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GENERAL NOTES

Laysan Albatross in Flight. Photo by Harvey I. Fisher

THE OCEANIC DISTRIBUTION OF THE LAYSAN ALBATROSS, *DIOMEDEA IMMUTABILIS*

Harvey I. Fisher and James R. Fisher

The purpose of this paper is to portray the oceanic distribution of the Laysan Albatross (*Diomedea immutabilis*) as indicated by records in the literature and by recoveries of birds banded by us. An attempt is also made to understand the reasons for the general distribution, as well as for changes associated with season and age.

The distribution of breeding colonies has been reviewed by Rice and Kenyon (1962), but no one has yet attempted an analysis of the pelagic range of the species. Present knowledge of the range is based upon incidental sightings at sea and recoveries of a few banded birds. Several publications list Laysan Albatrosses observed during transects of the North Pacific Ocean (for example, Clark, 1946; Hamilton, 1958; and Cogswell, 1946), and there are regional surveys as by Sanger (1965) off the coasts of Oregon and Washington, by Kuroda (1955) in the northwest Pacific Ocean, and by King (1970) near the eastern end of the Hawaiian Islands.

METHODS

Data used in the analysis consisted of 109 recoveries of birds we banded, 53 published records of birds banded by others, and 113 sight records. Of the 109 recoveries, 64 birds were less than 3 years of age, 23 were 3 to 7 years old, and 22 were adults, including 19 known breeders. No significance can be attached to the relative numbers of the different age classes; we banded several times as many young as juveniles or adults. The sightings date from 1897 (Kaeding, 1905), but most are since 1945. Sight records prior to 1897 were not included because of possible confusion between records of the Laysan and the Short-tailed Albatross (*D. albatrus*) prior to that date. Attempts have been made to verify all records and to eliminate questionable sightings, but data collected over such a long period and by so many different persons are subject to some error. Gathering of data over three-fourths of a century does have one advantage; it tends to smooth out annual vagaries such as Ingham (1959) and Tickell and Scotland (1961) noted in the annual patterns of dispersal of Giant Petrels (*Macronectes giganteus*).

The paucity of verified records (276) spread over the millions of square miles of the North Pacific Ocean is troublesome and in several instances makes impossible more than tentative statements. The problem is ameliorated, however, by multiple records in certain regions. Another question is whether our data reflect the distribution of albatrosses or of persons recapturing albatrosses. A minimum of 69 per cent and a maximum of 89 per cent of the recaptures were made by Japanese tuna fishermen; 9 per cent were taken as scientific specimens. The uncertainty in actual figures arises because the codes used by the U.S. Fish and Wildlife Service to indicate the method of recovery are not mutually exclusive.

This possible confusion as to the distribution being indicated is perhaps immaterial, for we can assume that most tuna fishermen are where tuna are or where tuna can be expected. The evidence also indicates a probable similarity in the distribution of tuna and albatrosses in the North Pacific because both derive a large proportion of their food from squid. Our studies on Midway indicate that at least 90 per cent of the Laysan's diet consists of squid. Nakamura (1965) reported that the main molluscan food item of skipjack tuna (*Katsuwonas pelamis*) in 1957–59 was squid. Waldron and King (1963) found that in Hawaiian waters squid constituted 35 to 83 per cent of the food items of: skipjack tuna; yellow fin tuna (*Neothunnus macropterus*); and bigeye tuna (*Parathunnus sibi*).

In analyzing the variation in oceanic distribution with age, three categories were established: young birds (to 3 years of age); juveniles (3–7 years); and adults (7 plus years). Separation into these classes is based upon differences in behavior. Until they are three or more years old, the young Laysans are at sea and seldom return to the breeding colony (Fisher and Fisher, 1969). Between three and seven years the juveniles establish patterns of return, territories, and pairs. They visit the breeding colony at intervals between January and June. After the age of seven, the birds can be expected to be breeders, or within a year of breeding. They tend to return to the colony initially between November and February. Such differences in the relationship between albatrosses of different ages and the breeding grounds may affect oceanic distribution despite the remarkable flight powers of the albatross.

All oceanic records in the immediate vicinity of the Hawaiian Island breeding colonies were omitted. Records associated with these colonies add nothing to our knowledge of oceanic distribution, and their inclusion in analyses of latitudinal and longitudinal movements or even of distribution introduces a bias. Breeding albatrosses are of necessity restricted in their oceanic travels, although perhaps less than many other species.

Sea-surface temperatures are 20-year means (1947–66) furnished by R. A. Schwartlose of Scripps Institution of Oceanography.

RESULTS

All 276 records reported here lie within the limits of 8 to 59° N lat. and 132° E to 116° W long. Published reports of occurrences within these limits include: 1) 25 sightings off Japan made by Kuroda (1955). Macdonald and Lawford (1954) and Wilhoft (1961) reported incidental sightings in the western and central Pacific area, as did Clark (1946), Dixon and Starrett (1952) and Hamilton (1958); 2) 11 sightings around the Aleutian Islands made by Kenyon (1961), Kuroda (1955), Macdonald and Lawford (1954), and Murie (1959); 3) Sight records off the west coast of North America by Sanger (1965), Love (1958), Willet (1913), Stager (1958), Thompson (1951), McHugh (1950), Kenyon (1950), Fredrich (1961), Holmes (1964), Kaeding (1905), and Yocum (1947); and 4) Occurrences around the Hawaiian Islands and other eastern North Pacific islands were recorded by Fisher (1948), Munro (1945, 1946), Hanson (1959), Jensen (1949), Cogswell (1946), Eastman and Eastman (1958), and Thompson (1951).

Few Laysan Albatrosses have been found south of approximately 28° N. except around the breeding colonies which are essentially between 28 and 22° N. According to Amerson (1969), Laysans are "accidental on islands in the

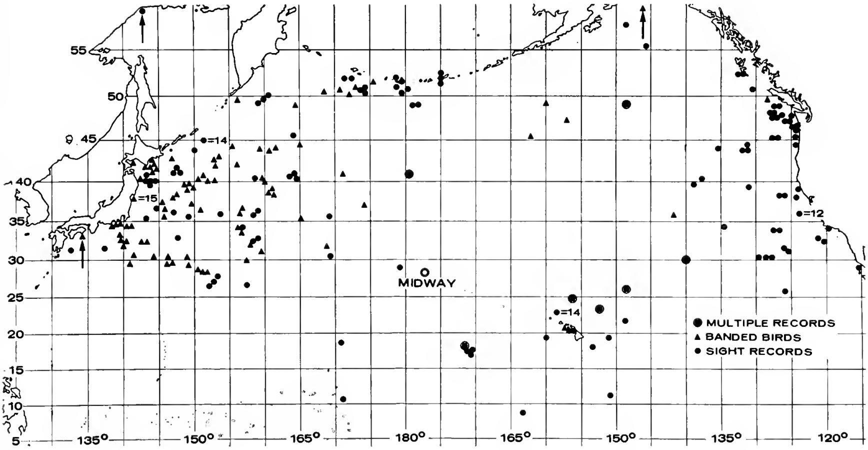

FIG. 1. Records of Laysan Albatrosses in the North Pacific Ocean: sight records and banded birds more than 3 years of age.

northern Marshalls [approx. 13° N] probably at-sea-visitor." However, he reported a Laysan Albatross at Mejit Island in the Marshalls, 10° 17′ N and 172° 52′ E. And there is the lone record at 8°. Dixon and Starrett (1952) stated that Laysans are "Noted south of 30th parallel only to eastward of Wake Island." Baker (1951) in his review of Micronesian ornithology reported no records of Laysan Albatrosses in the Micronesian Islands.

The plot of all the sightings of birds of unknown age and of recaptures of our banded birds more than three years of age (Fig. 1) indicates that the primary oceanic range of the Laysan Albatross lies between 28 and 52° N and

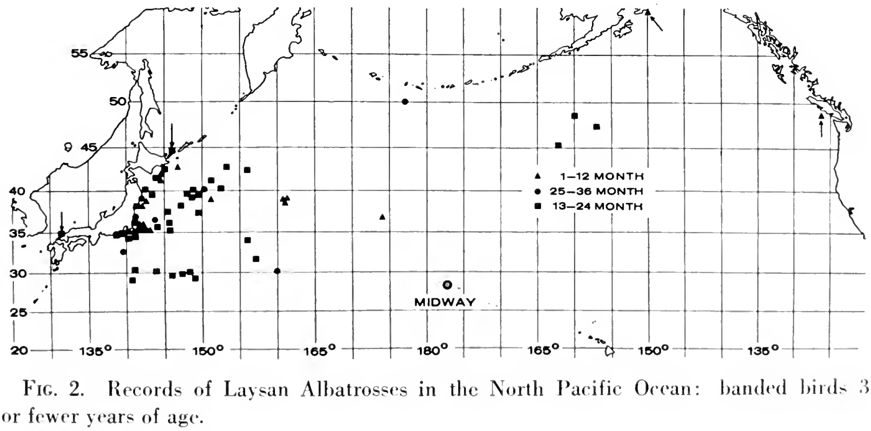

FIG. 2. Records of Laysan Albatrosses in the North Pacific Ocean: banded birds 3 or fewer years of age.

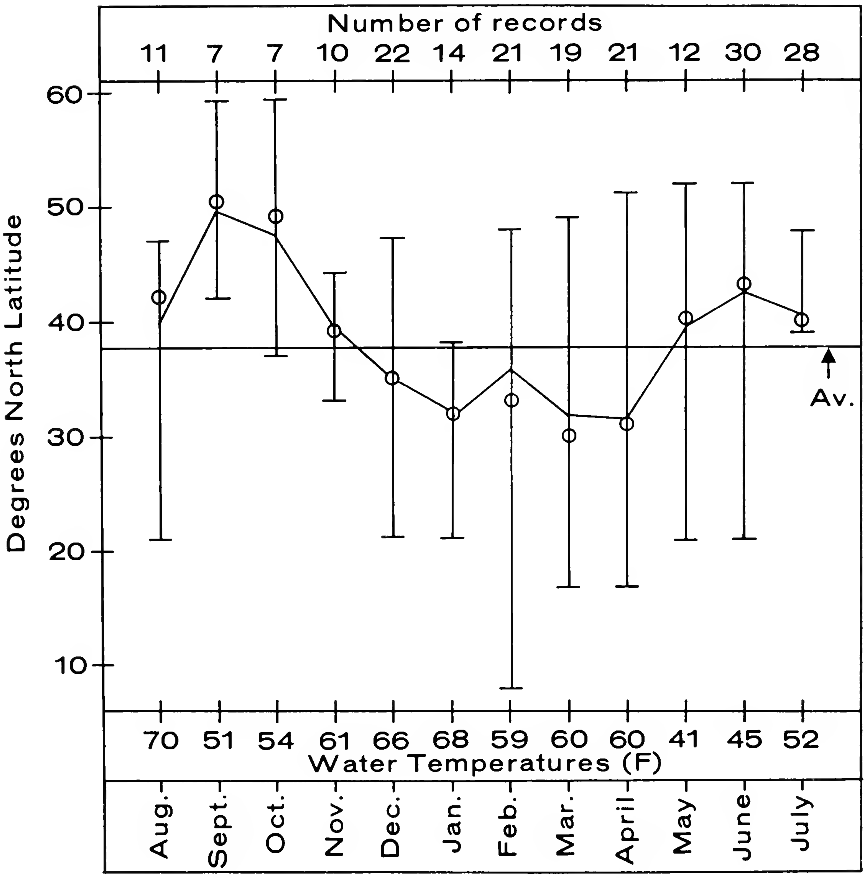

FIG. 3. Distribution of Laysan Albatrosses in the North Pacific Ocean by latitude, month and surface water temperature: birds of all ages.

between 140° E and 120° W. This area includes 83 per cent of all records. Within this general range are four areas of concentration: 1) east of Japan and the Kurile Islands; 2) south of the western Aleutians; 3) off the west coasts of British Columbia and the United States; and 4) at sea around the eastern end of the Hawaiian Islands.

Certain regions contiguous to the general range have few or no instances of sightings or recaptures of Laysans: 1) the Sea of Okhotsk and the Sea of Japan; 2) the Bering Sea; 3) west of lower California; and 4) a vast circle of ocean between the eastern Aleutians and the Hawaiian Islands, centering at 40° N and 170° W. The only evidence of Laysan Albatrosses in the seas west of Japan consists of the recovery of a banded bird off the southwest coast

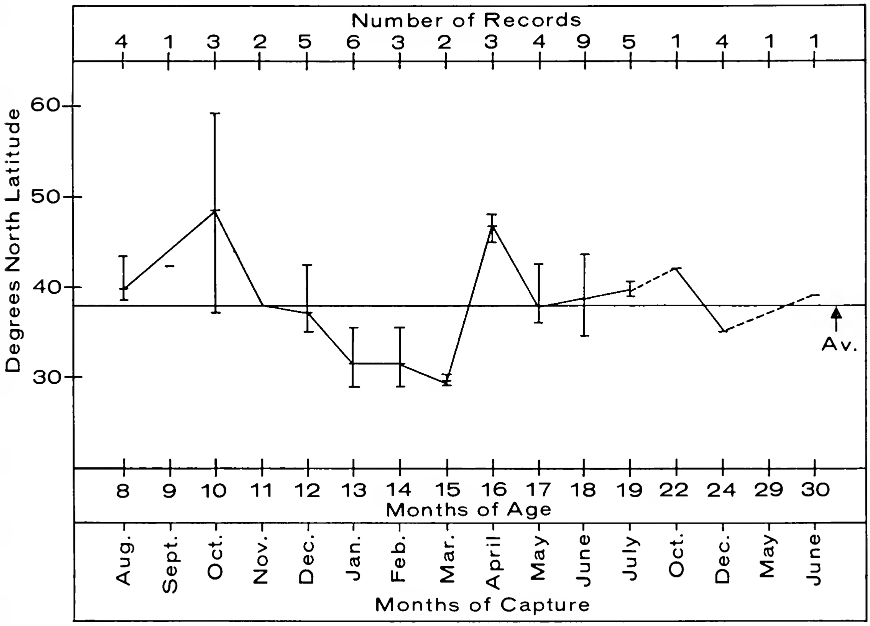

FIG. 4. Distribution of Laysan Albatrosses in the North Pacific Ocean by latitude, month and age: banded birds less than 3 years of age.

of Japan and another off the city of Okhotsk. Dement'ev et al. (1951) reported that the Laysan is a casual straggler "in Russia" but listed as evidence only one Laysan obtained in Kamchatkan waters. Kenyon (1950) reported no certain records in the Bering Sea, and Arnold (1948) and Kuroda (1955) saw no Laysans north of the Aleutians.

Records of birds three or fewer years of age are concentrated (87 per cent) in an area east of Japan and roughly bounded by 30 to 45° N and 140 to 160° E (Fig. 2). With only two exceptions, all birds recaptured at a year or less of age have been between 35 and 45° N and 140 and 175° E.

Seventy-two per cent of the 3- to 7-year-old birds recaptured (23) were in this area, and 17 per cent were nearby. One bird in the Aleutians and one in Hawaiian waters represented the records most distant from the concentration.

Although the 22 banded adults were recaptured in widely separated places, two-thirds were in this same area east of Japan.

The mean latitude of all recaptures or sightings is 38° N. The monthly mean latitude of these records and the 20-year means of sea-surface temperatures at these mean latitudes are shown in Figure 3. From May through November the albatrosses are most frequently north of 40° N and in temperatures of 41 to

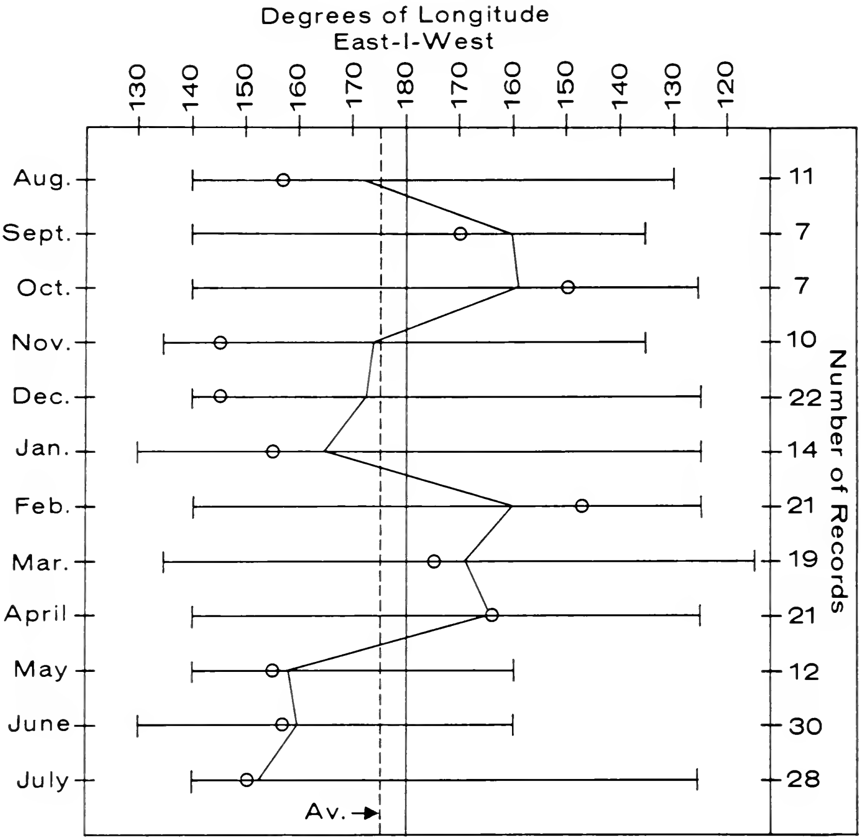

FIG. 5. Distribution of Laysan Albatrosses in the North Pacific Ocean by longitude and month: birds of all ages.

61° F (except in August). From December into April the majority of the albatrosses are south of 35° N and in water temperatures of 59 to 68° F.

Albatrosses less than three years of age exhibit essentially the same seasonal shift in latitude (Fig. 4). However, in their first 12 months (excluding, of course, approximately 5 months in the natal colony) the young birds are found mostly north of 38° N. Although they are south of this during the winter months at the beginning of their second year, none have been retaken below 30° N. They shift north a full month ahead of the older birds (March versus April, Figs. 3 and 4, respectively).

When the recaptures and sightings of all albatrosses are plotted by month and mean longitude (Fig. 5), the average longitude of occurrence appears to be 176° E. Seasonal shifts are apparent. From May through August and from

November through January the majority of albatrosses are found between 150 and 160° E; from February to April and from September–October most are found between 155 and 175° W.

DISCUSSION

General Considerations.—The Laysan Albatross ranges in significant numbers over most of the North Pacific Ocean north of 28° N and exclusive of the contiguous seas to the west and north. Continental land to the northwest, east, and northeast is an obvious barrier to this pelagic species. Islands to the north and west may function similarly, as is discussed later. But no land masses, even intermittent ones, delimit the southern extent of the range.

It is suggested that food is the most important single factor in determining the southern limits of the range and the relative abundance of Laysan Albatrosses within the range. Such a positive correlation between the occurrence of oceanic birds and their food supply is not new, of course. Kurochkin (1963), for example, regarded food as a primary determinant of distribution for many species including several procellariiform species. Voous (1965) stated that the distribution of many antarctic birds corresponded with the distribution of surface plankton. The papers of Jameson (1961) and of Gibson and Sefton (1959) on the Wandering Albatross (*D. exulans*), of Thompson (1951) on the Black-footed Albatross (*D. nigripes*) and of J. Fisher (1952), Salomonsen (1965), and Brown (1970) on the Fulmar (*Fulmarus glacialis*) also emphasized the importance of plankton.

With these views in mind, and recognizing that Midway Laysans obtain 90 per cent of their food from plankton-feeding squid whose distribution is less known than that of plankton, it is logical to relate the occurrences of plankton and these albatrosses.

Four factors directly and indirectly affect the volume of plankton in an area—nutrients, water movements, water temperature, and water salinity. Water movements, as in currents, convergences of currents, and upwellings, affect available nutrients, temperature, and salinity. Any type of turbulence that mixes deep and surface layers of the sea increases the availability of nutrients in the surface layers and lowers temperatures, and both actions are basically favorable to the growth of plankton. It is also established (Marr, 1956, for example) that the larger euphausids upon which both squid and albatrosses feed occur primarily in the near-surface, eutrophic waters and are virtually limited to cold currents. Thus, Laysans, plankton, squid, certain temperatures, and turbulence should coincide in their distribution. The available data support this view.

Laysan Albatrosses occur most frequently and in larger numbers where water temperatures range from 40 to 65° F (King, 1970, said below 72° F),

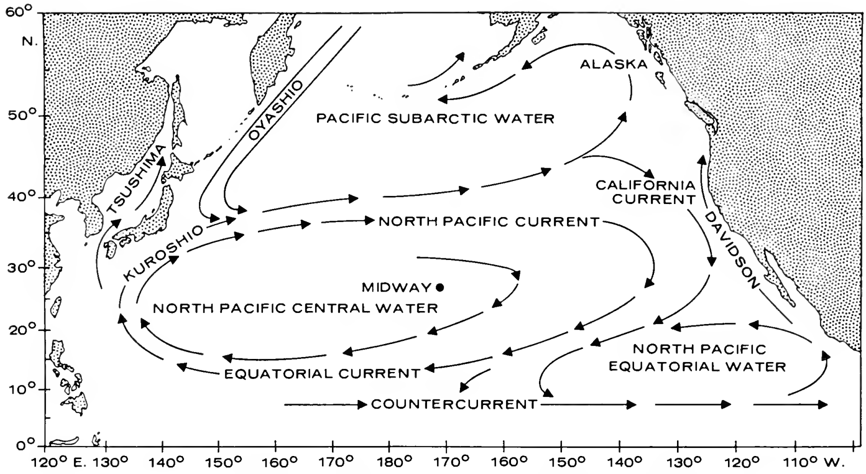

FIG. 6. Major water masses and currents in the North Pacific Ocean.

although the temperature variance over their general range is 36 to 84° F. And this temperature zone of preference coincides with the zone of highest plankton productivity—between 28 and 35° N (King and Iversen, 1962). In this zone, the south edge of the North Pacific Current, they obtained approximately 14,500 organisms per hour of trawling. North of 35° and in the Aleutian area the catch was 9,500 per hour. Between 28 and 5° N (Hawaiian and North Equatorial waters) King and Iversen reported less than 500 organisms per hour.

Therefore, the southern limit of the range of the Laysan Albatross appears to be formed by a major drop in the abundance of food organisms. Temperature may be the primary factor, but salinity may also be significant as Sanger (1970) suggested for the offshore waters west of North America. King (1970:96) stated that albatrosses ". . . tended to be most numerous over high-salinity water. . . ." but later ". . . it appears unlikely that surface salinity is a significant limiting factor in the distribution of sea birds in the study area." However, Seckel and Yong (1970:191) noted that "Hawaii is located in the vicinity of a relatively high salinity gradient that delineates the boundary of the North Pacific Central Water." The southern limit of the range of the Laysan thus appears to coincide with major, though gradual, changes in temperature and salinity. The limit can also be identified as the northern edges of the westward-trending Equatorial Current west of the Hawaiian Islands and of the North Pacific Equatorial Water between Hawaii and Central America (Fig. 6).

The correlation of turbulence and records of Laysan Albatrosses, mentioned earlier, is discussed in connection with the four major concentrations of birds (p. 15–18).

Extralimital areas.—The few records west of Japan and the Kuriles, north of the Aleutians, and west of Lower California, despite the presence of numerous fishing boats (Ommaney, 1963) which have been the main source of records elsewhere, support the hypothesis that these areas are indeed outside the regular range of the species.

The Japanese, Kurile, and Aleutian islands may form partial barriers to the seas behind them, since these albatrosses do not normally approach land other than that of the breeding grounds. Even more significant is the fact that to reach these outer, fringe areas an albatross would have to pass through or over rich seas which are presumably attractive feeding grounds for the species. It is probable that the Tsushima Current just west of the Japanese islands. with its warmth and its low productivity (Sorokin and Koblentz-Mishke, 1958), is a major deterrent to the Laysan Albatross. The warm North Pacific Equatorial Water west of Lower California may be a similar factor.

The Central North Pacific area, in the south edge of and just south of the Pacific Subarctic Water (Fig. 6), also lacks significant numbers of records. Less than 10 per cent are from this several-million-square-mile region which is devoid of strong currents, turbulences or upwellings and which is lower in plankton productivity than the regions to the north or south (King and Iversen, 1962). The occasional records within this vast expanse of sea are in either the fringes of the Aleutian Current or the eastward extension of the North Pacific Current, and the birds may be assumed to be vagrants from the richer areas near the source of these currents. However, the scarcity of records may reflect the lesser human use of this region, despite our earlier discounting of this possibility for other parts of the North Pacific.

Areas of concentration.—Four major concentrations of albatrosses are evident on Figure 1: 1) east of Japan; 2) south of the western Aleutians: 3) west of North America; and 4) around the larger, eastern islands of Hawaii.

There are reasons for the Laysan Albatrosses to be numerous in each of these areas. In each instance the conditions within the region of the concentration are generally constant from year to year within a certain range of coordinates. Bourne (1967:141) has noted that seabirds ". . . are normally restricted to very limited sea-areas by strict preferences for certain types and temperatures of surface water. . . ." Bailey (1968) noted this same phenomenon among seabirds in the western Indian Ocean. The Laysans apparently respond to permanently profitable foraging areas and do not utilize intermittent, locally enriched seas. The first reason may be the time and space lag between surface enrichment and the resulting production of suitable food. Secondly, the exigencies of amount of food, of time, and of distance probably make it impossible for the Laysans to rely on spotty food resources during such critical times of the year as the immediate pre-egg stage and the chick-feeding period (Fisher, 1967). And last, species in which each member is so closely restricted to its own island and natal colony for breeding (Fisher, 1971*b*) might be expected to be similarly related to its feeding areas.

The major concentration of records is east of Japan where the cold waters of the Oyashio Current collide with the warmer waters of the Kuroshio Current (Fig. 6). The resulting turbulence and many eddies occur between 35 to 40° N and 140 to 160° E (Seckel, 1970) and subside into the North Pacific Current still farther east. This region has been identified by Koblentz-Mishke (1965, Fig. 2) as having the greatest primary production in the North Pacific Ocean. More than a third (36 per cent) of the records are within the longitudinal limits of the turbulence and 30 to 45° N. Nearly half (45 per cent) are here, if sightings and recaptures on the immediate fringes of the region are included. Kuroda (1955) said of the Laysan in the northwest Pacific "This species was most plentiful 180–200 miles eastsoutheast of Shinshiru Island, where we saw 14 birds in one day." This is within the area of turbulence. Because of the turbulence and the consequent abundance of nutrients, plankton and squid occur year-round, with only minor seasonal changes, and the albatrosses find a plentiful food supply which they exploit constantly.

Although the second area of concentration, the western Aleutian region, includes only 7 per cent of the records, we believe the Laysan Albatross uses this area more extensively than the data may indicate. One reason is that Laysans tend to move into cooler waters during the summer months where plankton and presumably squid, are seasonally more abundant (King and Iversen, 1962). Another is that the Aleutian Current courses northeastward through the islands while the Oyashio comes southward in the western part of this region. Such flows may produce major eddies and turbulence and rich waters around islands (Wyrtki, 1967), as has been demonstrated behind the islands of Johnston and Hawaii (Manar, 1969). Larrance (1971) has noted the higher primary productivity in Aleutian coastal waters, as compared to areas to the south. Bourne (1963:836) also noted the higher productivity of seas around islands. The Aleutian region thus has all the features of a major seasonal feeding ground.

Along the west coast of North America (120–140° W and 30–50° N) is the third concentration (25 per cent of the records). Only two of our banded Midway birds have been found here. Few of these North American records are inshore, and winter reports are negligible. It appears that the Davidson Current, which in winter flows north along the coast to about 48° N, rather than the continental shoreline, forms the eastern boundary of the Laysan range in these latitudes. The Davidson and the various northward extensions of the North Pacific Equatorial Water are probably responsible for the absence of Laysan Albatrosses in the area south of 30° N and east of 145° W. The warmth of this water and its low oxygen and salinity are not typical of waters frequented by albatrosses.

Considering the amount of ship traffic, the number of scientific voyages, and the number of persons involved here in the past 75 years, it is apparent that this is a lesser concentration of Laysan Albatrosses than occurs east of Japan. Although these offshore waters are reportedly rich and upwellings are prevalent from March through July (Sverdrup et al., 1942), there are a number of reasons why albatrosses may occur here less frequently. 1) The richness of these waters, as in the Aleutians, may be only seasonal and also considerably less because of the admixture of warmer, southern waters. 2) It has been suggested that Laysans avoid waters of low salinity, as found at least off Oregon (for example, Sanger, 1970). 3) Prevailing winds and water currents are not as advantageous for movement to and from this area as to the waters off Japan, and the distances are greater. 4) Another possibility about which we known little is that Laysan Albatrosses breeding on different islands may go to different parts of the ocean. Tickell found some indication of this segregation in young *D. melanophris* (1967) and in *D. exulans* and *D. epomophora* (1968). Our data indicate that Midway birds are for the most part (90 per cent) recaptured west of 180°. However, nearly half of all known oceanic records of Laysans (117 of 276) are east of the date line. This could be an indication that Laysan Albatrosses breeding in the western end of the Hawaiian Chain move northwest to sea and the Japanese or Aleutian concentrations and that albatrosses breeding farther to the east move into either the Hawaiian or North American concentrations referred to earlier. However, the picture is clouded by the fact that virtually all Laysans now breed east of 180°. 5) There is still another explanation for the lesser number of recaptures and sightings off the North American coast. At least 61, and perhaps 85 per cent since reporting techniques vary, of the recaptures were made by fishermen. The Japanese tuna fishermen of the western and central Pacific are predominantly surface fishermen of the open sea, and they recapture albatrosses on their long-line sets of tuna hooks or in their surround nets. Fishing in the far northeastern North Pacific, aside from a minor component of surface trolling for sport fishes, is closer inshore and directed more toward deeper dwelling fishes. Hence we should not expect as many albatross recaptures in these waters as in the Japanese area, even though the number of birds and fishermen were the same as in the western Pacific.

Nevertheless, a significant number of Laysan Albatrosses have been recorded in the cool offshore waters of North America, waters formed by the California Current or the lower limits of the Aleutian Current.

Ten per cent of our Laysan records are from the fourth area, the vicinity of the five large, easternmost islands of the Hawaiian Chain, all of which are east and south of the primary sea range indicated earlier. Several factors, some factors unique, some perhaps common to other concentrations, may influence the number of birds observed here. This concentration is no more than 800 miles from the breeding grounds, compared to 2,000 miles for the Japanese concentration, 1,200 for the Aleutian area, and the nearly 3,000 miles between the American concentration and the breeding grounds. There are major water eddies, turbulence and subsequent rich waters in the lee of these large Hawaiian islands (Manar, 1969), which may provide adequate feeding grounds in the otherwise generally unproductive Hawaiian waters (King and Iversen, 1962). A large fleet of sportfishing boats and an active Audubon Society probably increased greatly the number of sight records. But the concentration of Laysan Albatrosses appears to be factual, and the primary reason may be that the North Pacific Current, which turns southward at about this longitude (Fig. 8), brings cooler, more productive water and Laysan Albatrosses with it. And the prevailing northeast trade winds, moving essentially parallel to this current, may further influence albatrosses to move southward into this region.

Because of this Hawaiian concentration it is necessary to extend the primary oceanic range of the Laysan south to 20° in the region of 155° W long.

Distribution by age.—Eighty-seven per cent of the 64 young birds were recovered in and around the Oyashio-Kuroshio turbulence east of Japan. The 13 per cent retaken outside this area are considered to be exceptions. Other than the two occurrences west of Japan, the sites of recapture are ones to which inexperienced birds may well have been transported by ocean currents (Figs. 2, 6).

The offshore waters of Japan constitute a nursery area, at least for Midway birds, in which the young remain until they begin their annual visits to the breeding colonies (Fisher and Fisher, 1969). Tickell (1967) reported similar concentrations of *D. melanophris* in their first 3 years of age. While adults are commonly recaptured on both sides of the Atlantic, Falkland Islands young go to the western Atlantic and South Georgia young move into the eastern Atlantic. Within a few months of fledging, Fulmars from West Greenland and St. Kilda go to the Newfoundland Banks (J. Fisher, 1952:325; J. Fisher and Lockley, 1954:138). And Robertson has suggested recently (1969) that young Atlantic Sooty Terns (*Sterna fuscata*) may congregate in the Gulf of Guinea in Africa while those of the Pacific assemble in the central Philippines. It seems probable that as we learn more of the oceanic distribution of seabirds of different ages we shall discover that many species exhibit at least a partial segregation by age which reduces intraspecific competition.

Factors other than the richness of these Japanese waters are important in attracting young Midway Laysans. The area is closer to Midway than is any other known and abundant food source, and it is more easily reached by inexperienced birds with relatively poor powers of flight. As the young bird leaves Midway it is subjected to westward trending water currents (Fig. 6) and generally consistent winds from the east-northeast sector (U.S. Naval Oceanog. Office, 1966). As it rests or feeds on the water it is carried west by south; its weak flight is greatly affected by the wind, and the bird in the air also drifts southwest. Should it drift too far to the south, another factor increases the rate of its westward trend—the westerly flow of the Equatorial Current. One might compare this latter current to a drift fence along which the young birds move until they reach the Kuroshio Current which then moves them north to the nursery area. Conditions in these critical months of July–September may be particularly advantageous to these birds. King and Hida (1957) obtained their largest plankton catches then and reported that surface catches at night were 1.5 times as large as in daytime. These data may mean that not only are the squid attracted to the abundant food, they are attracted presumably in greater numbers to the surface and at night. This, of course, means greater accessibility for the initial foraging efforts of the young birds. The abundant supply and greater availability of suitable food organisms to inexperienced birds could be expected to hold the birds there until initial sexual development stimulates them into migratory patterns.

The 23 juveniles were recaptured at sites more widespread than those of young birds, but 72 per cent were taken in the rectangle described as the nursery area. An additional 17 per cent were retaken nearby. Thus even juveniles, most of which have already made one or more trips to the Midway breeding colonies, return to the offshore waters of Japan.

The 22 adults were widely scattered at the time of recapture, but 68 per cent were secured off Japan. One was recovered off California, one in the Hawaiian area, and four in the Aleutians. Since 19 of these adults were known to have bred on Midway, it is plausible to suggest that a majority of Midway's breeders return at times to feed in this area. It is unfortunate that we did not know the current breeding status of each of these adults, for then we might know whether they move between the breeding colony and this area during the nesting season. Other studies in progress show that Midway adults feeding chicks may fly east and north at least 1500 miles.

It is evident that Midway birds of all ages feed in the turbulent convergence of currents east of Japan, that a high percentage remain there for the first three years of life, that juveniles return there as they initiate periodic visits to the breeding colony between the ages of 3 and 7 years, and that many of Midway's breeding Laysan Albatrosses feed there at least from time to time.

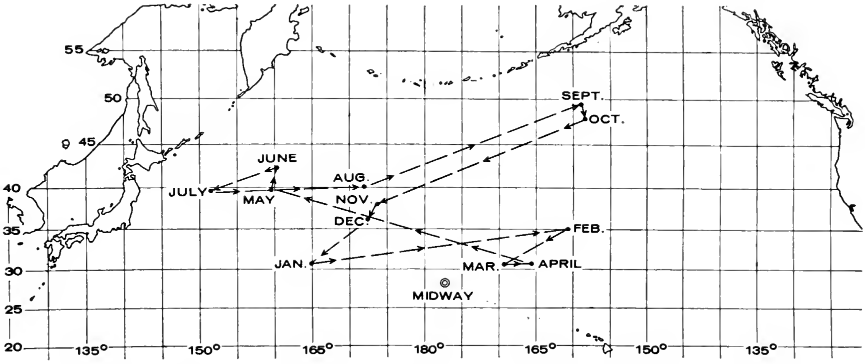

Fig. 7. Distribution of Laysan Albatrosses in the North Pacific Ocean by latitude, longitude and month: mean locations of birds of all ages.

Seasonal distribution.—Figure 5 illustrates the occurrence of four periods of longitudinal shift: eastward (into west longitude) in January and August and westward in April and November. In Figure 3 three latitudinal shifts are shown: northward in April–May and August–September and southward in October–December. Figure 7 is an attempt to portray graphically the combined results of the longitudinal and latitudinal shifts for birds of all ages. We believe the directions of movement are accurately shown, but the extent of the shifts is probably unduly influenced by the use of averages including extreme records.

Starting in August, the first month of the year in which no Laysans are involved with reproduction, there is a shift in concentration toward the northeast along the North Pacific Current and perhaps into Pacific Subarctic Water. This continues until October. The birds move from water near 70° F into 50-degree and presumably more productive water. In November the birds are back in the central reaches of the North Pacific Current where the sea-surface temperatures are now in the low 60s. In December and January the albatrosses are near 30–35° N and 170° E where temperatures gradually climb into the upper 60s. The birds then move eastward, with no change in latitude, to 165° W where water temperatures are 60° or below. The birds are probably in the same water as in December–January, water that has cooled as it moved eastward in the southern fringe of the North Pacific Current. In April the move is west and north to the 40–50° F waters east of Japan, waters brought to this temperature by the cold waters of the Oyashio Current. The albatrosses remain until late July. In all the above statements we are referring to "average moves," not necessarily to movements of the entire populations.

It might be suggested that Figure 7 reflects at least in part the movements to and from the breeding grounds. And one might justifiably speculate, on the

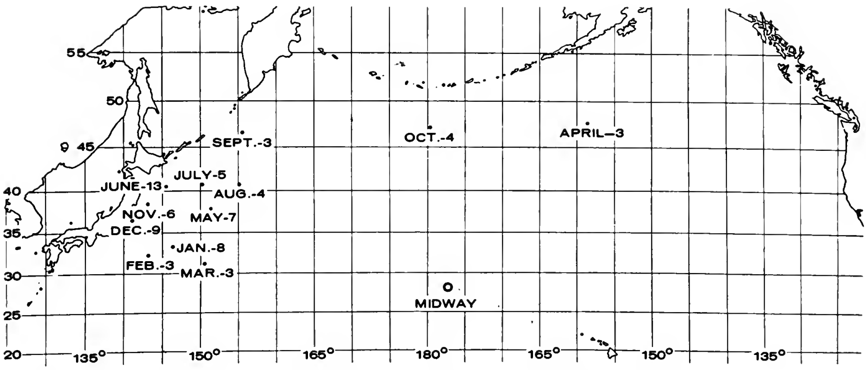

FIG. 8. Distribution of Laysan Albatrosses in the North Pacific Ocean: mean location of birds 4 or fewer years of age.

basis of this study and published information on the biology of the Laysan Albatross, that: 1) virtually all of the birds less than 3 years of age are in the May–July plotting; 2) the August to November roundtrip is made mostly by breeders, along with some older juveniles; and 3) the December to May plotting consists primarily of breeders, with 3- to 7-year-olds contributing to the March to May portion (Fisher and Fisher, 1969). It is perhaps equally logical, with regard to the December–May period, to suggest that incubating birds (November–January) with their longer periods of relief from nest duties (8–20 days, Fisher, 1971*a*) can subsist in less productive areas. But when the food requirements of the chick are added to those of the foraging parents and when the total time for travel and foraging between chick feedings averages 2 days (February–April) the adults shift eastward to presumably better food sources. Also during this time, nestling mortality has released additional parents and the chicks are fed smaller amounts and less frequently, as evidenced by the fact that their weight declines after May (Fisher, 1967). These factors may permit failed or even current breeders to move northwest in April and May.

However, we believe that the movements of breeding birds are not significantly involved in the conclusions to be reached from study of Figure 7. First, the Laysans four or fewer years of age show the same directional shifting (Fig. 8), and most of these are not yet making their periodic visits to the natal colonies. Second, only 37 per cent of the banded portion of the sample is of an age to visit the colony or to breed. And third, Laysan Albatrosses in short periods of time are capable of traversing distances greater than those involved in the latitudinal shifts. Kenyon and Rice (1958), for example, showed that Laysans removed from eggs or young chicks home at the rate of nearly 200 miles per day.

Furthermore, evidence from the literature, though scanty, tends to support the concept of these movements and concentrations. King (1970:9) in recording Laysan Albatrosses at sea east of the Hawaiian Islands and between 10 and 25° N and 148 and 150° W, gave their status as "Uncommon visitor February–April, rare or absent May–January." He also noted that the decline in numbers in April was accompanied by ". . . a contraction of range to the northern end of the study area."

Amerson (1969:293) wrote of the Laysan "Found at sea normally south to 15° N in the Central Pacific during the *breeding seasons. . . .*" [italics mine], thus indicating his belief in a seasonal shift. However, his reasons were not stated, and we now know that Laysans seldom penetrate this far south.

The northward movement of the albatrosses in summer may well be related to the seasonal northward advection of southern water into the latitudes of the Hawaiian Islands (Seckel and Yong, 1970). This advection brings warm water of lower salinity into the southern part of the albatross range.

The observations of McHugh (1950), Holmes (1964), and Sanger (1970) that Laysan Albatrosses were more abundant off the North American coast "in winter" lends some strength to our view of eastward shifts in February and March.

Hamilton's observations (1958) during a June transit west to east and between 35 and 48° N tend to substantiate the midsummer concentration around the 40th parallel.

Austin and Kuroda (1954) believed that the Laysan was a regular visitor off the Pacific coasts of Honshu and Hokkaido from early spring to late autumn, and Kuroda (1957) said that it arrives off Japan in March. We presume he meant greater numbers were present there at that time. It is probable that this influx is of young birds which we think move north in March (Fig. 4). He further wrote (p. 448) of a "post-breeding movement northward in spring." This may correspond to the April shift or perhaps the greater occurrence off Japan in July. He indicated this was a movement with the northward trend of the warm Bonin Island Air Mass. We regard it as a seasonal movement away from the increasingly warm waters of the Kuroshio Current. The average water temperatures in July drop from 81° F at 30° N to 53° F at 45° N in these longitudes, and Kuroda had earlier (1955) stated that the Laysan ". . . seems to avoid water above 13° C." In 1960 he indicated that the Laysans congregated off the Kuriles in June and July at sea temperatures slightly above 40° F, which is in basic agreement with the data in Figure 3. He did not find many Laysans in either the colder or warmer waters of this region. Szijj (1967) noted that albatrosses in southern seas were most numerous at water temperatures between 6 and 13° C.

The implication is that Laysans seek out these temperatures, for one reason or another, probably food. It is probable that the Laysan adult, like the Fulmar (J. Fisher, 1952:325; Brown, 1970; and Salomonsen, 1965), regularly moves to a food source that is adequate, accessible and predictable on a time and place basis. This seasonal phenomenon is also reported for the Wandering Albatross (Tickell, 1968; Gibson and Sefton, 1959, 1960; and Jameson, 1961). Dixon (1933) and Tickell and Gibson (1968) believed that Wanderers, especially those of pre-breeding age, had a regular migratory path between South Georgia and the sea off New South Wales. And Gibson (1963: 216) has said of the Wanderer: ". . . when free from breeding commitments at their home islands, these birds returned regularly to an assured natural food supply, contrary to the generally held conception of a free-ranging ocean wanderer unbound by conventional migrations." The Royal Albatross regularly moves between Campbell Island and South America (Dixon, 1933; Tickell, 1968). Falla (1963) noted that "several albatrosses" breeding in the Subantarctic moved into colder waters in late summer, a shift perhaps comparable to the September–October move of Laysans.

Our data (Fig. 7) do not support Bourne's view (1967) that seabirds tend to move clockwise around anticyclonic stationaries in the middle latitudes of the Northern Hemisphere.

SUMMARY

All 276 oceanic records of Laysan Albatrosses are within the limits of 8 to 59° N and 132° E to 116° W in the North Pacific Ocean. The primary range, however, is between 28 and 52° N and 140° E–120° W.

The northern boundary of their distribution is the Aleutian Islands and the relatively non-productive waters of the Bering Sea. The Kurile and Japanese islands, along with the warm Tsushima Current, constitute a western barrier. The North American continent with its warm inshore Davidson Current forms the eastern limit. The southern border is marked by warm equatorial waters of low salinity and low productivity.

Within these limits Laysan Albatrosses tend to congregate in four regions: 1) east of Japan (35–40° N and 140–160° E); 2) south of the western Aleutians (50° N and 165° E–175° W); 3) off the west coast of North America (30–50° N and 120–135° W); and 4) near the large, eastern islands of Hawaii (20° N and 150—160° W).

The Japanese region serves as a nursery foraging area for birds fewer than 4 years of age; seldom are they recaptured elsewhere. However, older juveniles and adults from Midway also return there to feed.

There is evidence of seasonal shifts in concentrations; the birds move east in January and August, west in April and November; they move north in April–May and in August–September, south in October–December. In general these movements are associated with changes in surface water temperatures.

Laysan Albatrosses tend to be associated with turbulent seas, eddies and currents; the birds most frequently are in water temperatures of 40 to 65° F. Such waters are generally most productive, and it is suggested that food is the primary determinant of the Laysan's distribution.

ACKNOWLEDGMENTS

It is impossible to thank individually the many persons who have so obviously contributed to this study, but our appreciation is no less sincere. We do want to note particularly the contributions of the unknown men of the Japanese tuna fleet, for without their cooperation in recapturing significant numbers of albatrosses at sea this study would have been impossible.

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LITERATURE CITED

Amerson, A. B., Jr. 1969. Ornithology of the Marshall and Gilbert Islands. Atoll Res. Bull. No. 127.

Arnold, L. W. 1948. Observations on populations of North Pacific pelagic birds. Auk, 65:553–558.

Austin, O. L., Jr., and N. Kuroda. 1954. The birds of Japan, their status and distribution. Bull. Mus. Comp. Zool., 109:277–637.

Bailey, R. S. 1968. The pelagic distribution of sea-birds in the western Indian Ocean. Ibis, 110:493–519.

Baker, R. H. 1951. The avifauna of Micronesia, its origin, evolution, and distribution. Univ. Kansas Publ. Mus. Nat. Hist., 3:1–359.

Brown, R. G. B. 1970. Fulmar distribution: a Canadian perspective. Ibis, 112:44–51.

Bourne, W. R. P. 1963. A review of oceanic studies of the biology of seabirds. Proc. 13th Internatl. Ornithol. Congr. Ithaca 1962, 2:831–854.

Bourne, W. R. P. 1967. Long-distance vagrancy in the petrels. Ibis, 109:141–167.

Clark, T. O. 1946. Bird observations to San Francisco aboard a transport. Elepaio, 7:1–3.

Cogswell, H. L. 1946. Bird study aboard a transport to the Western Pacific. Elepaio, 6:46–48, 53–54, 62–63.

Dement'ev, G. P., R. N. Meklenburtsev, and A. M. Sudilovskaya. 1951. Birds of the Soviet Union. Vol. 2.

Dixon, C. C. 1933. Some observations on the albatrosses and other birds of the southern ocean. Trans. Roy. Canadian Inst., 19:117–139.

Dixon, K. L., and W. C. Starrett. 1952. Offshore observations of tropical seabirds in the Western Pacific. Auk, 69:266–272.

Eastman, W., and K. Eastman. 1958. Bird study in the Hawaiian Islands is a stimulating experience. Elepaio, 19:1–5.

Falla, R. A. 1963. Distribution patterns of birds in the Antarctic and high-latitude Subantarctic. Biol. Antarctique, Prem. Symp., Sept. 2–8, Paris, 1962, pp. 367–376.

Fisher, H. I. 1948. Laysan Albatrosses nesting on Moku Manu Islet off Oahu, T. H. Pacific Sci., 2:66.

Fisher, H. I. 1967. Body weights in Laysan Albatrosses, *Diomedea immutabilis.* Ibis, 109:373–382.

Fisher, H. I. 1971*a.* Incubation hatching, and associated behavior in the Laysan Albatross, *Diomedea immutabilis.* The Living Bird, 10:19–78.

Fisher, H. I. 1971*b.* Experiments on homing in Laysan Albatrosses, *Diomedea immutabilis.* Condor, 73:389–400.

FISHER, H. I., AND M. L. FISHER. 1969. The visits of Laysan Albatrosses to the breeding colony. Micronesica, 5:173–221.

FISHER, J. 1952. The Fulmar. Collins, London.

FISHER, J., AND R. M. LOCKLEY. 1954. Sea-birds. Houghton Mifflin Co., Boston.

FREDRICH, L. A. 1961. An occurrence of the Laysan Albatross on the northwestern coast of Oregon. Condor, 63:506.

GIBSON, J. D. 1963. Third report of the New South Wales albatross study group (1962) summarizing activities to date. Emu, 63:215–223.

GIBSON, J. D., AND A. R. SEFTON. 1959. First report of the New South Wales albatross study group. Emu, 59:73–82.

GIBSON, J. D., AND A. R. SEFTON. 1960. Notes on some albatrosses of coastal New South Wales. Emu, 60:128–130.

HAMILTON, W. J. III. 1958. Pelagic birds observed on a North Pacific crossing. Condor, 60:159–164.

HANSON, C. 1959. [Field notes]. Elepaio, 19:67.

HOLMES, R. T. 1964. Notes on the occurrence of the Laysan Albatross near the California Coast. Condor, 66:302–303.

INGHAM, S. B. 1959. Banding of Giant Petrels by the Australian National Antarctic Research Expeditions, 1955–58. Emu, 59:189–200.

JAMESON, W. 1961. The Wandering Albatross. Rev. ed., Doubleday and Co., New York.

JENSEN, S. 1949. Field notes: from Johnston Island. Elepaio, 9:66.

KAEDING, H. B. 1905. Birds from the west coast of Lower California and adjacent islands. Condor, 7:105–111.

KENYON, K. W. 1950. Distribution of albatrosses in the North Pacific and adjacent waters. Condor, 52:97–103.

KENYON, K. W. 1961. Birds of Amchitka Island, Alaska. Auk, 78:305–326.

KENYON, K. W., AND D. W. RICE. 1958. Homing of Laysan Albatrosses. Condor, 60:3–6.

KING, J. E., AND T. S. HIDA. 1957. Zooplankton abundance in the Central Pacific, Part II. Fish. Bull., 57:365–395.

KING, J. E., AND R. T. B. IVERSEN. 1962. Midwater trawling for forage organisms in the Central Pacific 1951–1956. Fish Bull., 210:271–321.

KING, W. B. 1970. The trade wind zone oceanography pilot study. Part VII: Observations of sea birds March 1964 to June 1965. U.S. Fish and Wildl. Serv. Spec. Sci. Rept. Fish. No. 586.

KOBLENTZ-MISHKE, O. J. 1965. [The magnitude of primary production of the Pacific Ocean]. Oceanography (Russian), 5:325–337.

KUROCHKIN, E. N. 1963. [Distribution of some seabirds in the North Pacific.] Zool. Zhur., 42:1223–1231.

KURODA, N. 1955. Observations on pelagic birds of the northwest Pacific. Condor, 57: 290–300.

KURODA, N. 1957. A brief note on the pelagic migration of the Tubinares. Yamashina's Inst. Ornithol. and Zool. Misc. Rept. No. 11:436–439.

KURODA, N. 1960. Analysis of sea bird distribution in the Northwest Pacific Ocean. Pacific Sci., 14:55–67.

LARRANCE, J. D. 1971. Primary production in the mid-subarctic Pacific region, 1966–68. Fishery Bull., 69:595–613.

LOVE, C. M. 1958. Preliminary report: *Brown Bear Cruise* 188 off the coasts of Washington and Vancouver Island, 19–28 February 1958. Univ. Washington Dept. Oceanog. Ref. 58–16. (ditto).

MACDONALD, J. D., AND P. A. LAWFORD. 1954. Sight records of birds in the Pacific: compiled from the bird log kept during the recent cruise of H.M.S. *Challenger.* Emu, 54:7–28.

MANAR, T. A. 1969. Progress in 1967–68 at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu. Bur. Comm. Fish. Circ. 321.

MCHUGH, J. L. 1950. Increasing abundance of albatrosses off the coast of California. Condor, 52:153–156.

MARR, J. W. S. 1956. *Euphausia superba* and the Antarctic surface currents. Norsk. Hvalfangst-Tid., 45:127–134.

MUNRO, G. C. 1945. The Laysan Albatross on Kauai. Elepaio, 5:70.

MUNRO, G. C. 1946. [Field notes.] Elepaio, 6:79.

MURIE, O. J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. N. Amer. Fauna No. 61.

NAKAMURA, E. L. 1965. Food and feeding habits of skipjack tuna, *Katsuwonus pelamis,* from the Marquesas and Tuamotu Islands. Trans. Amer. Fish. Soc., 94:236–242.

OMMANNEY, F. D. 1963. The Fishes. Time Inc., New York.

RICE, D. W., AND K. W. KENYON. 1962. Breeding distribution, history and populations of North Pacific albatrosses. Auk, 79:365–386.

ROBERTSON, W. B., JR. 1969. Transatlantic migration of juvenile Sooty Terns. Nature, 223:632–634.

SALOMONSEN, F. 1965. The geographical variations of the Fulmar (*Fulmarus glacialis*) and the zones of marine environment in the North Atlantic. Auk, 82:327–355.

SANGER, G. A. 1965. Observations of wildlife off the coast of Washington and Oregon in 1963, with notes on the Laysan Albatross (*Diomedea immutabilis*) in this area. Murrelet, 46:1–6.

SANGER, G. A. 1970. The seasonal distribution of some seabirds off Washington and Oregon, with notes on their ecology and behavior. Condor, 72:339–357.

SECKEL, G. R. 1970. The trade wind zone oceanography pilot study. Part VIII: Sea-level meteorological properties and heat exchange processes July 1963 to June 1965. U.S. Fish and Wildl. Serv. Spec. Sci. Rept. Fish. No. 612.

SECKEL, G. R., AND M. Y. Y. YONG. 1970. Harmonic functions for sea-surface temperatures and salinities, Koko Head, Oahu, 1956–69, and sea-surface temperatures, Christmas Island, 1954–69. Fish. Bull., 69:181–214.

SOROKIN, U. I., AND O. J. KOBLENTZ-MISCHKE. 1958. The primary production of the Sea of Japan and the part of the Pacific adjoining Japan, during spring 1957. Papers Acad. Sci. U.S.S.R., Moscow, 122:1018–1020.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING. 1942. The Oceans. Prentice-Hall, New York.

STAGER, K. E. 1958. A record of the Laysan Albatross from Southern California. Condor, 60:404–405.

SZIJJ, L. 1967. Notes on the winter distribution of birds in the western antarctic and adjacent Pacific waters. Auk, 84:366–378.

THOMPSON, D. Q. 1951. Notes on distribution of North Pacific albatrosses. Auk, 68: 227–235.

TICKELL, W. L. N. 1967. Movements of Black-browed and Grey-headed Albatrosses in the South Atlantic. Emu, 66:357–367.

TICKELL, W. L. N. 1968. The biology of the great albatrosses, *Diomedea exulans* and *Diomedea epomophora.* Antarctic Res. Ser., 12:1–55.

TICKELL, W. L. N., AND J. D. GIBSON. 1968. Movements of Wandering Albatrosses. Emu, 68:7–20.

TICKELL, W. L. N., AND C. D. SCOTLAND. 1961. Recoveries of ringed Giant Petrels, *Macronectes giganteus.* Ibis, 103:260–266.

UNITED STATES NAVY. 1966. Pilot chart of the North Pacific Ocean, No. 1401, July 1966. U.S. Naval Oceanog. Office, Wash., D.C.

WALDRON, K. D., AND J. E. KING. 1963. Food of skipjack in the Central Pacific. Proc. World Sci. Meet. Biol. Tunas and Related Species, FAO Fish. Rept. No. 6:1431–1457.

WILHOFT, D. C. 1961. Birds observed during two crossings of the Pacific Ocean. Condor, 63:257–262.

WILLET, G. 1913. Pelagic wanderers. Condor, 15:158.

WYRTKI, K. 1967. The spectrum of ocean turbulence over distances between 40 and 1000 kilometers. Deut. Hydrog. Z., 20:176–186.

YOCOM, C. F. 1947. Observations on bird life in the Pacific Ocean off the North American shores. Condor, 49:204–208.

VOOUS, K. H. 1965. Antarctic birds. Monogr. Biol., The Hague, 15:649–689.

Unfortunately, we did not know of the significant report by V. P. Shuntov (Zool. Zhurnal, 47:1054–1064, 1968) until after our paper was in press. His study of the distribution of the Laysan Albatross, based on approximately 800 records obtained at sea over a 10-year period, is in nearly complete agreement with ours in relation to basic distribution and its correlation with land masses, oceanic currents and primary productivity, to major areas of concentration, to temperature preferences, and to seasonal movements. The major difference is that Shuntov found a summer and fall penetration of the western and southern parts of the Bering Sea by significant numbers of Laysans and lesser numbers throughout the Sea of Okhotsk in these seasons. We thank Dr. Isaac Shechmeister of Southern Illinois University for translating this article for us.

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HABITS OF THE CRIMSON-CRESTED WOODPECKER IN PANAMA

Lawrence Kilham

I studied the Crimson-crested Woodpeckers (*Campephilus* [*Phloeoceastes*] *melanoleucos*) in the Panama Canal Zone in February 1965 and from November 1970 to February 1971, a period which included the end of the rainy season when nesting began and the onset of the dry season when young were fledged. The behavior of this species resembles that described by Tanner (1942) for the Ivory-billed Woodpecker (*Campephilus principalis*) and has not hitherto been the subject of any detailed reports, with exception of notes by Short (1970*b*), as far as I am aware. In Short's opinion (1970*a*), *Phloeoceastes* should be merged in *Campephilus* and I have adopted this terminology.

While the aim of present studies was to learn as much as possible about the total behavior of *C. melanoleucos*, the problems raised by its similarity in size and coloration to the sympatric Lineated Woodpecker (*Dryocopus lineatus*) were kept in mind, thanks to the ideas of Cody (1969) on why this parallelism exists. Actual field observations, however, failed to support his interesting theories, which are dealt with in greater length in a final discussion.

STUDY AREAS

I studied Crimson-crested Woodpeckers in five localities of which three, Madden Forest Reserve, Limbo Hunt Club, and Barro Colorado Island (BCI), were, for the most part, mature forests. Of the other two areas, one was of second growth forest 10 to 20 m in height at Cardenas Village where I lived and the other at Frijoles, an area under partial cultivation opposite Barro Colorado Island. The Crimson-crested and Lineated Woodpeckers were sympatric in all five of these localities, as indeed they are in much of South America.

METHODS OF COMMUNICATION

Instrumental Expressions

Drumming.—Drumming is typically a strong blow followed by short, weak, vibratory roll, "DA-drrr." Such bursts usually come at a rate of one to two per minute, three per minute being a fast rate. This drumming serves a number of functions. Single "DA-drrs," given occasionally throughout the day, enable members of a pair to keep in touch as they travel through woods together; duets of them continuing for periods of up to 20 minutes may occur at the height of courtship and just prior to copulation; while louder drumming, delivered against a resonating stub, is usually related to territorial disputes and assertions of dominance. This abbreviated drumming of *C. melanoleucos*,

FIG. 1. Female Crimson-crested Woodpecker drum-taps at rim of recently completed nest hole as mate approaches.

which at times can be no more than a single "DA," appears to be the same as that described by Tanner (1942) for the Ivory-billed and by Short (1970*a* and *b*) for the Magellanic (*C. magellanicus*) and other *Campephilus* woodpeckers in South America. Although both sexes of *C. melanoleucos* drum, males drum far more than females during the nesting season.

Pileated Woodpeckers (*D. pileatus*) (Kilham, 1959) strike a sharp rap with their bills against any surface they happen to be on when nervous or excited. According to Bock (1963), the genus *Campephilus* is an offshoot, phylogenetically, of *Dryocopus* and one might wonder whether the single drumming of *Campephilus* is not derived from the rapping of the latter genus. An observation of Tanner (1942) on the Ivory-billed Woodpecker is of interest here, for he noted that "The adults always were disturbed and excited whenever I first found a nest." In addition to giving calls they "often double-rapped or pounded on stubs or limbs of the nest tree and nearby trees." Thus, the drumming was done in the same context as the rapping would be done for *D. pileatus*.

Drum-tapping.—As discussed in a preceding report (Kilham, 1959), most woodpeckers tap at a regular and countable rate at the time of excavation of a nest hole. Pileated Woodpeckers, on the other hand, have a more rapid

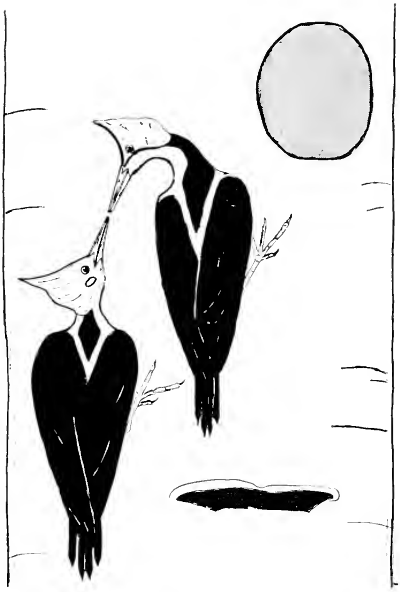

FIG. 2. Female Crimson-crested Woodpecker backs down from nest hole to touch bills with her mate who reaches up toward her.

roll taking the place of tapping, which I have called "drum-tapping." Crimson-crested Woodpeckers drum-tap in the same manner as Lineated and Pileated Woodpeckers, both at the rim of the nest hole at time of excavation (Fig. 1), but also down inside the nest at time of relief at the nest, a habit also described by Sielmann (1958) for the European Black Woodpecker (*D. martius*).

Wing noises.—Crimson-crested Woodpeckers can fly silently. They often, however, make a heavy sound, even in flying short distances, that doubtless keeps each member of a pair informed when the other moves and in what direction. Heavy wing noises are a feature of conflicts.

Displays

Bill-touching.—At times of most active courtship, the woodpeckers of a pair may come close to one another, crests raised and even curled forward, then fence gently, making contact for roughly half the length of their bills. This interest in bills at time of courtship may be related to the way a male pecks down at the bill of the female while copulating. Ivory-billed Woodpeckers touch bills in courtship according to Tanner (1942) and Allen and Kellogg (1937) wrote that as a female climbed up a pine toward her mate "he bent his head downward and clasped bills with her." Although I noted a

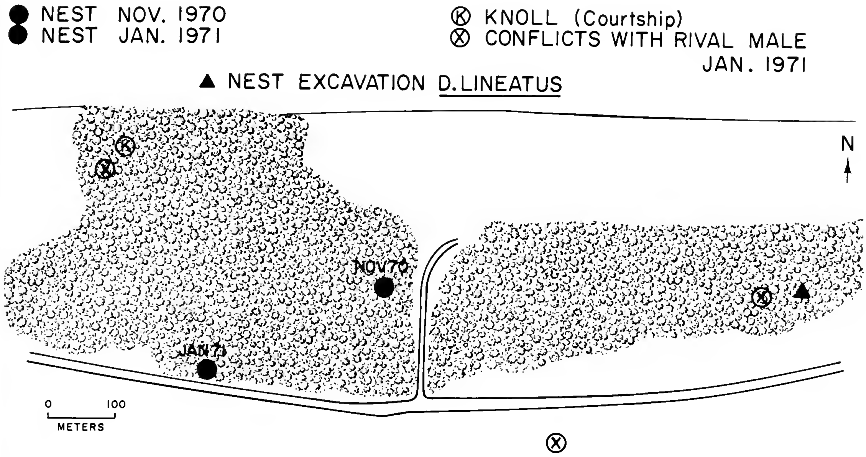

FIG. 3. Territory of Pair A of Crimson-crested Woodpeckers at Cardenas Village.

similar bending down on several occasions, as illustrated in Figure 2, I never observed bill clasping with *C. melanoleucos.*

Vocalizations

Alarm notes.—Notes of moderate disturbance made, for example, when one comes too close to a nest excavation are *ca* and *ca-wa-rr-r* often repeated. A sharp, high-pitched *ca* given alone was the only vocalization heard in several conflicts between males. Shrill, piping *put put puttas* given by both males and females are expressive of high excitement. These may be kept up for minutes on end. On the whole, however, Crimson-crested Woodpeckers are relatively silent birds, giving way to alarm notes with far less frequency than the related Lineated Woodpeckers.

Intimate notes.—These low notes are expressive of closeness of pair bonds, being given just prior to coition and at times when one partner relieves the other at excavating. Variations include *wuk wuk, wrr wrr, wun wun,* and *uh uh* among others.

Main breeding call.—A tree-frog-like *kwirr kwirr-ah* or *squeer squeer-ah-hah.*

Comparisons to other species.—Short (1970*b*) records a three-noted call *wink-at-chew* for *C. melanoleucos* in Argentina. Vocalizations of *C. magellanicus* (Short, 1970*b*) are given in more detail and here the double-noted calls, *wieeer* and *kee-argh* (harsher, more drawn out) appear somewhat similar to the *kwirr-ah* and *ca-wa-rr-r* notes described above for *C. melanoleucos.*

COURTSHIP AND COPULATION

The following activities of Crimson-crested Woodpeckers, as well as the excavation of nest holes, with exception of Pair E, took place in the rainy season.

Pair A.—The woodpeckers of Pair A frequently came to a knoll (Fig. 3) at the edge of woods by Cardenas Village for early morning courtship and preening, the male (MA) always to a special place on his tree and the female (FA) to hers. These trees were about 14 m tall and 10 m apart. Here the two began a duet of drumming at 06:10 on 22 November 1970. After 15 minutes of low bursts, one or two per minute from each, MA flew to FA's tree and I heard low notes then as well as five minutes later when FA moved out onto a horizontal limb. Here she crouched low in a crosswise position as MA approached. He mounted in full coition, pecking gently down at her bill four or five times as he gradually fell to the left in establishing cloacal contact.

This copulation suggested that the pair must have a nest nearing completion and on 26 November I was led to it at 16:00 by the sound of FA excavating. She took alarm and flew out, then drummed on nearby trees as if disturbed. I returned again in the late afternoon. The woodpeckers were feeding in trees close-by when, at 17:20, FA flew to the hole and clung to its lower rim. When MA alighted a meter below, she drum-tapped on the rim of the hole (Fig. 1) and as he hitched upward, she moved down to meet him, bending over to fence bills (Fig. 2) as he stretched upward. All now looked well for actual nesting. The way a pair of Collared Araçaris (*Pteroglossus torquatus*) dispossessed the woodpeckers of their completed hole 20 minutes later is described beyond.

Five days later, on 2 December, the two Woodpeckers, now without a nest, had returned to the knoll (Fig. 3). MA drummed at an uneven rate of 11 times in 10 minutes at 06:23, but FA, on her tree, did not respond. When he flew to her, however, the two fenced lightly with their bills. FA moved on a less horizontal part of the trunk and crouched low, but MA, taking no apparent interest in this invitation to coition, flew away. On the following morning MA drummed again, with only one burst in reply from FA. The two preened in leisurely fashion for 35 minutes, then left. It thus appeared on succeeding days that, with loss of their nest, the woodpeckers gradually lost interest in courtship.

I now felt there would be little to observe further with this pair when on 15 December I heard *kwirr-kwirra* notes by the knoll when MA alighted on the trunk of a slender tree, to be joined almost immediately by FA, both being at the same level as they bent heads together to touch bills. The crests of the two were raised to the full and curled forward. They returned to their original positions, only to bend heads together on the other side of the trunk to fence again. Both now flew to the knoll and drummed a brief duet before a longer period of leisurely preening. Had the woodpeckers found a new nesting site as the renewal of courtship activities suggested? I had no further indication of this until 1 January when at the comparatively late hour of 18:45 I saw the pair on a bare tree near the knoll in full copulation. From here, after feeding for five minutes, they flew east. With this direction as a clue I was able to find their nest, in which they were to hatch young, a few days later.

Pair B.—At 06:10 on 26 November drumming led me to find a male Crimson-crested Woodpecker on the limb of a dead tree above Madden Forest. A female Lineated Woodpecker alighted briefly on the same limb but after she had left, the female Crimson-crested, whom I could not see, drummed five or six times, then flew to her mate. I heard low notes, then witnessed full coition lasting possibly 10 seconds. Afterwards the two birds preened in leisurely fashion for 10 minutes, then flew to feed in the forest. At 07:00 the female gave a single *kwirr-a*. After a pause, the male flew to her, there were more low notes, and a second copulation, not well seen, followed. This was 35 minutes after the first one.

EXCAVATION OF NEST HOLES

Trial nest stub.—Not all pairs of Crimson-crested Woodpeckers were able to find suitable nest stubs. Pair C, for example, had already tried to excavate one stub when, at 09:25 on 24 December, I found the male carving an entrance in a second one. His mate remained nearby making querulous *wer wer* and *wuk wuk* notes until she took over the excavating at 09:40. Her interest, however, waned after five minutes and she circled up the stub, pecking here and there as if to test the nature of the underlying wood, which was probably too hard to excavate, before flying away. She thus appeared more critical of the stub as a nesting site than her mate. Little further progress was ever made with entranceway and by early February Pair C had still failed to find a place to nest. From such observations I came to believe that suitable stubs in this and other parts of Barro Colorado Island, as well as other localities, were generally in short supply.

Successful nest stubs.—Both males and females excavated and their greetings at times of changing over were expressive of attachment to the nest hole as well as to each other. At 10:45 on 26 December, for example, the male at Nest D drum-tapped when inside the hole with head still visible, made low notes, then drum-tapped again when his mate flew over to take his place. She tossed some sawdust from the entrance but spent most of her time looking out. When Male D returned in 15 minutes, she immediately disappeared to drum-tap at the bottom of the cavity. He peered in at her several times before she squeezed out by him to fly away. MD then tossed out sawdust. As with FD, however, he was soon looking out idly and I believed from this and subsequent behavior that the nest was ready for egg laying.

The woodpeckers of Pair E were late in excavating in comparison with Pair D, for they did not begin until late in January. Their hesitancy to use the stub finally chosen was probably due to the mass of epiphytes at the top, together with the lianas that might have encouraged arboreal mammals or other unwanted neighbors. The pair had, however, carved an entrance by 22 January. The female did most of the excavating at this nest and change-overs, when they did occur, were much the same as for Pair D with one exception. This was on 31 January. Male E had been excavating when his mate flew to the hole making low notes. Instead of dropping out of sight to drum-tap, ME remained by the hole to meet his mate directly and the two touched bills a number of times before he flew away.

NESTING

Greeting ceremonies in the first few days of incubation were much the same as in the previous period in regard to drum-tapping, but changes soon became evident when the birds became silent, increasingly undemonstrative, and no longer looked out from entrances. When MD came to his nest hole at 16:00 on 8 January, his mate swung out of the hole in silence, the two woodpeckers resting side-by-side below the hole momentarily without other ceremonies before she flew away.

Times between change overs are long for *C. melanoleucos.* In waits of one and a half hours or more I never saw a woodpecker return after leaving. Skutch (1969), however, in waiting for extended periods at a nest of the closely related Pale-billed Woodpecker (*C. guatemalensis*), noted the female as spending four and a half hours on the eggs and her mate as remaining on them from 12:15 until dark without being relieved.

Nestling period.—The behavior of the woodpeckers at Nest D changed with the hatching of the eggs, their greater restlessness being exemplified by the following observations: On 15 January MD, after looking out from the hole for five minutes, flew out at 13:45 to preen for a few minutes on an adjacent tree, then re-entered to brood the nestlings. The longest time he spent away from the nest in the course of two and a half hours was 10 minutes.

On 22 January FD had been brooding for a half hour when she flew out, leaving the young unattended for 45 minutes before MD arrived and entered. FD returned almost immediately, replacing him within a few minutes. Her attention to the nest was closer than that of her mate on this and succeeding days, as she would generally stay near the nest when not in it, whereas MD might, at times, be away for more than three hours.

Other events of special interest at Nest D during the nestling period can be summarized as follows:

1) Neither parent ever brought visible prey to feed their young. It is conceivable, however, that they might have done so had the young survived longer, for Tanner (1942) describes Ivory-billed Woodpeckers as carrying large grubs to well-grown nestlings.

2) FD and MD were both together in the nest on two occasions. Thus, on 30 January MD entered while his mate was inside, only to leave a few minutes later and on the following day, under similar circumstances, he remained inside with her for five minutes.

3) MD became increasingly apprehensive as the nesting period progressed, delaying each entry by much looking about and bowing into the hole, only to withdraw. Whether the predator that finally destroyed the nest (if predation was the cause) was in the vicinity I did not know, but on nearly every visit

to Nest D I did see a pair of Spectacled Owls (*Pulsatrix perspicillata*) almost within sight of it.

I found Nest D devoid of activity when I came to it on 7 February. The entrance was undamaged and I could find no clue as to why the nest had failed. In looking about in woods nearby I was able to locate the parents and to follow them for one and a half hours. Their behavior was now much as in the pre-nesting season, with no sign that they any longer had young to feed.

Tanner (1942) speaks of three nests of Ivory-billed Woodpeckers from which the young disappeared mysteriously and the nest of the Pale-billed Woodpecker observed by Skutch (1969) also failed. He noted a large black snake in the vicinity. It would seem that snakes may be likely predators of such woodpeckers when entrances are undamaged.

YOUNG AFTER LEAVING NEST

I was watching a male Crimson-crested Woodpecker digging out grubs from a well-rotted stub on 22 January on Barro Colorado Island when a second woodpecker in adult female plumage alighted 25 cm away. She made no effort to feed herself but preened lightly, making *k-da k-da* begging notes much of the time. The male paid no seeming attention until, on encountering a huge larva (4 cm long and 1½ cm in breadth), he leaned over and fed it to her. Meanwhile, a second female, I believed the mate of the male, joined the other two. This second female, unlike the first one, dug out her own food. The two females got along peacefully although later on I had evidence of a brief conflict between them.

The male did not feed the begging female again in the course of the hour that I followed them. She foraged for herself occasionally but much of the time she followed him so closely that she was almost at the tip of his tail, whether he was feeding along the under or top side of a limb. It seemed possible that she was a young of the year before and while this may seem a long time for a young one to stay with parents, it does fit a situation described by Short (1970*b*) for *C. melanoleucos* in Argentina as well as by Tanner (1942) who wrote of *C. principalis* as follows:

> "The young birds usually leave or are driven away by the following nesting season, but the single male that was raised by the John's Bayou birds in 1938 stayed in that territory through the following spring. The female of the pair frequently tried to drive him away, but he would only dodge, sulk, and return. The old male paid little or no attention to his yearling son."

The first juvenile I encountered on Barro Colorado was on 31 January when continued *k-arr k-arr* disturbed notes attracted me to one at the edge of a gap in the forest. Its mother in the same clearing gave her *k-wirr k-wirr-a* notes, then flew off. The young one followed and later I found it close beside her as she dug for grubs in a dead stub. The only other encounter with juveniles was on 19 February 1965 when, as described below, one adult female, attended by two juveniles, had a confict with a second female.

TERRITORIAL AND AGONISTIC BEHAVIOR

Female vs female.—Two females alighted low on a series of trees on the morning of 19 February 1965, shifting around trunks as one tried to strike the other, or made a display of doing so for over 15 minutes. The presence of several juveniles indicated that the conflict, possibly a territorial one, had come at the end of the nesting season.

Male vs male.—Sounds of much drumming had come from Territory E on the morning of 27 December. When I followed these into the woods at 13:00, I found two males, one pursuing the other in short, heavy-sounding flights from one to another of four trees centering on a tall stub, to which they often returned. The stub, although unsuitable in a number of aspects, was large enough for nesting. When the woodpeckers came to rest, I noted two types of more direct conflicts: In one that lasted five minutes, one male clung almost upside down below a large limb, while the other, perched on top, half-opened his wings each time the first one tried to come around from below. When the two flew, it was to continue with an even milder type of encounter on a tree trunk nearby. Here one backed down as the other retreated backward. Finally both flew in opposite directions with the territory owner going to a large dead limb where he drummed in slow but resounding fashion for six minutes. He then attacked the intruder again. All of the fighting was silent except for two sharp *ca* notes. The males were still engaged when I left 50 minutes later.

A somewhat different and even milder conflict between males took place on 12 January at Cardenas Village, where Female A was probably incubating eggs. MA was preening and occasionally drumming at "the knoll" (Fig. 3) on what was usually FA's drumming tree when, at 07:08, a second male arrived on MA's usual drum tree 10 m away. MA did not appear disturbed. He continued to preen and drum as before, giving about five bursts to every single one given by the intruder. The latter clung almost immobile the whole time. Possibly, being well within the territory of MA, he was intimidated. This was suggested when he suddenly flew toward MA, then changed his mind in mid-air, and returned to his original position. Five minutes later he again flew, but this time in an opposite direction.

The intruder again returned some minutes later to a tree close by MA. The conflict ended at the knoll when MA left soon afterward, followed in a minute or two by the second male. This was possibly the first of a series of encounters taking place on subsequent mornings between the two males.

The above encounters were all mild in nature. There were no accompanying vocalizations, no bill-wavings, or for the most part any threat displays, and no direct clashes such as one can observe among temperate zone species such as the Pileated Woodpecker (Kilham, 1959). It may be that tropical species, being under more pressure from predators, cannot afford to attract attention to themselves when engaged in conflicts. Short (1970*b*), however, gives a description of a more conspicuous conflict between two males of *C. robustus*.

INTERACTIONS WITH OTHER SPECIES

Collared Araçaris.—The mildness and seeming lack of aggressiveness of Crimson-crested Woodpeckers was exemplified, in a different context, when several Collared Araçaris took over the just completed nest hole of Pair A on 26 November. After drum-tapping and bill-touching by the hole, these woodpeckers had appeared comfortably on the way to nesting when MA entered the hole to roost for the night at 17:33. He was soon looking out, however, as if nervous. Seven minutes later he slipped out and moved around to the rear of the stub, being joined by his mate as a toucan flew to the hole and put its bill in several times. The woodpeckers made a few low *krr* notes but gave no sign of resistance. They simply flew off and as far as I know they never returned. A feature of this performance was that the toucans did not appear too confident. They did not roost in the hole on the 26th and when I returned to the nest stub at 17:25 four evenings later, I found them still chary about entering, for they rested nearby for 20 minutes as if looking the situation over before doing so. A few nights later, on the contrary, they arrived at dusk and entered directly. They had thus won the hole without any show of aggressiveness.

Reaction to a marmoset.—On 24 February 1965 I watched a male Crimson-crested Woodpecker feeding in a mass of vines at the top of a tall stub in company with two marmosets (*Oedepomidas geoffreyi*). A marmoset came down a vertical liana on which a woodpecker was working. Neither species paid any attention to the other, even though they passed within 5 to 7 cm of each other on either side of the vine. Crimson-crested Woodpeckers did, however, become much excited by monkeys on one occasion. This was when the members of Pair E were excavating a nest not far from a cage of *Cebus* monkeys on Barro Colorado on 26 January. Loud screaming from the cage upset both birds to the extent that they made almost continuous *put-put-putta* notes for 10 minutes.

On the whole, however, I found Crimson-crested Woodpeckers relatively unexcitable as compared with Lineated Woodpeckers. Their tameness in fact was of great aid in observing them. It would seem that Tanner (1942) had a similar experience in noting that Ivory-billed Woodpeckers became used to people so rapidly that "in a day or so (they) would pay little or no attention to one a moderate distance away."

FEEDING BEHAVIOR

Methods of Foraging.—The feeding behavior of Crimson-crested Woodpeckers was separable into the following categories:

Pecking.—The uncovering of prey with relatively few blows against bark of superficial layers of wood.

Percussion.—While a woodpecker may deliver many blows per minute in pecking, not all of these are to uncover prey. Some appear to be exploratory, given here and there without digging into the wood, either to cause a wood-boring larva to move within its tunnel and thus reveal its location or to sound out difference in resonance between a hollow tunnel and solid wood.

Scaling.—When working on limbs that have been dead for some time, Crimson-crested Woodpeckers may combine pecking with sidewise, glancing blows that dislodge sizeable pieces of loose bark and other debris that may shower to the ground as the woodpecker moves along. On the other hand, almost nothing may fall when a woodpecker is working on the closely adherent bark of a dying limb; the powerful, rapid, occasionally prying blows involved in its straightforward pecking being sufficient to uncover prey.

Probing.—Putting the bill into natural cavities or clumps of epiphytes, etc., presumably to explore their interstices with their tongues, although these are seldom visible.

Digging.—When working on well rotted stubs for deeper lying prey, Crimson-crested Woodpeckers may dig cavities 10 cm or more deep, seizing and tossing larger slivers of rotten wood to the ground as they do so. The sizes of such cavities are usually no larger than those made by Hairy Woodpeckers (*Dendrocopos villosus*) and never as large as the deep troughs dug by Pileated Woodpeckers in North America. This doubtless reflects the fact that conditions of decay and location of insects are different in tropical climates.

The listing of these categories of feeding and foraging does not provide a full picture. As pointed out lucidly by Bock and Miller (1959) the *Campephilus* group of woodpeckers have remarkable adaptations not only in the forward direction of all their toes, but particularly in having legs directed away from the center of the body in such fashion that the full tarsus can be pressed against trunks and branches. The result is that such a species as *C. melanoleucos*, in whatever position it is working, whether on the underside of a limb, on the smooth bole of a large tree, or out on smaller branches, appears to be solidly stabilized for delivering powerful blows.

Feeding of non-breeding pairs in dry season.—Observations on a pair without attendant young, followed for 140 minutes on 24 February 1965 on Barro Colorado Island, brought out some aspects of feeding when the woods were relatively free of leaves. The two birds were usually within 15 m and often much less of each other as they moved through the mature forest feeding at heights varying from 6 to 25 m, the latter height bringing them close up under the canopy of larger trees. Most of their feeding, however, was at intermediate levels. An almost constant feature with this pair was the greater activity of the female, for she was not only the first to fly on the six occasions when the woodpeckers flew from one part of the woods to another, but she also moved along a greater extent of limbs and tree trunks in feeding than the male. At one time, for example, both woodpeckers flew to a dead limb 4 m long. During the next 10 minutes she progressed nearly the whole length of the limb in knocking off bark and debris while he moved only a fifth as far as he probed thoroughly in a limited area, which he continued to do after she had left. His inclination to work one place thoroughly was again exemplified later in the morning. This time he was on a tree with a relatively smooth bole where he found large numbers of grubs under a strip of discolored bark and fed on them for 15 minutes. When any fell, he would press his belly against the bark to recover them.

Foraging in the rainy season.—The dry season arrived late in Panama in 1971 so that essentially all observations made from November into the latter part of January were made in the rainy season. They were divisible into two categories of which the first was in the second-growth woods at Cardenas Village. Here at 16:40 on 4 January, when Female A was presumably incubating, I found MA working alone on a small semi-dead tree, 3 to 4 m above the ground and at the level of my eye as I stood on a slope above. At times he moved out onto branches of 2.5 cm in diameter. Clinging securely by grasping small branchlets, two of his forward-directed toes on one side and two on the other, he pecked steadily on the still adherent bark, as if finding considerable amounts of prey. At one time, for example, I saw him extract a larva grub about 3 cm long. At another time he clung to the underside of a slightly larger branch, his forward directed toes serving well for hanging in this position. It is likely that insect larva are particularly abundant on the underside of limbs and branches where moisture collects and persists longer than on the uppersides. The male also worked on a limb of 10 cm in diameter. Here I could see that he delivered three or four powerful pecks in one place, then moved along to another, pecking rapidly and nowhere penetrating deeply into the wood. With a background of watching woodpeckers in the temperate zone, I would have thought the branches more suitable for a Hairy or even a Downy (*D. pubescens*) Woodpecker, than for a large species such as *C. melanoleucos*. Short (1970*a*) noted *C. magellanicus* feeding on small branches in a similar manner.

Crimson-crested Woodpeckers are versatile feeders whether in second-growth woods, such as those in Cardenas Village, or on Barro Colorado where the mature forest contained many large stubs and branches. Methods of feeding in these habitats are illustrated in the following examples. 1) Feeding directly under bark. MA delivered hard blows on the firmly adherent bark of a dead stub near Cardenas Village and as bits of bark came loose, I could see tunnels of wood-boring larvae directly below. The woodpecker's blows were straight on, followed by a few at slight angles, together with prying motions. 2) Excavations into wood. A pair of Crimson-crested Woodpeckers on BCI dug holes 3 to 5 cm deep in a large stub finding not only small grubs, but also several large ones measuring approximately ½ by 4 cm. 3) Tree with smooth bark. A female fed under strips of loose bark on the unusually smooth bole of a large tree by splaying her legs well out to the side. 4) Possible feeding on termites. A lone female fed for 40 minutes on a dead stub arising from a small, understory tree. She dug so industriously into its basal portion that the upper part broke off and fell to the ground. Later examination of this portion revealed that it contained many termites along with a few tunnels, all old, of large larvae.

The foraging habits of Crimson-crested Woodpeckers were easy to observe for several reasons. First, the woodpeckers would often move from one tree to the next, finding plenty to look for without taking long flights from one good tree to another as is often the case with other woodpeckers, such as the Pileated or Hairy in northern woods; and second, when feeding high up on dead limbs, they would often move along the underside where one still had a good view of their activities.

COMPARATIVE FEEDING BEHAVIOR AND INTERACTIONS WITH *D. LINEATUS*

Crimson-crested and Lineated Woodpeckers fed in the same locations and occasionally on the same trees on Barro Colorado Island without signs of hostility or indeed special reactions of any kind.

I heard, for example, vocalizations of both species, then found the four woodpeckers of two pairs intermixed as they fed among a small group of trees on 24 December. When the Crimson-cresteds left, the Lineated Woodpeckers moved into the tree where they had been. Here the male probed into holes and crevices of a dead limb, then moved out onto a dead branch 2.4 cm in thickness that one would have thought suitable only for a smaller species. I had noticed a female Lineated Woodpecker doing much probing a short while before and an impression that this method of foraging was a characteristic habit of *D. lineatus*, more so than of *C. melanoleucos*, was re-enforced by further observations on 5 February. Thus, at 09:00 I heard both the *kwirr-as* of Crimson-crested and the *wer-wer-wer* notes of Lineated Woodpeckers coming from close by a trail. Sounds of digging then led me to a male Lineated. He pecked only briefly, then began probing a spot on the upper side of a large limb, 15 cm below a decaying branch stub. This was probably a ramifying area of decay, for the male turned and twisted his head for the next five minutes, as though reaching into deep tunnels or interstices with his tongue, the whole performance being identical with what I have witnessed with Pileated Woodpeckers on many occasions. It seemed probable, therefore, that the Lineated Woodpecker was foraging on ants and their larvae.

At 09:10 a male Crimson-crested suddenly alighted only a meter below the male

Lineated Woodpecker. As the Crimson-crested Woodpecker hitched upward, neither he nor the Lineated Woodpecker raised their crests in even mild excitement. When the two were within 30 cm, the Lineated flew to a limb a meter away, remaining there quietly while the slightly larger Crimson-crested Woodpecker took over his feeding place. The latter gave only a few pecks, as though finding nothing of interest, then moved on to drum once on the broken branch stub, preen briefly, and leave. The Lineated now returned to continue at his feeding spot for another 10 minutes.

A number of aspects of this episode were noteworthy. First, the Crimson-crested Woodpecker had not replaced the Lineated in a supplanting attack, for there was no sign of hostility, the situation appearing to be one of simple dominance at a food situation. The Crimson-crested was the larger woodpecker and this, plus having a longer, heavier bill, may have explained his dominance.

A second feature of the episode was that whereas the Lineated Woodpecker had started making *put-air* notes when I had arrived, he stopped making these notes when the larger woodpecker replaced him, appearing thus, if anything, to have become calmer, rather than more excited. What was the most significant feature of the encounter, however, was the light it threw on the feeding habits of the two species. The Lineated obviously found much to feed upon in the one spot, for he was able to feed there actively for a total of 15 minutes, quite possibly on ants and their larvae. On the other hand, the tree itself provided feeding places of a different kind, such as decaying dead limbs, attracting *C. melanoleucos*, for I had watched the male and female feeding here a few weeks before. These observations suggested the two species of woodpecker, instead of having the similar "ecologies" needed to support Cody's (1969) theory, can forage on the same trees for quite different sorts of prey. While they do undoubtedly overlap in some of their feeding habits, as indeed Tanner (1942) showed for Pileateds and Ivory-bills, this is not of sufficient degree to interfere with their being sympatric.

That the Lineated Woodpecker is specialized is seen most clearly, as is well discussed by Skutch (1969), in its attacks on *Cecropia*s and the colonies of *Azteca* ants harbored in their hollow trunks and branches. These trees grow in abundance nearly everywhere and their prevalence at edges of woods may explain why Lineated Woodpeckers come to these situations. On 9 January, for example, I found a male digging into a *Cecropia* at the edge of the laboratory clearing at Barro Colorado Island. He worked first on the trunk where it was 7 cm in diameter, then on a limb of half that thickness. Although I had many more observations on *C. melanoleucos* than on *D. lineatus*, I never saw it even alight on one of these fast growing trees which, in general, bear little dead wood.

I found it more difficult to observe the feeding habits of *D. lineatus* than those of *C. melanoleucos* for three reasons, namely that *D. lineatus* was more easily disturbed, often starting *put-air notes* on seeing me; that it was more thinly distributed, being only one-third as numerous as *C. melanoleucos* on Barro Colorado Island; and finally that, whereas *C. melanoleucos* usually foraged from one tree to another close by, *D. lineatus*, after spending some time on one tree, might take a long flight to another and was hence easily lost to further observation. The last two situations suggested that *D. lineatus* requires larger feeding territories than *C. melanoleucos.* Whatever the differences between the two species, it was striking that they thrive together whether in old and mature woods such as at Madden Forest, Limbo, and Barro Colorado, or the second growth ones at Cardenas Village and Frijoles. It is of interest here, finally, that Slud (1964) found *D. lineatus* less common than *C. guatemalensis* in Costa Rica.

COMPARATIVE BREEDING BEHAVIOR OF LINEATED WOODPECKERS AND INTERACTIONS WITH *C. MELANOLEUCOS*

Skutch (1969) has provided a general account of the Lineated Woodpecker. Additional aspects based on recent observation are given below to bring out mainly how it is that *D. lineatus* and *C. melanoleucos* can live in sympatry without undue competition or overlap in any aspects of their lives. Reproductive isolation is, of course, complete. Not only are patterns of plumage colors about the head different, but also, and this may be of special importance, *C. melanoleucos* has a bright yellow iris while the iris of *D. lineatus* is strikingly white. This situation is depicted in color for *D. lineatus* and *C. guatemalensis* by Sutton (1951). The latter woodpecker forms a superspecies with *C. melanoleucos* and is also similar in plumage to *D. lineatus* with which it is sympatric. Short (1970*b*) noted that the eyes of an immature female of *C. melanoleucos* were white.

The drummings and vocalizations of *C. melanoleucos* and *D. lineatus* are also different. Thus, in *C. melanoleucos* the main call is a *kwirr-a* while in *D. lineatus* it is, according to Skutch (1969), a flicker-like *wic wic wic.* I have found, however, that this latter is actually part of a spectrum, becoming at high intensity a *wuk wuk wuk* of about 17 notes, falling off at the end, that one recognizes at once as being similar to the high call of the Pileated Woodpecker (Kilham, 1959), while at low intensities the notes become a *wer wer wer* that one might never consider as coming from a woodpecker. The drummings differ to an equal degree. Thus, much of the communication between members of a pair as well as between rivals in *C. melanoleucos* is by their peculiar drumming, vocalizations being infrequent. Comparable communications of *D. lineatus,* on the other hand, are more by vocalizations, while the long rolling drum, again like that of *D. pileatus*, is used less frequently.

Nest excavation.—Crimson-crested and Lineated Woodpeckers are further

TABLE 1

SIMPLIFIED OUTLINE OF DIFFERENCES IN BREEDING AND OTHER HABITS OF CRIMSON-CRESTED AND LINEATED WOODPECKERS THAT PERMIT SYMPATRY WITHOUT UNDUE COMPETITION*

Differences	*C. melanoleucos*	*D. lineatus*
Main breeding season	Last of rainy season and first of dry season (Nov.–Jan.)	Last of dry season (March–April)
Relative size of territories	Small	Large
Type of stub used for nesting (optimal)	Large (45–50 cm diam.); substantial	Stubs or tops of stubs small in diam. (18–23 cm); more risk
Food	**Larvae of wood-boring beetles primarily and possibly termites	*Azteca* and other ant larvae, overlaps with *C. melanoleucos* otherwise in feeding on beetle larvae
Temperament	Relatively tame	Easily alarmed

* It should be emphasized that this outline is based on observations of relatively few individuals.

** Special adaptations of feet and legs (Bock and Miller, 1959) make *C. melanoleucos* especially efficient at extracting this type of prey. (See text.)

isolated reproductively by the timing of their nestings, that of *C. melanoleucos* coming at the end of the rainy season and that of *D. lineatus* toward the end of the dry season (Table 1). W. John Smith (pers. comm.), for example, found a pair of *P. melanoleucos* nesting at Frijoles on 27 January 1967 not far from where a pair of *D. lineatus* had nested in May 1966, and Chapman (1929) mentions the young of a pair of *C. melan-oleucos* as leaving their nest on Barro Colorado in February. Skutch (1969) stresses that the closely related *C. guatemalensis*, which replaces *C. melanoleucos* northward of Panama and is also sympatric with *D. lineatus*, is an unusually early nester. Although Lineated Woodpeckers nest later than Crimson-crested, they may, in some cases, start trial nest excavations early in January, as indicated by the following observations: On 2 January I found a pair of Lineated Woodpeckers excavating a hole in the dead top (Fig. 4) of a living tree, one of the Bombacaceae. The cavity was already deep but the two birds continued to toss out sawdust from the entrance until 4 January, when the excavation appeared to have been completed. Yet with exception of a brief view on 5 January I never saw the pair by the hole again. Strong winds came with the beginning of the dry season later in the month and on 1 February I found that the top of the tree had broken off where the cavity of the woodpeckers had weakened it (Fig. 4).

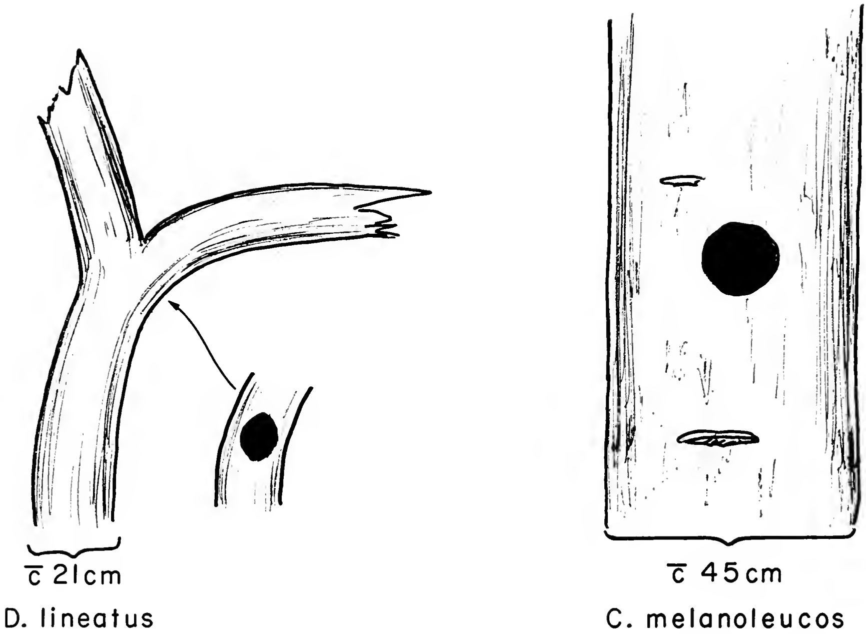

FIG. 4. Contrasting sites of nest excavations of Lineated and Crimson-crested Woodpeckers. (The entrance hole of the Lineated's nest having been under the curving arch of the limb above, is shown as seen from below, looking up.)

On 8 January on BCI a pair of Lineated Woodpeckers were excavating a hole they had pirated from a pair of the smaller Black-cheeked Woodpeckers (*Melanerpes pucherani*). The hole was in an arching limb 18 cm in diameter at the top of a tall dead stub. Both members of the pair of larger woodpeckers could enter their excavation completely by 9 January. The male was still excavating a week later but on 17 January the entire stub crashed to the ground.

In summary of these and other observations it would seem that *D. lineatus* differs from *C. melanoleucos* in the locations as well as in the timings of its nest excavations. Thus, while *C. melanoleucos* is particular about finding a large stub (Fig. 1) that will be a secure place to nest and appears wary about even attempting to nest otherwise, *D. lineatus* is attracted to inherently more risky situations, whether in stubs or in dead tops of trees so narrow that the nest cavity is barely accommodated. Its walls, therefore, are necessarily thin, offering too little support in case of wind or storm. Advantages of using such situations, however, must outweigh disadvantages. They may include such things as freedom from competition with the sympatric *C. melanoleucos* for nest stubs, locations so high above ground as to be less within reach of usual climbing predators, and in being less attractive in their fragile nature to nest hole competitors of various species such as Collared Araçari.

Finally it should be noted that this habit of making nest excavation in places that would seem too narrow and too risky is not confined to *D. lineatus.* As previously described (Kilham, 1959) the same situation holds for Pileated Woodpeckers in central Florida where, in absence of any large trees, they may nest in narrow pole-like dead pines where a full nest cavity may be supported by little more than outer bark. Truslow (1967), who happened to be present at the dramatic moment, has recently photographed the breaking up of one such nest under only a light wind.

DISCUSSION

The Crimson-crested and Lineated Woodpeckers, whose breeding and feeding habits have now been compared, are a remarkable pair of species in being alike in size and general coloration, yet sympatric within the same monsoon-rain forest habitat. Thanks to Cody's article (1969), I became interested in studying these species concomitantly. If it were true, as Cody claimed, that these two are so alike in habits that they can coexist sympatrically only by means of an interspecific territoriality promoted by convergence in size and plumage patterns, then here was a remarkable biologic phenomenon. Unfortunately, I could find no evidence supporting Cody's ideas, for I was struck, as also was Karr (1971), that the two species are mutually tolerant. Every time I encountered Lineated Woodpeckers on Barro Colorado Island, for example, they were within the territories of one or another of pairs of Crimson-crested Woodpeckers under study. At no time did I observe conflicts such as might arise from mutually exclusive territoriality. The general peacefulness between the two species was notable not only when pairs happened to be feeding on adjacent trees, but also on one occasion when a male Crimson-crested, coming close to a male Lineated Woodpecker, temporarily displaced it from a feeding spot without show of hostility on the part of either the dominant or of the submissive species.

Having concluded early that interspecific territoriality did not exist. I wondered whether Cody's theory might not be modified to apply to spacing out in relation to nest sites. This hypothesis, however, likewise became untenable in the light of experience. The two species are divergent in such important aspects of their lives as the time of their breeding, the nature of nesting sites they look for, as well as in their feeding habits, as summarized in Table 1. Such a situation is, of course, the usual outcome of natural selection. What is unusual, if not very rare, would seem to be interspecific territoriality based on any long term evolutionary process.

An interesting example of limited interspecific territoriality among very closely related woodpeckers is given by Selander and Giller (1959). They found that, seemingly due to man's interference with natural ecologic barriers, morphologically similar members of the same superspecies, *Centurus carolinus* and *C. aurifrons*, met in Austin, Texas, and, in a limited area of sympatry, held mutually exclusive territories. This situation would appear different from what must be the historically long sympatry that has existed between *C. melanoleucos* and *D. lineatus.*

From one point of view an instructive example of a species pair comparable in some ways to the Crimson-crested and Lineated Woodpeckers, and even more alike in plumage although dissimilar in size, are the Hairy and Downy Woodpeckers. I have found (Kilham, MS) that in spite of wide differences in prey and feeding habits, in type of nesting sites, as well as in the time of onsets of breeding behavior, these species must still be acted upon by many selection pressures in common, such as predation, survival over winter months when trees are bare of leaves, and many others, in relation to which their plumages represent one of many optimal compromises for survival. While the selection pressure may differ from tropical rain forest to north temperate woodlands, the principles of why certain birds are similar in plumage would seem to be the same.

SUMMARY AND CONCLUSIONS

Reproductive and feeding habits of Crimson-crested Woodpeckers were followed in mature as well as in second-growth woods of the Panama Canal Zone.

The double drum *DA-drrr*, characteristic of *Campephilus* woodpeckers, was a main method of communication, whether used to express mild alarm, territorial dominance, or in duets between members of a pair at time of courtship.

Copulations and excavations were seen in November but most pairs had difficulty finding suitable nest stubs and either began nesting in December or January or, in some cases, failed to nest.

Territorial conflicts between rival males were marked in January, the intrusions being largely by males of pairs that were failing to establish nest holes.

Both sexes excavate and the bird excavating drum-taps on the inside or outside of the cavity on the arrival of its mate. This drum-tapping ceremony is identical in *Campephilus* and *Dryocopus.*

Bill-touching or fencing between members of a pair takes place at the nest excavation or elsewhere at the height of courtship.

Crimson-crested Woodpeckers become silent and difficult to observe in the incubation period, sitting on their eggs for prolonged periods without looking out from nest holes.

After hatching, either sex may look out and in the first few days when brooding young, drum-tap on the arrival of a mate. Prey was never visible in the bills of parents coming to feed young in the first three weeks.

A bird in adult female plumage, seeming by her begging behavior to be a young one of the year before, was seen accompanying a pair of Crimson-crested Woodpeckers in January. The male fed her a large grub on one occasion. Juveniles of recent nestings were first seen late in January and in February.

Crimson-crested Woodpeckers have remarkable adaptations of legs and toes which enable them to cling securely when feeding in such difficult situations as the undersides of limbs, small branches, or on boles of large trees. Larvae of wood-boring insects appear to be their chief prey.

Crimson-crested Woodpeckers live in the same woods and even feed in the same trees with Lineated Woodpeckers, which appear remarkably like them in size and general coloration. The two species differ in feeding habits, in time of onset of nesting, and in types of nest sites chosen. No signs of interspecific hostility or territoriality were observed.

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LITERATURE CITED

Allen, A. A., and P. P. Kellogg. 1937. Recent observations on the Ivory-billed Woodpecker. Auk, 54:164–184.

Bock, W. J. 1963. Evolution and phylogeny in morphologically uniform groups. Amer. Naturalist., 97:265–285.

Bock, W. J., and W. D. Miller. 1959. The scansorial foot of woodpeckers with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Novitates, no. 1931:1–95.

Chapman, F. M. 1929. My tropical air castle. Appleton, New York.

Cody, M. L. 1969. Convergent characteristics in sympatric species: A possible relation to interspecific competition and aggression. Condor, 71:222–239.

Karr, J. R. 1971. Ecological, behavioral, and distributional notes on some Central Panama birds. Condor, 73:107–111.

Kilham, L. 1959. Behavior and methods of communication of Pileated Woodpeckers. Condor, 61:377–387.

Selander, R. K., and D. R. Giller. 1959. Interspecific relations of woodpeckers in Texas. Wilson Bull., 71:107–124.

Sielmann, H. 1958. Das jahr mit den spechten. Verlag Ullstein, Berlin.

Short, L. L. 1970*a*. The habits and relationships of the Magellanic Woodpecker. Wilson Bull., 82:113–240.

Short, L. L. 1970*b*. Notes on the habits of some Argentine and Peruvian woodpeckers (Aves, Picidae). Amer. Mus. Novitates, no. 2413:1–37.

Skutch, A. F. 1969. Life histories of Central American birds III. Pacific Coast Avifauna, no. 35:1–580.

Slud, P. 1964. The birds of Costa Rica. Bull. Amer. Mus. Nat. Hist., 128:189.

Sutton, G. M. 1951. Mexican birds. Univ. Oklahoma Press, Norman.

Tanner, J. T. 1942. The Ivory-billed Woodpecker. Res. Rept. No. 1, Natl. Audubon Soc., New York.

Truslow, F. K. 1967. Egg-carrying by the Pileated Woodpecker. Living Bird, 6:227–236.

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TERRITORIAL BEHAVIOR IN SAVANNAH SPARROWS IN SOUTHEASTERN MICHIGAN

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THE Savannah Sparrow (*Passerculus sandwichensis*) is a bird of open grasslands, bogs, coastal marshes, and tundra. In southeastern Michigan its thin insect-like song is heard wherever farming has produced pastures and fallow fields. It migrates south in late summer and fall and returns in April and early May. For three successive breeding seasons (1965–67) I observed the territorial behavior in Savannah Sparrows in a field five miles west of Ann Arbor, Washtenaw County, Michigan. The population ranged from about 18 pairs in 1965 to 12 pairs in 1967.

METHODS

The study area was measured off in a grid, with tape markers placed along border fences and metal ground markers at the grid intersections in the field. Song perches were marked with colored pipe cleaners, some with colored foam plastic balls attached. Adult birds were netted and marked with aluminum and color-coded plastic bands. Sex was determined by behavior since there is no discernible difference in appearance. Nestlings were marked only with aluminum bands. (Only one bird banded as a nestling later returned to the study field to breed.) Fifty-two adults were banded in 1965, 12 in 1966, and 6 in 1967, a total of 70. Seventy-five young were banded in 1965, 29 in 1966, and 26 in 1967, a total of 130. (Banding in 1966 and 1967 was more selective, aimed at birds evidently linked to a territory. In several instances, females on their nests were flushed into nets posted near them. Only one non-resident Savannah Sparrow was caught in each of those years, contrasted to 19 in 1965.)

I observed the birds mostly on Fridays and Sundays from 06:00 to 12:00. Occasionally, I made evening visits. In all, I spent 490 hours in observation.

Because Savannah Sparrows spend so much of their time on the ground, it was impossible to determine their territorial boundaries where vegetation was dense. "Walking" the birds around their territories was not feasible since they would leave their territories when pressed. Neither did many territories touch others, where the males might have clashed and revealed the borders. It was necessary, therefore, to fall back on the device of marking the males' singing perches to provide an approximation of the territorial areas. When singing was done on the ground, usually during pauses in foraging among the hummocks of grass, adjacent grass clumps or weed stalks were marked.

Gradually the accumulation of markers described areas the edges of which appeared to be defended consistently. Furthermore, the birds did not appear to go much beyond these markers to defend their territories. Thus, the variation between the edges of those areas described by markers and the actual territorial boundaries seemed slight enough to make the location of the territories clear and the measurement valid.

STUDY AREA

The study field contained 4.74 hectares (11.72 acres) and was essentially level and poorly drained. It was bounded on the south by a gravel road and a brushy field, to the north by cropland, and on either side by wet pastures.

Most of the study field was covered by bluegrass (*Poa pratensis*) fallen over or blown down in successive layers to form hummocks 30 to 50 centimeters in diameter and up to 30 centimeters high. The bluegrass and interspersed timothy (*Phleum pratensis*) grew up to 45 centimeters tall by mid-June. In widely separated locations were slowly-spreading circles of sedge (*Carex stipata*) ; chickweed (*Stellaria graminea*) was also prevalent.

The northern half of the field was free of woody plants except for a small copse of willows (*Salix sp.*) up to 4.5 meters tall at one place along the northern fence. The southern half contained scattered clumps of willow (*Salix petiolaris*) from one-half to two meters tall. The field had occasionally been used as pasture for cattle in previous years, including the year immediately preceding the study period, but no cattle were there during the study period itself. In those three years there was an increase in the amount of thistle (*Cirsium sp.*), goldenrod (*Solidago sp.*), spirea (*Spirea sp.*) and asters (*Aster sp.*).

ARRIVAL DATES

The earliest recorded dates of the birds' spring arrival at the field during the study period were 9 April in 1965 and 1967, and 15 April in 1966. Males were singing on those dates.

Twenty-two males color-banded in 1965 were first observed in 1966 from 15 April to 13 May, and 17 color-banded males in 1967 from 9 April to 7 May. A color-banded male first seen as late as 21 May 1967 was not seen again.

In both years most of the returning males (20 out of 22 in 1966 and 16 out of 18 in 1967) arrived within a ten-day period in April (9–18 April 1966 and 15–24 April 1967.)

In 1966 and 1967, the first color-banded females were seen on 1 May and 30 April respectively. The earliest estimated start for nesting in any year was 30 April 1967. Returning color-banded females were first seen in 1966 as late as 14 June and in 1967 up to 27 May. Usually inconspicuous unless alarmed by the observer's proximity to a nest or fledgling, some females could have been in the field several weeks before being seen for the first time.

TERRITORIAL DEFENSE

Singing.—Males began singing on arrival in their territories or shortly thereafter. In all three years of the study some singing, however limited, had begun by 15 April. In two of those years the field was full of song on that date. In the third year (1965) full song came on 23 April.

Singing did not appear to be done by other than territorial males. I never heard a female sing or make any other sound other than a chip of alarm and a buzz when rejecting the advances of a male.

Songs differed from one bird to another and in one bird's repertoire, but I have no detailed notes on this. I did time one singing individual and recorded 25 songs in four minutes—an average of one song every 9.6 seconds.

Borror (1961) found that individual Savannah Sparrow songs last two to three seconds.

Several birds were usually singing by 06:00 in April. They ceased as late as 19:40 in late April, and as late as 20:20 by the end of June. Singing tapered off after 09:00 and the birds were usually still after 12:00. Singing in the evening was less than in the morning but occurred regularly. It was also less or absent in strong wind or rain.

Song was sometimes distorted by wind, making the birds difficult to hear or locate, especially when they sang from behind hummocks on the ground during pauses in foraging.

Singing decreased by mid-June, since the male stopped singing during the incubation period and did not resume until the fledglings were on their own. (He also used the perches less frequently and was less frequently seen.) When a nest was lost through predation, the male soon resumed singing.

Singing occurred mostly from perches in thistle, goldenrod and willow, and on the barbed wire fence around the field. Certain perches were used more than others.

Fighting.—The ultimate defense of Savannah Sparrow territory is a fight between males, but fights were infrequent. (No female was seen in a fight or any other defense of a territory.) Typically, the two birds rose straight up about a meter above ground and went back down, breast to breast and clawing all the way. The fights were of short duration—I never saw a rise repeated—and the birds quickly went their separate ways. I heard no sound during the fights.

Chases.—Chases by territorial males were more common than fights, especially early in the season when the territories were first established. They ceased with molt.

In all chases in which I was able to identify the pursuer, the chase was made by the territorial defender and ended at the border or shortly past it. The pursuer usually made a buzzing noise during the chase. In one instance the defender rose almost straight up about 6 meters to intercept and chase a Savannah Sparrow flying over its territory.

The pursuer often ended the chase by flying to a perch in his territory and making a chipping noise or singing. One pursuer, apparently agitated by the chase, flew from a grass clump out in his territory to a fence at the border, then back and forth two more times, singing constantly.

If the chased bird flew through more than one territory, the chase sometimes became a relay event, the first defender stopping at his border and the neighboring defender taking up the pursuit.

On three occasions a week apart in April, 1967, I saw gang chases involving as many as five or six male Savannah Sparrows. The first incident began with a two-bird chase, the rest converging and all going down into the grass. The birds started scattering before I arrived, but I was able to identify four from their color bands. The second chase involved four birds, only one identifiable. The third incident involved five or six birds, one or two flying in from as far away as 15 meters. It broke up quickly but not before a fight occurred.

The location in all three incidents was the same "no-man's-land" between several territories. The birds identified were all territorial residents in that area. I was unable to determine if they were ganging up on a bird from outside the area—a transient, perhaps, or a new arrival—or whether a single chase between two area residents excited others into general aggression.

Border-crossings did not always end in chases, perhaps because even Savannah Sparrows have difficulty finding each other in tall grass.

On 15 May 1966, for example, a territorial male flew onto a grass tuft and, his crown feathers raised, looked around quickly in many directions but started no chase. Another Savannah Sparrow soon flushed from the base of of a nearby fence post and flew off, whereupon the first bird, his crest now down, perched quietly on the fence and no longer looked around so rapidly.

Generally, however, Savannah Sparrows stayed within their territories throughout the breeding season except when the momentum of chasing an intruder carried a male into an adjoining territory or when a parent accompanied a wandering fledgling across boundaries.

Other defenses.—Most adjustment of borders between the few territories that touched occurred without either fights or chases. Instead, the opposing males sang on either side of the line, about a meter apart, silently crowded each other back and forth across the line, or walked along the line side by side, a few centimeters apart. There were also combinations of these.

Examples:

1) M-44 was challenged at his border by another male, M-39. The birds ran side by side, occasionally buzzing and fighting. At times they were only 30 cm apart and both singing.

2) I flushed M-64, and he flew to a grassy area at his boundary. He was instantly met there by M-38 of the adjoining territory. Both then walked side by side, sometimes only centimeters apart, along their border. At one point M-64 stopped and M-38 walked on, whereupon M-64 crossed the "line." M-38 immediately rushed back at M-64 and buzzed; M-64 returned to his side and the side-by-side walking resumed. M-64 occasionally sang as he walked. After a few minutes I moved away and M-38 flew to a perch in the center of his territory and sang, ending the confrontation.

3) M-53 resisted intrusions by M-40, who had part of M-53's territory as his own the previous year. On one occasion M-40 sang from the ground in M-53's territory but was escorted back across the border. That is, M-53 flew to the ground about 30 cm from M-40 and followed M-40 as the latter walked back into his own territory. There was no audible sound.

Among encounters on fences bordering adjacent territories, one observed 12 May 1967 was typical. M-29 and M-33 approached each other, facing first one way, then another as they perched crosswise on the barbed wire. They fluttered their wings slightly, fanned their tails, raised their body feathers as if swelling, teetered forward with their heads lower than their tails, and opened their bills. At times they were only 30 cm apart.

One would back up after depressing his body feathers, while the other advanced. Then the action would be reversed. The birds see-sawed a distance of not greater than 1.5 m, more often within a one-half-to-one-meter span. All was done silently except for a few very soft buzzes.

The confrontation ended when M-33 hopped up onto a fence post a little farther away and sang. M-39 hopped down into the grass a short distance in the opposite direction and began foraging.

Other encounters on fences lacked the buzzing, wing movements and feather-raising, but the see-sawing and teetering were the same. None of the encounters resulted in fights.

Immunity from defense.—Parent birds apparently could follow their fledglings anywhere without being attacked by territorial defenders. The parents were very excitable at this stage, both birds (but particularly the male) perching closer to the observer than usual and chipping rapidly and loudly.

In June, 1966, female F-69 from an adjacent territory, possibly foraging for her nestlings, perched and chipped in M-64's territory without being chased out. But when her mate, M-18, also intruded, M-64 approached him and buzzed and M-18 retreated to his own territory.

Six days later, however, the situation changed. The nestlings had left the nest and were being tended by M-18 and F-69. The parent birds again moved into M-64's territory. Although I was unable to see whether they were following their fledglings, this time neither bird was bothered by M-64. On the contrary, M-18 approached M-64 and buzzed.

Interspecific aggression.—Aggression toward birds of other species was observed in only a few instances.

A territorial male was seen chasing a Field Sparrow (*Spizella pusilla*) which shifted only a meter or two at each rush but eventually left the territory.

A Savannah Sparrow landed beside a Song Sparrow (*Melospiza melodia*) and buzzed until the latter flew away, but in another case a Savannah Sparrow flew when approached by a Song Sparrow. In all other encounters, these two species appeared to ignore each other.

Goldfinches (*Spinus tristis*) and Bobolinks (*Dolichonyx oryzivorus*) nested in the field without being approached. On the contrary, I once saw a Bobolink chasing a Savannah Sparrow.

I saw no cases of Savannah Sparrows being aggressive toward other animals except in pursuit of insects for food.

Cessation of defense.—Nesting activity tapered off in late July, accompanied by lessening and cessation of territorial defense. The females left the study area, none being seen despite repeated inspection walks throughout all territories. The males went into molt, stopped singing and skulked through the brush. When flushed, they flew only a short distance and disappeared into the brush again. Any chipping was low in volume and not persistent. Eventually the males also left the field.

The earliest date on which molt was noticed during the study period—that is, when the males first looked ragged—was 17 July. For some males it was noticed 30 July. In all cases molt was accompanied by a cessation of territorial activity. In no case was molt seen as long as the male was still tending fledglings.

I was never able to observe molt in a female. Quite often a female would appear to be in sleek plumage while her mate looked ragged. Generally the females left earlier and may have molted during this dispersal.

The cessation of territorial defense throughout the field seemed to occur within a week's time except for a few birds still busy with nestlings or fledglings. In each of the three years there came a particular day when I noted that territorial behavior seemed to have ended. Twice it was on 25 July and once on 31 July.

DEPARTURE

The females usually left the study area within two weeks after the end of their last nest, whether the end was from predation or fledging and although both males and females tended fledglings. While they no longer defended their territories, the males stayed on as long as a month and a half, the average being about a month. By 31 July, most had gone, but a few stayed on until mid-August. One was seen as late as 10 September in 1965.

The last resident birds of 1966 were seen on 14 August. Observations in 1967 ended on 31 July, with four males and three females remaining, representing only 22 per cent of the full adult population that season. The seven birds included three pairs with late broods.

In general, the females left gradually through June and July, while most of the males left the last two weeks in July.

NATURE OF TERRITORIES

Shape.—The territories varied considerably in shape from almost square to long and rectangular and roughly triangular, with no apparent correlation between territory shape and success in attracting a mate.

Although the fields adjacent east and west were breeding areas, the Savannah Sparrows I observed generally adopted the barbed wire fences not only as much-used singing perches, but also as territorial boundaries. The birds did not cross the fences except when approached by me or for a short distance in pursuit of an intruding Savannah Sparrow. I also recorded one instance in which a female apparently followed her fledglings into the adjacent field.

One of the two exceptions to adoption of the fences as boundaries was a Savannah Sparrow which frequently sang from a small sapling about two m beyond the fence, although the bulk of his territory was in the study field. Another bird clearly had territories which straddled the fence line in 1965 and 1967.

The fences were observed as boundaries even when they merely separated open grassland rather than being paralleled on one side by something different, such as a road, a ditch or a thicket.

Nest location.—Nests occurred anywhere in a territory, even at the border. In 1965 I discovered two nests only 2.2 m apart in adjacent territories. Both nests were successful.

Size.—Fifty-eight per cent of 62 territories marked during the three years ranged from 601 to 1200 m^2—about one-sixth to one-third of an acre. Fifteen per cent were smaller, 27 per cent larger.

The average for the 62 territories was 1,068 m^2 (0.26 acre). For the 27 territories in which no nest was found, the average size was 845 m^2; for the 35 in which nests were found it was 1,239 m^2.

The literature on the size of sparrow territories is limited. What there is indicates the Savannah Sparrows I observed had territories considerably smaller than the other species noted. I found reports of territory sizes for ten species in addition to my own figures for the Savannah Sparrow.

A comparative list follows, all figures translated into square meters:

Savannah Sparrow (*Passerculus sandwichensis*)—From 120 to 2,920 m^2, averaging 1,068 m^2 (0.26 acre). Present study.

Grasshopper Sparrow (*Ammodramus savannarum*)—4,850 to 13,330 m^2, averaging 8,200 m^2 (2.03 acres). Smith, 1963.

Baird's Sparrow (*Ammodramus bairdii*)—4,730 m^2 (1.17 acre). Cartwright, et al., 1937.

LeConte's Sparrow (*Passerherbulus caudacutus*)—1,020 to 6,300 m^2, averaging 3,320 m^2 (0.82 acre). Calculated from maps by Murray, 1967.

Henslow's Sparrow (*Passerherbulus henslowii*)—Average of 3,238 m^2 (0.80 acre). Robins, 1971.

Sharp-tailed Sparrow (*Ammospiza caudacuta*)—Female less than 4,047 m^2 (1 acre), males not territorial. Woolfenden, 1956.

Seaside Sparrow (*Ammospiza maritima*)—Nesting area, 5,830 m^2; shoreline feeding area, 4,170 m^2; total, 10,000 m^2 (2.47 acres). Woolfenden, 1956.

Tree Sparrow (*Spizella arborea*)—5,580 to 39,100 m^2 (1.38 to 9.66 acres). Heydweiller, 1935.

Chipping Sparrow (*Spizella passerina*)—4,047 to 6,070 m^2 (1 to 1.5 acre). Walkinshaw, 1944.

Field Sparrow (*Spizella pusilla*)—Less than 3,640 to 8,094 m^2 ("less than 0.9 acre" to 2 acres). Walkinshaw, 1945.

Song Sparrow (*Melospiza melodia*)—For mainland, 2,000 to 6,000 m^2 (0.5 to 1.5 acre),

TABLE 1

DISTRIBUTION OF TERRITORIES ACCORDING TO SIZE AND PRESENCE OF NESTS

Size (m²)	Territories without nests	Territories with nests	Total no. of territories in size range	% of all territories	Nests found	% of territories in size range with nests
0–600	8	1	9	15	1	11
601–1200	16	20	36	58	27	56
1201–1800	1	8	9	15	12	89
1801–2400	1	4	5	8	5	80
2401–3000	1	2	3	5	2	67
Totals	27	35	62	101	47	

Nice, 1937; for lakeshore, 1,250 to 2,750 m² (0.31 to 0.68 acre), Suthers, 1960; for island, 160 m² (0.04 acre), Beer, et al., 1956.

Nest occurrence.—Fifty-four Savannah Sparrow nests were found. Behavior by adult birds indicated the probable existence of 15 more nests, for a total of 69. Thus the nests found represented about 80 per cent of those believed to have been in the field.

A breakdown of territories by size and known presence of nests is presented in Table 1. Only 47 of the 54 nests found are included. The other seven were in five territories also not included because of inadequate marking or because the nests were discovered too late to map the territories. Figure 1 shows the territories for the three years of the study.

As might be expected, most of the nests were found in the size range which also included a majority of the territories—601 to 1,200 m². But a comparison of the percentages of nest occurrence in the several size ranges revealed a roughly similar distribution (56 to 89 per cent) except where territories were smaller than 601 m². Only one of the nine territories in that range had a nest, a distribution of only 11 per cent.

Female occurrence.—The same pattern of distribution could be applied to the presence of female Savannah Sparrows in the territories. This was so because in only nine out of 45 territories in which adult females were known to be present were there no nests found, and even in eight of those nine behavior of the adult birds indicated the probable existence of nests.

It appeared, therefore, that the size of the territory had some influence on the attraction of a female, with territories larger than 600 m² being more attractive.

Territorial compression.—Two males experienced severe territorial compression.

In 1965, M-24 attracted a mate, F-23, to a territory originally 890 m² in

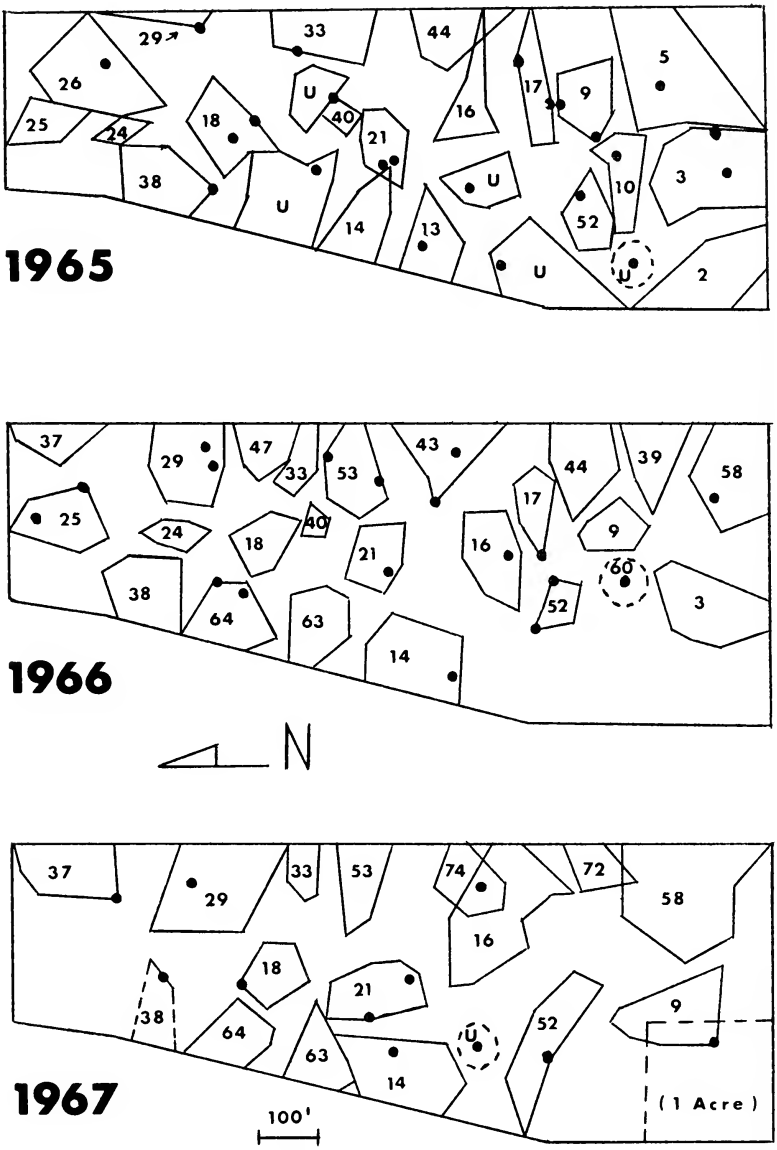

FIG. 1. Savannah Sparrow territories in field near Ann Arbor, Michigan, 1965–67. Numbers = identified males. U's = unidentified males. Dots = nests. Broken circles surround nests found too late to map territories. Broken territory at bottom, 1967—Male 38, is estimated from partial sightings.

size. Much of this was later used by another male as part of his own territory, and M-24's area shrank to 200 m^2. M-24 and F-23 apparently nested once but abandoned the field after 26 June. The following year, M-24 returned to the same spot, established a territory only 360 m^2 in size and did not mate.

The other male, M-40, first established (in 1965) a 970 m^2 territory, and F-35 became his mate. Encroachments by other males establishing adjacent territories compressed M-40's area first to 360 m^2 and then to only 200. Nevertheless, there was at least one nest and probably two. In 1966, however, M-40 returned to the same spot, established a territory only 120 m^2 in size and did not mate. He was surrounded by five other territories, the males all aggressive.

Neither M-24 nor M-40 returned to the field in 1967.

(The original sizes of their territories in 1965, before compression, are used in Table 1, since these sizes existed when the females were attracted to the areas and began nesting.)

Territorial expansion.—With the exceptions just discussed, early-arriving Savannah Sparrows did not seem consistently to claim large areas that were later scaled down by population pressure, although there sometimes was considerable border adjustment at the beginning. On the contrary, there seemed to be room between most territories for the small expansion the male frequently indulged in at the onset of a second nest.

However, I was not able to determine whether part of the old territory was abandoned so that the total area remained the same size. This was because once his territory was established, each male favored only certain perches.

Late arrivals (there were attempts to establish new territories even in July) would sometimes choose unclaimed areas between territories and attempt to crowd their way in, expanding to either side and reducing the sizes of the adjacent territories. If the unclaimed spaces were small to begin with and the attempts at expansion failed, the late arrivals were often gone the next day but sometimes stayed as long as two weeks.

Abandonment of territories.—Abandonment by one mate or the other is impossible to prove except when a missing bird shows up elsewhere. Otherwise, predation is assumed to be the cause of disappearance. During this study no males were proven to have abandoned well-established territories, although three disappeared, all in 1967. One of them had a mate, which disappeared nine days before the male and long before the usual departure time.

After having successfully reared a brood in 1966, F-69 followed her fledglings into the adjacent territory of M-64 and remained there to mate with him for a second, successful nest. Deserted M-18 spent the rest of the season singing in his own territory but did not acquire another mate. A similar occurrence was noted among Field Sparrows by Walkinshaw (1945).

Another female, F-20, disappeared after her first nest in both 1965 and 1966 with the same male, M-21, although the male remained each time. Oddly enough, after M-21's first mate of 1967 (not F-20) disappeared after laying four eggs, F-20 reappeared to mate with him again for the second nest, which was successful.

SUMMARY

Territorial behavior of Savannah Sparrows in a field in southeastern Michigan was observed for three successive breeding seasons.

Most males arrived within a 10-day period in mid-April. Females arrived over a one-month period starting at the end of April. The males established territories immediately, often returning to the same area of the field claimed in previous years.

Males defended their territories by singing from border perches, chasing intruders, walking side-by-side along the boundaries with males of adjoining territories or by assuming threatening postures face-to-face at the borders.

Birds seldom left their territories except under stress, but adults accompanying fledglings could cross boundaries with impunity.

Fifty-eight per cent of the territories ranged in size from 601 to 1,200 m^2. Fifteen per cent were smaller, 27 per cent larger. There was some enlargement between nestings.

The Savannah Sparrow territories observed were considerably smaller than those of 10 other species of sparrows reported in the literature.

The success of attracting a mate was apparently linked to territorial size, with a better chance in territories larger than 600 m^2.

Nesting activity tapered off in late July, territorial defense ended and the males molted. The females left the study area usually within two weeks after their last nests were emptied, through June and July. The males usually remained about a month after the last nests were emptied, most of them departing the last two weeks in July.

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LITERATURE CITED

Beer, J. R., L. D. Frezel, and N. Hansen. 1956. Minimum space requirements of some nesting passerine birds. Wilson Bull., 68:200–209.

Borror, D. J. 1961. Songs of finches (Fringillidae) of eastern North America. Ohio Journ. Sci., 61:172.

Cartwright, B. W., T. M. Shortt, and R. D. Harris. 1937. Baird's Sparrow. Trans. Roy. Canadian Inst., 21:Part 2:163–197.

Heydweiller, A. M. 1935. A comparison of winter and summer territories and seasonal variations of the Tree Sparrow. Bird-Banding, 6:1–11.

Murray, B. G., Jr. 1967. A comparative study of the LeConte's and Sharp-tailed Sparrows with comments on the ecology of sympatric species. Unpubl. Ph.D. thesis, Univ. Michigan, Ann Arbor.

Nice, M. M. 1943. Studies in the life history of the Song Sparrow. II. Trans. Linnaean Soc. New York, 6:152.

Robins, J. D. 1971. A study of Henslow's Sparrow in Michigan. Wilson Bull., 83:42–48.

Smith, R. L. 1963. Some ecological notes on the Grasshopper Sparrow. Wilson Bull., 75:159–165.

Suthers, R. A. 1960. Measurement of some lake-shore territories of the Song Sparrow. Wilson Bull., 72:232–237.

Walkinshaw, L. W. 1944. The Eastern Chipping Sparrow in Michigan. Wilson Bull., 56:193–205.

Walkinshaw, L. W. 1945. Field Sparrow 39–54015. Bird-Banding, 16:1–12.

Woolfenden, G. 1956. Comparative breeding behavior of *Ammospiza caudacuta* and *A. maritima.* Univ. Kansas Publ. Mus. Nat. Hist., 10:45–75.

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FLOCKING ASSOCIATES OF THE PIÑON JAY

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The Piñon Jay (*Gymnorhinus cyanocephalus*) is a noisy, restless bird that normally forms large flocks. Our investigations of the annual flocking cycle of this corvid (Balda and Bateman, 1971) showed that several other species regularly joined and foraged with flocks of Piñon Jays.

In most interspecific flocks of the North Temperate Region reported on to date (Odum, 1942; Wing, 1941; Austin and Smith, in press; and the extensive review by Morse, 1970) the species involved are mainly insectivorous, flocks form primarily in the fall or winter, and the "flock leaders" or "nuclear species" are not present in overwhelming densities compared to the associate species. By contrast, this report deals with five associate species that join relatively large flocks of Piñon Jays: Hairy Woodpecker (*Dendrocopos villosus*), Downy Woodpecker (*Dendrocopos pubescens*), Red-shafted Flicker (*Colaptes cafer*), Clark's Nutcracker (*Nucifraga columbiana*), and Starling (*Sturnus vulgaris*). The Piñon Jay flock is maintained in a number of forms throughout the year, thus permitting interspecific association the year around. The main foods of the Piñon Jay during the fall and winter months when attendant species are most numerous are seeds of ponderosa (*Pinus ponderosa*) and piñon (*P. edulis*) pine, and occasional arthropods (pers. observ.).

The efficient procurement of food has often been used as at least a partial explanation for flocking (Miller, 1921; Rand, 1954; Short, 1961; Morse, 1970). Our observations were made on two Piñon Jay flocks, one on its undisturbed home range and the other when it visited a local feeding station where food was diverse and super-abundant. Comparisons were made of the foraging and agonistic behavior of the jays and associates in both situations.

STUDY AREAS AND PROCEDURES

We studied intensively a flock of about 250 Piñon Jays on a home range of eight square miles located 10 miles NE of Flagstaff, Arizona for over 480 hours from February 1968 through January 1971. Movements, foraging sites (ground, trunk or branch, tip of foliage), and intra- and inter-specific social interaction were recorded. At periodic intervals foraging sites were recorded by counting all birds foraging at each site. Six hundred and forty-nine counts of the entire flock were made in this way. Aggressive encounters, either "supplantings" (overt chases) or "displacings" (retreats) were recorded (after Willis, 1966). We also noted reactions to potential predators and stuffed Great Horned Owls (*Bubo virginianus*).

The third author has a 0.25-acre feeding station which was visited almost daily by a flock of about 70 Piñon Jays for the past five years. On some fall and winter days the flock visited the station up to four times daily; during spring and summer groups of young and adults often spent hours at the station. A number of different foods including

TABLE 1

FORAGING LOCATIONS OF MEMBERS OF THE LARGE PIÑON JAY FLOCK THROUGHOUT THE YEAR (IN PER CENT)

Foraging Location	Jan., Feb., March	April, May, June	July, Aug., Sept.	Oct., Nov., Dec.
Ground	40.0	59.4	48.9	39.7
Foliage	31.8	23.3	42.1	35.6
Crevices	29.1	12.8	4.1	24.7
Hawking In Air	0.0	4.4	4.9	0.0
Total Number of Counts Made	213	172	116	148

mealworms, sunflower seeds, Spanish peanuts, commercial pigeon grain, bacon grease-bread crumb-popcorn mix, white millet, piñon pine seeds, raisins, and suet were always available at the feeding station. Qualitative notes were kept concerning the behavior and aggressive interactions of the Piñon Jays and four of the associates. The Clark's Nutcracker did not visit the feeding station.

FLOCKING CYCLE OF THE PIÑON JAY

Descriptions of interspecific flocks often include a designation of one or more species as nuclear species without adequately describing the movements and behavior patterns of these important species in mixed flocks. We have described the flocking cycle of the Piñon Jay elsewhere (Balda and Bateman, 1971). Here we will only summarize and enlarge on behavior patterns essential to understanding the role of Piñon Jays as a nuclear species in mixed flocks.

Fall and early winter.—During this period blue adults and gray first-year birds formed a loosely organized flock which foraged primarily in ponderosa pine forest. During early morning feeding the flock moved at an average rate of about one mile per hour. Short flights below tree-top level advanced the birds in either leapfrog fashion or as a broad front with all members simultaneously moving in one direction. Longer flights taken over large meadows often consisted of rolling and swirling movements and were accompanied by loud calling of the flock members. Flocks moved up to 13 miles per day while foraging. In the forest some of the flock walked on the ground, either probing for insects and/or pine seeds or caching pine seeds, while other members of the flock foraged off the ground. Some of these gleaned in the foliage, hammered open pine cones to extract seeds or tore out the tender new growth at the tips of the branches. The rest of the birds picked food items out of crevices on the trunks and branches, or hammered vigorously to flake bark to

TABLE 2

NUMBER OF INDIVIDUALS AND FREQUENCY OF OCCURRENCE OF ATTENDANT SPECIES WITH THE PIÑON JAY FLOCK

	Jan., Feb., March n = 49*	April, May, June n = 77	July, Aug., Sept. n = 29	Oct., Nov., Dec. n = 64
Hairy Woodpecker				
Average Number (when present)	5(2–7)**	1(1)	0	4(1–7)
Frequency of Association (%)	100***	14	0	88
Downy Woodpecker				
Average Number	2(1–3)	1(1)	0	1(1–2)
Frequency of Association	80	6	0	42
Red-shafted Flicker				
Average Number	6(4–9)	5(3–7)	2(1–4)	5(3–9)
Frequency of Association	100	71	62	81
Clark's Nutcracker				
Average Number	1(1–2)	2(1–3)	9(6–15)	7(4–12)
Frequency of Association	12	16	45	67
Starling				
Average Number	7(3–14)	9(5–16)	0	4(2–7)
Frequency of Association	39	74	0	28

* Number of visits.
** Range.
*** Per cent of visits when associates were present.

extract food (Table 1). All five associate species foraged with the large Piñon Jay flock at this time (Table 2).

During this period, the feeding station was visited from one to four times daily by a flock of 70 Piñon Jays. While at the station the birds fed on piñon seeds, bacon grease-bread crumb-popcorn mix, peanuts, sunflower seeds, suet, and mixed small grains in that order of preference.

Winter and early spring.—During courtship which commenced in mid-December adult blue birds radiated out in pairs from the feeding flock leaving the gray first-year birds plus a few blue birds to forage as a unit. The foraging flock varied in size from 35 to 70 birds. The foraging birds spent about equal time on the ground and in the foliage. The birds feeding at arboreal sites divided their activities almost equally between foliage gleaning and cone feeding, and crevice picking and bark flaking. The entire flock reassembled periodically and moved to a new feeding location at a loud rapidly repeated *krawing* signal given by most individuals in the feeding flock. The resultant din could be heard for over three-quarters of a mile. During the nest building period the flock fed as a unit in the morning and evening. However, small groups of 4–12 birds often formed autonomous feeding units. Throughout the incubation period the main flock was divided into incubating females, a flock of adult males seeking and bringing food to the females and a flock of gray yearling birds. This latter subunit foraged quietly and moved rather long distances per flight.

When nest building began the visits of the smaller flock to the feeding station diminished to one each morning and evening. Small groups of jays, however, visited the station throughout the day. Later, males visited the feeding station regularly.

Late spring and summer.—After the young fledged, family groups of adults and juveniles foraged together as a unit. Adults failing in their first nesting attempt formed smaller nesting colonies and subsequent family-group feeding flocks. By late July the single winter flock was divided into a flock of year-old birds that did not breed, and five or six independent feeding groups. In late July or early August these flocks moved into the piñon-juniper woodland, where the birds opened piñon pine cones, extracted seeds and carried them into the ponderosa pine forest where they were cached. From this time on the birds remained together as a large flock.

ANTI-PREDATOR BEHAVIOR

Protection from predators is often described as a benefit of inter- and intraspecific flocking (see Morse, 1970 for discussion). Piñon Jays have two behavioral mechanisms which can be termed anti-predator behavior. These are in addition to the protection afforded the birds by their mere presence in a flock (Allee, 1938; Tinbergen, 1953).

Sentinels.—Throughout the year each subflock (feeding group; gray yearling flock) and the entire flock when assembled was commonly surrounded by sentries as reported by Cary (1901). The number of sentries was rather constant around feeding aggregates and the yearling flock (3–5 birds) but varied greatly (3–12 birds) around the large feeding flock that existed during the non-reproductive period. Sentinels were positioned at high vantage points, either exposed or concealed in foliage. At the approach of an aerial or terrestrial intruder the sentinel(s) gave a loud rhythmic *krawk-kraw-krawk* which was often repeated. On occasion, a ground-feeding bird also gave this warning call. This call was often sufficient to cause an immediate cessation of feeding and flight of all individuals up into the trees. During these rapid ascents, birds flew in all directions and it would seemingly be difficult for a predator to focus on and capture an individual. If the warning call was not repeated the flock resumed feeding. Individuals foraging in the trees when a warning call was given simply stopped feeding and remained still. The associate species responded to the warning calls in the same manner. Even though Steller's Jays did not participate in the activities of the mixed flock they responded to the warning calls. Piñon Jays in turn responded to the *shook* call (Brown, 1964) given by the Steller's Jay at hawks or owls.

Mobbing.—After the rhythmic warning call was given a number of birds (3–15) including the sentinel(s) often approached the intruder, circling it if it was perched or on the ground. If flying or running the intruder was chased. During this performance the mobbing Piñon Jays called loudly, often attracting numerous other birds including Steller's Jays, Red-shafted Flickers, Grace's Warblers, Chipping Sparrows, Acorn Woodpeckers, and juncos. Hawks and owls that flew off in response to this harassment were always chased by the Piñon Jays. The Sharp-shinned Hawk (*Accipiter striatus*) and Cooper's Hawk (*Accipiter cooperii*) often evaded the jays by flying an erratic but rapid course then landing and sitting quietly in a camouflaged location. Red-tailed Hawks (*Buteo jamaicensis*) and Rough-legged Hawks (*Buteo lagopus*) usually left the area by gaining elevation rapidly and then moving off. Great Horned Owls, however, seldom flew long distances and could not evade the jays. Consequently, Piñon Jays often mobbed them for up to 45 minutes.

FLOCKING ASSOCIATES

The following accounts are only for the five attendant species (Moynihan, 1962) which regularly occur with the Piñon Jay (passive nuclear species, cf. Moynihan, 1962) flock at least for a portion of the year but are not important for the maintenance of the flock.

Hairy Woodpecker.—One to seven individuals of this species were constant members of the jay flock from late October through early March (Table 2). An occasional individual accompanied the non-breeding flock during the spring and early summer. During this woodpecker's nesting period it did not associate with the flock. Nesting alone, however, cannot explain its seasonal appearance, as it left the flock before it began courtship and did not enter the flock until well after all its nesting duties were completed. During the period of association, however, the foraging pattern of the Piñon Jay was similar to that of the Hairy Woodpecker.

During fall and winter the jays spent considerable time searching the deep crevices of the ponderosa pine trunks, hammering and flaking bark to extract food from old dead branches and stumps, and extracting seeds from ponderosa pine cones. Whether foraging alone or with the jay flock, Hairy Woodpeckers used these same sites. Stallcup (1969) reported Hairy Woodpeckers spending 64.5 per cent of their time extracting seeds from ponderosa pine cones in Colorado. Stallcup's figures indicate that Hairy Woodpeckers spent about 83 per cent of their time foraging in the three sites listed above for the Piñon Jay. He noted that feeding on cones occurred mainly from mid-December through February, the very time these woodpeckers associate with the Piñon Jay flock in central Arizona. He reported as did Morse (1970) that the Hairy Woodpecker foraged throughout the winter in mixed flocks. Short (1961) reported the Hairy Woodpecker as a member of mixed flocks in Oaxaca, Mexico.

Hairy Woodpeckers were seen with the jay flock from sunrise to sunset and remained within the flock as it moved about in the forest and woodland. Interaction at foraging sites was minimal except at pine cones, where the jays successfully drove off the woodpeckers. Of 29 aggressive interactions observed, single jays or groups of jays were able to supplant the Hairy Woodpeckers 20 times. Nineteen of these encounters occurred at pine cones. Hairy Woodpeckers supplanted jays on 9 occasions. At other feeding sites woodpeckers of this species were always displaced by groups of seven or more jays.

During the short movements of the jay flock, the Hairy Woodpeckers always followed the Piñon Jays. The woodpeckers did not follow the flock when it made longer flights across fields, but remained in the trees at the edge of the field, calling loudly as the flock departed. Once, after the flock crossed a field one-quarter mile in width, three Hairy Woodpeckers rapidly flew around the edges of this small field to rejoin the jays. We have followed individual woodpeckers that spent four consecutive hours and traveled at least five miles with the flock.

At the feeding station, resident Hairy Woodpeckers fed alongside the Piñon Jays until the jays became too numerous at one location. Then displacement occurred and the woodpeckers perched silently in the trees until the jays left the station. The jays clearly dominated the woodpeckers: on one occasion an adult Piñon Jay took eleven peanuts, consecutively, from the bill of a Hairy Woodpecker. The woodpeckers did not come to the feeding station with the jays nor did they leave with them.

Downy Woodpecker.—This species associated with the jay flock during roughly the same months as did the Hairy Woodpecker (Table 2). Its foraging mode was somewhat different, however, as it spent most of its time on the trunks and branches of the ponderosa pines and on the dead trees, where it gleaned and flaked bark in search of food. Often it picked through pine cones on the ground, but it seldom worked on cones up in the foliage. Downy Woodpeckers occur in low densities in this area; consequently, more than three individuals were never seen with the jay flock at one time. Of 14 interactions between jays and this woodpecker, the latter was displaced 12 times and supplanted twice. Seven of these interactions occurred while this woodpecker fed on some object either on the ground or a short distance from it. Most direct conflicts were avoided because the Downy Woodpecker managed to stay away from Piñon Jays when they fed close together in groups. In other respects this species acted similarly to the Hairy Woodpecker. The calls of both species evoked no noticeable reactions from the jays.

At the feeding station the Downy Woodpecker did not feed at its usual sites when jays were present. It always left the area when the jays entered the station and returned when the jays left.

Red-shafted Flicker.—Flickers were the most regular associates of the Piñon Jay flock. Even during their breeding season a few flickers were almost always with the non-breeding gray bird flock (Table 2). During fall, winter, and spring as many as nine individuals were in constant association with the jay flock. One individual that was specifically followed spent seven hours with the jay flock and moved about nine miles with it.

The Red-shafted Flickers spent most of their time foraging on the ground among the jays. Their soil-probing activities greatly resembled those of the Piñon Jay. During slow movements through the forest and woodland the flickers flew with the group and were never segregated at the periphery or rear of the flock. During the winter months, Red-shafted Flickers spent considerable time probing into decaying logs for immature insects. This activity strongly resembled that of the Piñon Jay when caching food in these sites. Aggressive encounters were observed when jays and flickers foraged on the ground; groups of jays were observed driving flickers from cache sites in decaying logs. The jays either pointed their bills at the flickers or flew up at them. When a single jay came in contact with a flicker ($n = 48$) Piñon Jays were displaced or supplanted 46 per cent of the time, while jays dominated flickers 54 per cent of the time. When the jay flock moved over large fields some flickers often accompanied them, but others stayed behind, calling loudly as the flock departed. When sentry jays along the edges of the feeding flock gave their rhythmic *krawk-kraw-krawk*, signaling the approach of a potential predator, the flickers responded immediately by flying up into the trees in the same manner as the Piñon Jays. When the warning calls subsided, the Red-shafted Flickers returned to foraging on the ground with the jay flock. Thus, their movements between feeding sites, as well as their movements within the flock when it was stationary, were carried out in synchrony with the Piñon Jays and in a similar fashion.

During the non-breeding season the Red-shafted Flickers appeared to be paired, a male and a female often foraging near one another. On one occasion in May, a feeding group of jays moved through an area where a pair of flickers was excavating a hole. The birds stopped working, flew into the aggregate. and foraged with them for at least the next hour.

At the feeding station Red-shafted Flickers fed near the jays but did not enter or leave with them. The flicker used bill pointing and thrusting to supplant Piñon Jays when it was not badly outnumbered, however a flicker always retreated from groups of 11 or more jays.

Red-shafted Flickers are strongly attracted to Piñon Jay flocks (Table 2), and during the non-breeding season it was rare to find a solitary flicker or pair of flickers far from the jay flock. J. D. Ligon (in litt.) observed the same phenomenon in New Mexico. Short (1961) described the Red-shafted Flicker as an irregular attendant of mixed flocks in Oaxaca, Mexico. Its behavior in the vicinity of Piñon Jays appears to be quite different.

Clark's Nutcracker.—Nutcrackers descended the slopes of the San Francisco Peaks in late August to collect piñon seeds and carry them up the mountains to about 10,500 ft, where they were cached. During this period of seed collecting the nutcracker opened the green cones in such a manner that in poor light it was impossible for us to distinguish nutcrackers from Piñon Jays. The jays and nutcrackers worked on the piñon cones in close association, yet no aggressive interactions were noted. Johnson (1902) commented on such an association in central Utah. On one occasion a yearling Piñon Jay watched from a distance of about one meter as a Clark's Nutcracker opened a cone. At intervals spanning seven minutes the young jay fluttered its wings and begged softly while facing the nutcracker. The latter did not react to this begging. As the jay flock moved between feeding sites up to 15 nutcrackers moved with the flock. They responded to the danger *krawks* of the Piñon Jay by dropping the cones they were extracting seeds from and flying up to the tops of trees. They returned to seed collecting when the jays did. Twice the jay flock left the woodland and flew more than two miles to a watering hole. with eight Clark's Nutcrackers accompanying them. During these flights. the low throaty calls of the nutcrackers could be distinguished from the *krawks* given by the jays. The nutcrackers were always in the rear half of the flock during these flights.

During the spring and summer of 1969 from one to three nutcrackers were often with the yearling flock and also with feeding groups. The usual raucous calls given by nutcrackers during foraging and flight were not heard from these individuals. While foraging on the ground. they performed probing. insect capturing, and seed opening much as did the Piñon Jays.

Starling.—Beidleman and Enderson (1964) first described the association of Starlings with a flock of Piñon Jays in Colorado. In central Arizona, from 3 to 16 Starlings were associated with the jay flock during March, April, and May, and again during October and early November. Most Starlings left the jay flock during the nesting period and again in early winter when they became rare in rural central Arizona and conversely very common in the cities. Throughout the spring and summer months Starlings nested within the home range of the Piñon Jay flock but did not associate with it.

In late winter of 1968 the Starlings were first observed with the Piñon Jay flock when the male jays were roosting as a group and the females were incubating. During this period the Starlings roosted in holes, and on three mornings they stayed in their holes until the male jays called loudly and moved out of the forest to feed for the first time. The Starlings' initial response to these calls was to look out of the holes, squawk loudly, and fly directly to the flock of feeding jays.

Late in the winter of 1969 Starlings were first noted in the Piñon Jay flock at the time courtship activities had commenced. After feeding in a very deliberate fashion with the jays on the ground for an hour in the morning, the Starlings began courting. Pairs segregated from the jay flock and courted high in the foliage and examined old woodpecker holes. The Starlings' initiation of courtship agreed closely with the beginning of the daily courtship of Piñon Jay pairs. Courting activities were noted for six to ten Starlings each morning, and indicate not only a strong attraction to the jay flock, but also a close synchronization of daily events. The synchrony may be coincidence but also suggests the Darling effect (Darling, 1938).

During foraging the Starlings walked slowly and probed for seeds and insects in the same manner as the jays. Not only was their gait similar to that of the Piñon Jay, but in short flights made between feeding sites the Starlings displayed a very similar pattern of flight. At take off, both species beat their wings rapidly, but during sustained flight strong wing beats alternate with gliding. Neither of these species undulates in flight as do most woodpeckers, as the wings are partly outstretched during the glide phase of the flight. Jensen (1926) and Wetmore (1920) have pointed out these behavioral similarities. Under cloudy conditions, or when the jays and Starlings moved through heavy foliage, it was difficult to tell them apart.

Aggressive encounters between Piñon Jays and Starlings were not common as a Starling was not easily displaced by the mere presence of a Piñon Jay. Of 51 aggressive encounters observed, the Piñon Jay supplanted or displaced the Starling 57 per cent of the time; at least five other encounters resulted in both individuals leaving the area.

At the feeding station Starlings associated with the jays from November through mid-April. During the early winter, Starlings commonly entered

TABLE 3

SOLITARY SPECIES OCCURRING IN THE HABITATS USED BY PIÑON JAYS

Species	Mean Weights (g)
Selasphorus platycercus	3.4**
**Colaptes cafer*	110.9
Sphryapicus varius	50.7
**Dendrocopos villosus*	64.3
**Dendrocopos pubescens*	27.8
Tyrannus vociferans	47.0
Contopus sordidulus	13.7
Tachycineta thalassina	10.6
Cyanocitta stelleri	113.0
Parus gambeli	28.2
Sitta carolinensis	18.1
Certhia familiaris	7.8
Regulus calendula	6.5
Lanius ludovicianus	47.0
Dendroica auduboni	12.6
Dendroica graciae	7.8
Vireo solitarius	17.0
Piranga ludoviciana	29.7
Piranga flava	37.6
Chondestes grammacus	26.1
Spizella passerina	13.2

Total Number of Species = 21

Number of Associates = 3

* Indicates associates of Piñon Jay flocks.

** Sources for weights in this table are Baldwin and Kendeigh (1938), Hartman and Brownell (1961), Miller (1955), Poole (1938), Salt (1957), Hubbard and Ligon (in litt.). Whenever possible weights were obtained from specimens in the Museum of Northern Arizona and the Northern Arizona University Museum of Vertebrates.

and departed from the station with the jay flock. However, in late winter and early spring Starlings were much more prone to stay at the station. Early on winter mornings Starlings gathered just outside of the station but would not enter until the jay flock entered. If the jays did not appear by 09:30 the Starlings left without feeding at the station. When feeding at the station. Starlings mingled with even the largest groups of Piñon Jays and were not displaced.

On two occasions during the winter of 1969, groups of Piñon Jays were seen associating with an urban flock of Starlings. On both occasions, the flocks contained about 55 Starlings and eight to ten yearling Piñon Jays. The flocks moved silently through a forested area.

TABLE 4

GREGARIOUS SPECIES OCCURRING IN THE HABITATS USED BY PIÑON JAYS

Species	Mean Weights (g)
Zenaidura macroura	122.8**
Melanerpes formicivorus	66.0
Eremophila alpestris	43.0
Corvus corax	969.0
Corvus brachyrhynchos	479.0
**Nucifraga columbiana*	142.2
Psaltriparus minimus	5.8
Sitta pygmea	9.9
Turdus migratorius	80.7
Sialia mexicana	24.6
Sialia currucoides	34.7
Bombycilla cedrorum	32.9
**Sturnus vulgaris*	81.9
Sturnella magna	145.0
Molothrus ater	50.5
Euphagus cyanocephalus	64.8
Hesperiphona vespertina	53.6
Carpodacus cassinii	27.5
Spinus pinus	12.2
Spinus psaltria	10.4
Junco hyemalis	21.0
Junco oreganus	17.4
Junco caniceps	19.7

Total Number of Species = 23

Number of Associates = 2

* Indicates associates of Piñon Jay flocks.
** Same as Table 3.

DISCUSSION

Of the five species that associated with the jay flock, three are usually solitary, whereas the other two are often found in intraspecific associations (pers. observ.; Tables 3 and 4). Some of the species listed as solitary in Table 3 form intraspecific flocks at times of the year when not in the vicinity of Piñon Jays. Moynihan (1960) suggests that "many but not all species" that tend to form intraspecific flocks may also form interspecific flocks. Our data show, however, that 14 per cent of the solitary species and 9 per cent of the gregarious species that come in contact with the jay flock do associate with it. Innate social attraction cannot be used to explain interspecific flocking with Piñon Jays.

The ability of associate species to mingle and remain with the Piñon Jay flock is probably enhanced by the lack of intraspecific aggression among Piñon Jays. At any one time, less than 5 per cent of the jay flock was involved in intraspecific hostile behavior. Piñon Jays displayed similar aggressive behavioral patterns both intra- and interspecifically. These entailed crouching slightly, pointing the bill at the agressee and lunging, or flying up at an approaching intruder with legs extended and calling loudly. A direct thrust with the bill is also used to supplant other birds. These patterns could be easily learned and adjustments readily made. The Red-shafted Flicker and Starling used these same general agonistic behavior patterns to displace Piñon Jays. If the aggressive behaviors are easily learned or already in the behavioral repertoire of the species, actual combat that can result in injury and/or exhaustion is reduced or avoided (Moynihan, 1962). Once an interspecific association is established, the Piñon Jays tolerate the associate species and act with the same low level of aggressiveness towards them as to conspecifics. Therefore the associate species can efficiently reap what benefits are available without expending undue energy. In this regard, the Starling which arrived in northern Arizona in the early 1960's (pers. observ., G. F. Foster) has had only 10 years to learn and adjust to the behavior patterns of the Piñon Jay. Yet in many respects the Starling has the highest degree of behavioral compatibility with the jay flock. This must be due to the behavioral plasticity or preadaptation of this species.

The numerically superior Piñon Jay is also the socially dominant species in mixed flocks, in part because with superior numbers it can displace those associates individual Piñon Jays could not dominate. The associate species rank in an interspecific hierarchy (based partly on compatibility and tenacity when faced with large numbers of jays) as follows: Red-shafted Flicker, Starling, Clark's Nutcracker, Hairy Woodpecker, and Downy Woodpecker. The more abundant associates tend to have higher ranks.

Although the Piñon Jay is largely passive in its behavioral relations with the five associate species, it does possess many of the traits discussed by Moynihan (1960, 1962) which promote both intra- and interspecific gregariousness. The general noisiness and restlessness of the jay flock tend to focus attention on it. The neutral, rather drab blue coloration of the Piñon Jay may act as an attractant to species that are normally repulsed by a sharply contrasting plumage. The dorsal blue or blue-gray coloration is similar to that found in species that form mixed flocks in the Andes and Bolivia (Moynihan, 1968). The associate species show some of these same traits and others, including striking flash patterns on either wings, rump, or tail.

In our opinion the most important characteristics promoting this association are similarities of foraging strategies and similarities in size. Using the

TABLE 5

INDICES OF SPECIALIZATION (J′) OF FORAGING BY PIÑON JAYS AND SUM FREQUENCY OF ASSOCIATION

	Jan., Feb., March	April, May, June	July, Aug., Sept.	Oct., Nov., Dec.
J′	0.992	0.757	0.716	0.983
Sum* Frequency	3.31	1.81	1.07	3.06

* From Table 2; Average number of species to be seen with the flock during this period.

suggestions of Pielou (1966) we calculated the foraging diversities (H′) and indices of specialization (J′) (after Willson, 1970) of the Piñon Jay flock for four different periods of the year (Table 5). The higher the J′ the less specialized and consequently more diverse the foraging pattern. J′ was then compared to the sum frequency (see Table 2; expected number of associate species to be found with the Piñon Jay flock) and a very high positive correlation results. That is, when Piñon Jays are most diverse in their foraging sites, the number of associates is highest.

Numerous workers have pointed out the similarities in body size and weight of members of interspecific flocks. Tables 3 and 4 list weights for the species that occur in the home range of the Piñon Jay at least a portion of the year. The average weights of the associates range from a low of 28 g for the Downy Woodpecker to a high of 142 g for the Clark's Nutcracker. If we eliminate the Downy Woodpecker from this comparison because of its low numbers and obviously low social status, as indicated by the outcomes of interspecific hostile interactions, the weight range for the other four species is 64–142 g. The average weight of 27 adult Piñon Jays is 108 g, almost exactly intermediate to the weight of the associates. This range includes five potential associates, Mourning Dove, Acorn Woodpecker, Steller's Jay, Robin, and Brewer's Blackbird that do not associate. The Steller's Jay is found in high numbers year round, but appears to maintain definite winter home ranges. The other four species are either present in very low numbers throughout the year or are present only during the nesting season when they show strong affinities for nests or territories. Rather than join the flock, these birds all show signs of alarm when the jay flock comes into proximity with them. The typical response was to scold loudly and leave the area. During the warm winter of 1970–71 flocks of Robins occasionally mingled with the jays at watering or feeding sites but did not follow them. Thus, size must be only a secondary factor in determining flocking associates.

Flocking of the five species with Piñon Jays is probably due to their joining the jay flock when food is scattered widely throughout the habitat. The associates are then assured a share of the food. When food is super-abundant, as at the feeding station, attraction to the jay flock is not as evident. This assurance is best demonstrated in those cases of a species associating with the jays when they performed a specific type of foraging. The woodpeckers are most closely associated with the flock during the winter when many jays forage off the ground by flaking bark, probing crevices and opening ponderosa pine cones. The flicker associates most of the year, and there is always a portion of the jay flock feeding on the ground. The nutcracker shows a bond with the jay flock during the time both species are caching piñon pine seeds. Austin and Smith (in press) have shown that some flocking species increase their foraging diversity in winter. This is true in the Piñon Jay. Morse (1970) demonstrated that the associates modify their area of foraging in the presence of socially dominant species whereas Austin and Smith (in press) believe the numerically dominant species may alter their foraging pattern to accommodate the associates. We believe the Piñon Jay increases its foraging diversity during the more demanding winter months in order to obtain an ample supply of food. This, in turn, attracts the associate species. The Piñon Jay is probably more diverse in its foraging patterns than the associate species. This relationship between nuclear and associate species was also shown by Morse (1970) and Austin and Smith (in press).

The tendency of the associates to form mixed flocks is probably a species-specific trait, or set of traits expressed when advantageous, but not necessary for survival except under special conditions imposed by the local ecological situation. Harvesting of vast quantities of food by Piñon Jays may make it advantageous for other species to join them. At the feeding station, only Starlings actively joined the flock. Here food was constantly renewed and the woodpeckers and flickers did not move with the flock when it left the station but stayed to harvest the replenished food items.

Comparing the behavior of the associates at the feeding station to that of the flock in a more natural habitat, suggests that participation in the flock by the associates is directly related to the density and obviousness of the food items. When food is abundant, obvious, and easily obtained the tendency to form mixed flocks decreases. This has also been suggested for insectivorous flocks by Gibbs (1960) and Hinde (1952).

The advantages to be obtained from the association herein described are in all probability food and protection gained by mechanisms similar to those described and reviewed by Morse (1970), for insectivorous flocks. The above author rarely, if ever, observed raptors near or attempting to enter mixed flocks. In contrast, we observed raptors being scolded or mobbed on 12 per cent of the observation periods, and observed potential predators on 84 per cent of our visits to the home range of the Piñon Jay flock.

When sentries gave the rhythmic danger call, associates responded by flying up into concealing foliage and remaining still. This action was spontaneous and took less than five seconds to complete. The associates never lagged behind the jays in this movement and appeared to recognize the danger call as quickly as did the Piñon Jays. Although Piñon Jays were quick to mob potential predators, only the Red-shafted Flicker and Clark's Nutcracker participated in this behavior. Their participation in scolding and mobbing potential predators was meager as they joined the jays on less than 20 per cent of the scolding and mobbing performances. Thus, the associates gained appreciable protection from the actions of the Piñon Jays.

Associate species and also species that did not associate with the Piñon Jay flock were often, if not always, stimulated by social induction or facilitation (Rand, 1954) to feed when the jays were present. On numerous occasions Steller's Jays and juncos were observed to feed intently with the jays as they passed but these non-associates did not follow the flock when it departed, or only followed a short distance. Westcott (1969) made similar observations on Steller's Jays following a Piñon Jay flock in southern Arizona. Feeding activities of these non-associates ceased when the flock departed. This behavior suggests that all birds may derive some protection from the well organized sentinel system of the Piñon Jay flock. Not only are other species induced to feed in the presence of the jay flock, but they can do so intently because the predator warning system established by the jays allows these species to concentrate solely on feeding. One would suppose that this concentration would increase feeding efficiency. Thus, it is difficult to separate the benefits of associating with the jay flock into protection and feeding efficiency, as both appear to be important but not clearly distinguishable from each other (see Lack, 1968).

SUMMARY

The Hairy and Downy Woodpeckers, Red-shafted Flicker, Clark's Nutcracker, and Starling were observed to form interspecific flocks with the highly gregarious Piñon Jay. The general noisiness and restlessness of the jay flock, plus the drab coloration of its members probably acted to attract the associate species. The Piñon Jay flock was intact throughout the year, although in a number of different forms, thus offering attendant species an opportunity to participate in mixed flocking year round. The frequency of occurrence and numbers of associates varied with season and foraging site diversity of the Piñon Jay flock. A strong positive correlation exists between foraging site diversity of the jays and frequency of the associates.

The ability of the associates to remain in the Piñon Jay flock is enhanced by the lack of intraspecific aggression among the jays.

The important characteristics promoting this association are similarities of foraging strategies and secondarily similarities in size.

The benefits derived by associate species as a result of interspecific flocking are probably more effective utilization of the total food resources, indirectly resulting from efficient protection from predators while feeding and directly as a result of the greater ability of numerous individuals to locate scattered, but locally abundant, sources of food.

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LITERATURE CITED

Allee, W. C. 1938. The social life of animals. Norton & Co., New York.

Austin, G. T., and E. L. Smith. 1972. Winter foraging ecology of mixed insectivorous bird flocks in oak woodland in southern Arizona. Condor, 74:17–24.

Balda, R. P., and G. C. Bateman. 1971. Flocking and annual cycle of the Piñon Jay (*Gymnorhinus cyanocephalus*). Condor, 73:287–302.

Baldwin, S. P., and S. C. Kendeigh. 1938. Variations in the weight of birds. Auk, 55:415–467.

Beidleman, R. B., and J. H. Enderson. 1964. Starling-Piñon Jay associations in southern Colorado. Condor, 66:437.

Brown, J. L. 1964. The integration of agonistic behavior in the Steller's Jay *Cyanocitta stelleri* (Gmelin). Univ. California Publ. Zool., 60:223–328.

Cary, M. 1901. Birds of the Black Hills. Auk, 18:231–238.

Darling, F. F. 1938. Bird flocks and the breeding cycle. Cambridge Univ. Press.

Gibbs, J. A. 1960. Populations of tits and Goldcrests and their food supply in pine plantations. Ibis, 102:163–208.

Hartman, F. A., and K. A. Brownell. 1961. Adrenal and thyroid weights in birds. Auk, 78:397–422.

Hinde, R. A. 1952. The behavior of the Great Tit (*Parus major*) and some other related species. Behaviour Suppl., 2:1–201.

Jensen, J. K. 1926. The Piñon Jay (*Cyanocephalus cyanocephalus*). The Oologists' Record, 6:41–43.

Johnson, H. C. 1902. The Pinyon Jay. Condor, 4:14.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co. Ltd., London.

Miller, A. H. 1955. The avifauna of the Sierra del Carmen of Coahuila, Mexico. Condor, 57:154–178.

Miller, R. C. 1921. The flock behavior of the Coast Bush-tit. Condor, 23:121–127.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecol. Monogr., 40:119–168.

Moynihan, M. 1960. Some adaptations which help to promote gregariousness. Proc. XII Internatl. Ornithol. Congr.: 523–541.

Moynihan, M. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll., 143:1–140.

MOYNIHAN, M. 1968. Social mimicry; character convergence versus character displacement. Evolution, 22:315–331.

ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee. Auk, 59:499–531.

PIELOU, E. C. 1966. The measurement of diversity in different types of biological collections. J. Theoret. Biol. 13:131–144.

POOLE, E. L. 1938. Weights and wing areas in North American birds. Auk, 55:511–517.

RAND, A. L. 1954. Social feeding behavior of birds. Fieldiana Zool., 36:1–71.

SALT, G. W. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor, 59:373–393.

SHORT, L. L., JR. 1961. Interspecific flocking of birds of montane forest in Oaxaca, Mexico. Wilson Bull., 73:341–347.

STALLCUP, P. L. 1969. Hairy Woodpeckers feeding on pine seeds. Auk, 86:134–135.

TINBERGEN, N. 1953. Social behavior in animals. Methuen & Co., London.

WESTCOTT, P. W. 1969. Relationships among three species of jays wintering in southeastern Arizona. Condor, 71:353–359.

WETMORE, A. 1920. Observations on the habits of birds at Lake Burford, New Mexico. Auk, 37:221–247; 393–412.

WILLIS, E. O. 1966. The role of migrant birds at swarms of army ants. Living Bird, 5:187–231.

WILLSON, M. F. 1970. Foraging behavior of some winter birds of deciduous woods. Condor, 72:169–174.

WING, L. 1941. Size of bird flocks in winter. Auk, 58:188–194.

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ON THE EVOLUTION OF SOCIALITY, WITH PARTICULAR REFERENCE TO *TIARIS OLIVACEA*

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The behavior of the Yellow-faced Grassquit (*Tiaris olivacea*) apparently ranges from social and nonaggressive on the Central American mainland to territorial and very aggressive on the island of Jamaica (Pulliam, 1970). Why these differences?

This paper reports observations on the population size, habitat distribution, and social behavior of the Yellow-faced Grassquit on the island of Cayman Brac, West Indies, and speculations on factors influencing social behavior. Cayman Brac is a very small island (20 square miles) and this population of grassquits is extremely isolated from other populations, the nearest being found on Grand Cayman (80 miles southwest) and on Jamaica (190 miles southeast). The third of the Cayman Islands, Little Cayman Island, is about ten miles west of Cayman Brac, but grassquits are very rare or absent there perhaps because of a lack of suitable habitat.

The observations reported here are based primarily on a two-week field study beginning 27 November, 1969. Additional observations must be made at other times of year for confirmation of our findings. However, the social organization of the species has been noted by one author (Pulliam) to be stable throughout the year in Jamaica and Skutch (1954) indicates that Costa Rican grassquits can be found in flocks during all seasons of the year.

THE EVOLUTION OF SELFISH BEHAVIOR

Hamilton (1964) has demonstrated that kinship selection can limit the expression of behavior which decreases the fitness of a neighbor more than it increases the fitness of the actor (i.e., selfish behavior). Kinship selection encompasses the notion that an individual's overall fitness includes not only the effects of his genotype on his own ability to leave descendants but also the effects of his genotype on the fitness of relatives who carry some proportion of genes identical by descent to his own. Although Hamilton's model is formally correct, it is applicable only if the selfish behavior of a population is determined by the gene frequencies at one locus. We contend that aggression or selfish behavior is not coded at a single chromosomal locus (see Klopfer, 1969) but that the degree of aggression in an individual must be thought of as resulting from the interaction of the animal's environment with the epistatic effect of a large number of genes at very many loci. Thus, in an almost homozygous population, selfish behavior might be selected against because it decreases one's own inclusive fitness.

In this paper we argue that some forms of aggressive and territorial behavior constitute "selfish behavior" and, thus, their occurrence in natural populations must be restricted to relatively heterozygous populations.

An aggressive territory holder can decrease the fitness of a nonaggressive bird by excluding it from optimal habitat. It is less obvious that the decrease in fitness of the nonaggressive bird is greater than the increase in fitness of the aggressor. However, the territorial bird does lose some of the advantages of social behavior (whatever they are) and must spend considerable time defending his territory, time which might otherwise be applied towards maintenance and reproduction. The amount of time which the average aggressive individual spends defending his territory must necessarily increase as the proportion of the bird population which is territorial increases. Hence, the question: why are some grassquits territorial?

Suppose territorial individuals do have a lower reproductive capacity than social individuals would have in the absence of the former. This would result in a territorial population maintaining lower numbers than a social population even though the territorial individuals were superior in competition with the social individuals! If, for a given bird species, the social populations were shown to maintain a significantly higher population density than the territorial populations, we would have evidence that territoriality is a selfish behavior for that species.

Pulliam (1970) censused, during the breeding season, 11 similar habitats that appeared suitable for Yellow-faced Grassquits in both Jamaica and Costa Rica. Each habitat was visited twice. In Costa Rica, on a total of 25.9 acres, an average of 20.5 grassquits were seen. In Jamaica, on a total of 18.0 acres, an average of only 6.9 grassquits were seen. In both Costa Rica and Jamaica there were grassquits in four of the eleven habitats visited. The number of grassquits per acre in those sites containing some grassquits was 2.9 in Costa Rica, as compared to 0.7 in Jamaica. The increase in the density of the Costa Rican grassquits is especially surprising since there were many more individuals and species sharing sites with grassquits in Costa Rica than there were in Jamaica. Thus, it appears that the social grassquits of Costa Rica are able to maintain a population density two to three times as great as that of the territorial Jamaican grassquits. This accords with our supposition.

Very little is known about the degree of heterozygosity in natural populations of birds and we are not yet able to predict the degree of heterozygosity that might permit selfish traits to evolve. However, we do know that both isolation and population size exert considerable influence on the degree of genetic diversity of natural populations. In very small populations, random drift can lead to fixation or loss of genetic variability. This decay of genetic variation is counter-balanced by the forces of mutation and immigration. Soulé (1971) presents arguments and evidence that for lizards large population size and migration between adjacent populations is necessary for the maintenance of genetic diversity. Soulé showed that lizards from small, isolated island populations showed less variation in electrophoretically detectable isozymes than lizards from large island populations. The decrease in enzyme variation was correlated with a decrease in morphological variance. This result indicates that isolation and small population size result in a decrease in genetic diversity and could, therefore, limit the expression of selfish behavior traits.

Tiaris olivacea is an abundant inhabitant of the subtropical plateau region of Costa Rica (Slud, 1969). However, the grassquit is a bird of secondary growth habitats, never found in the dense forest, and is therefore restricted in distribution to areas near human habitation and agriculture. The human population of Costa Rica is largely limited to areas in close proximity to roads or rail lines. Thus, habitat suitable for grassquits is discontinuously distributed along the few roads and railroads in eastern Costa Rica. In May of 1969 Pulliam searched for grassquits along the road from San José to Turrialba and along the railroad between San José and La Lola Farms, which is about 30 miles west of Port Limon on the Gulf of Mexico. This journey made an east-west transect across almost the entire range of *Tiaris* in Costa Rica. Grassquits were first noted along the roadsides about 5 miles east of Cartego. From Cartego to Turrialba, grassquits were frequently recorded in suitable habitats but these habitats were distributed in patches. Along the railroad, grassquits were noted from Turrialba to La Lola Farms, where they were common. Suitable habitat along the railroad was distributed in discrete patches and often interrupted by many miles of forest habitat. In addition to the patchwork character of suitable habitat, the presence of a dozen or more sympatric seed-eating finches may further limit the distribution of grassquits. This combination of a patchwork habitat and many competitor species would tend to result in *Tiaris* being found in isolated groups of small size in Costa Rica. We expect their social behavior to be related to a high degree of genetic homozygosity maintained because of the patchiness of their distribution.

Tiaris olivacea is found in all parts of Jamaica with the possible exception of the very dry Southeast. Throughout the range of grassquits in Jamaica there are numerous roads and, therefore, much more habitat suitable for *Tiaris* than in Costa Rica. This suitable habitat is virtually continuous over the entire island except in the high mountains which are sparsely settled by humans. Also, in Jamaica there is only one other species of finch which feeds exclusively on grass seeds. The two factors combine to produce a continuous and therefore very large grassquit population. We expect such a population to be genetically more diverse than the discretely distributed Costa Rican population and, thus, to permit the occurrence of selfish behavior. In fact, the Jamaican birds, in contrast to those of Costa Rica, are territorial, as noted above.

These arguments are conjectural and were largely developed ex post facto, after our studies in Jamaica and Costa Rica. If, however, the argument is correct we would expect to find that any isolated, small populations of grassquits would exhibit social rather than selfish behavior, and be more similar in their social structure to the Costa Rican population than to the Jamaican population. With this idea in mind, we attempted to ascertain the population size and social structure of the isolated grassquit population on Cayman Brac Island.

ESTIMATE OF GRASSQUIT POPULATION SIZE ON CAYMAN BRAC

Data for population size estimates were collected by locating and then, only once, walking slowly through suitable habitats and recording all birds heard or seen. "Suitable habitat" was defined as those areas where trees and shrubs covered less than 80 per cent of the ground and where there was some grass growing. This definition of suitable habitat was consistent with our observations in Costa Rica and Jamaica that grassquits were found only in grassland and old-field habitats and the observations of Skutch (1954) in Costa Rica and Wetmore (1927) in Puerto Rico that the diet of grassquits consisted almost entirely of grass seeds. However, on Cayman Brac we often found male grassquits singing from the upper branches of trees and shrubs near the edges of fields. Figure 1 illustrates that the grassquits in trees were always very close to a grassy field. The data for Figure 1 were collected by pacing along a path which ran all the way across the island from North to South. The location of the bird is plotted as the location at which the bird was estimated to be at right angles to the path. Thus, those birds which appear, in the figure, to be in the fields may actually have been singing from trees and shrubs on the east or west sides of the fields. At any rate, the data presented in Figure 1 are consistent with our belief that the grassquits are found only in or near field habitats. Since the maintenance of such habitats on Cayman Brac depends entirely on their being accessible to people (due to the rapidity of successional growth), we felt confident that most such habitats could be found by traversing all roads and paths on the island.

One of the assumptions of the model (presented in the Appendix) used to estimate population size is that the probability of a call in any interval of time is constant throughout the time of observation. It is well known, however, that many birds show a pronounced decrease in singing in the middle of the

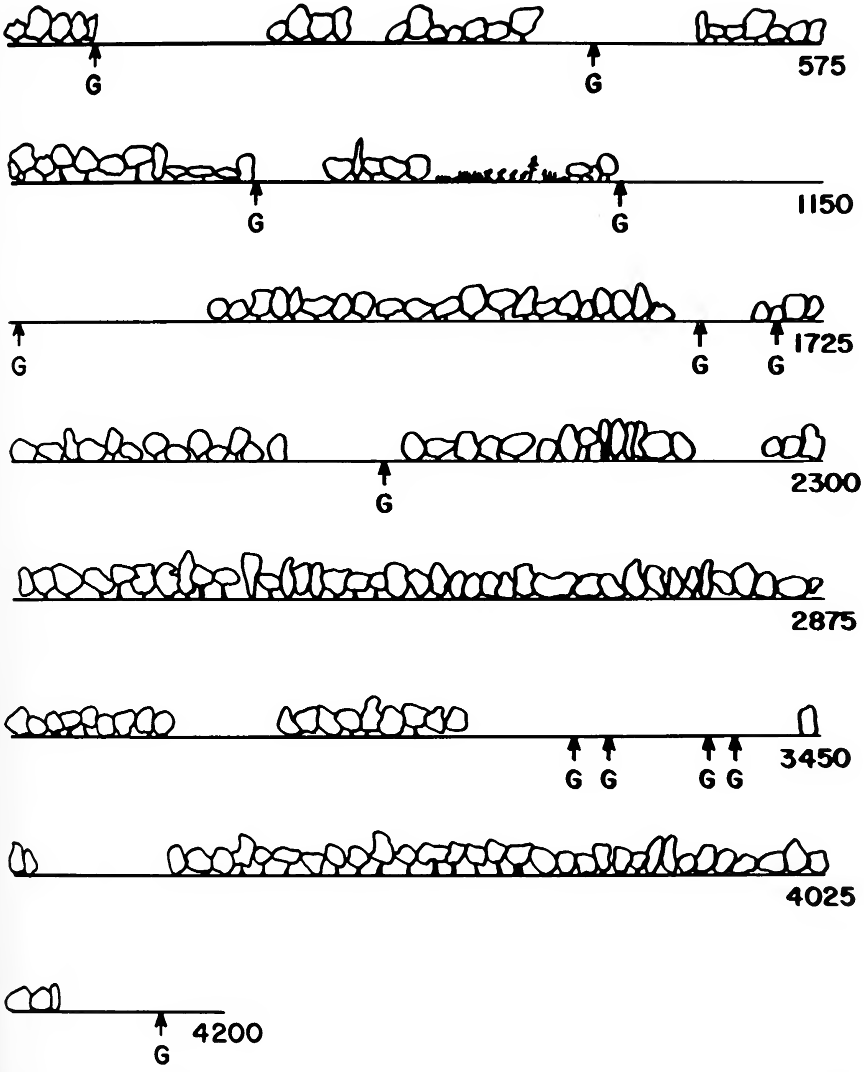

FIG. 1. Observations on the location of birds along a transect across Cayman Brac Island. The symbol G indicates the position of grassquits along the transect and the numbers on the right indicate the distance from the start of the transect. Grassy fields are indicated by the clear areas and forests and garden are indicated diagrammatically.

day. Thus, the probability of recording a bird in the middle of the day might be lower than, say, in the early morning. Table 1 shows the number of songs per thirty-minute interval for seven individual grassquits sampled at different times of the day. It appears from this sample of singing activity that there

TABLE 1

THE NUMBER OF BIRD SONGS IN THIRTY-MINUTE INTERVALS FOR SEVEN INDIVIDUAL GRASSQUITS WATCHED AT DIFFERENT TIMES OF DAY.

The times on the left indicate the beginning of each thirty minute interval.

	1	2	3	4	5	6	7	Average
7:00	60		20					40
7:30	38		18					28
8:00	48		20					34
8:30	118	3	61					60
9:00	23	17	80					40
9:30	0		82					41
10:00			85	36				60
10:30				17				17
11:00				1				1
11:30				46				46
12:00				3				3
12:30				40				40
13:00				57				57
13:30					40			40
14:00					76			76
14:30						28		28
15:00						18		18
15:30						21		21
16:00						4	43	23
16:30						9	56	32
17:00							51	51

may be a slight decrease in singing rate in the middle of the day. Since the sample size is so small, particularly for the mid-day period, this is not certain. Even if there is a decrease in singing rate at mid-day we believe it does not seriously effect our results, since the decrease appears to be small and less than 10 per cent of our censuses were taken in the mid-day period (between 10:00 and 14:00).

For three of the seven birds for which data are given in Table 1, we were able to record the occurrence of each song to the nearest second. From these data we could assess the reliability of our census technique (see the Appendix). Figure 2 indicates that the probability of recording a bird does not differ significantly from one time of day to the next.

For the total census we recorded 190 male and 24 female grassquits. Of the 190 males, 161 were heard singing and 29 were only seen. If we assume the sex ratio to be equal and that there must have been some suitable habitat which we did not locate, then we must conclude that there were at least 400 grassquits on the island. However, this is undoubtedly an underestimate since many

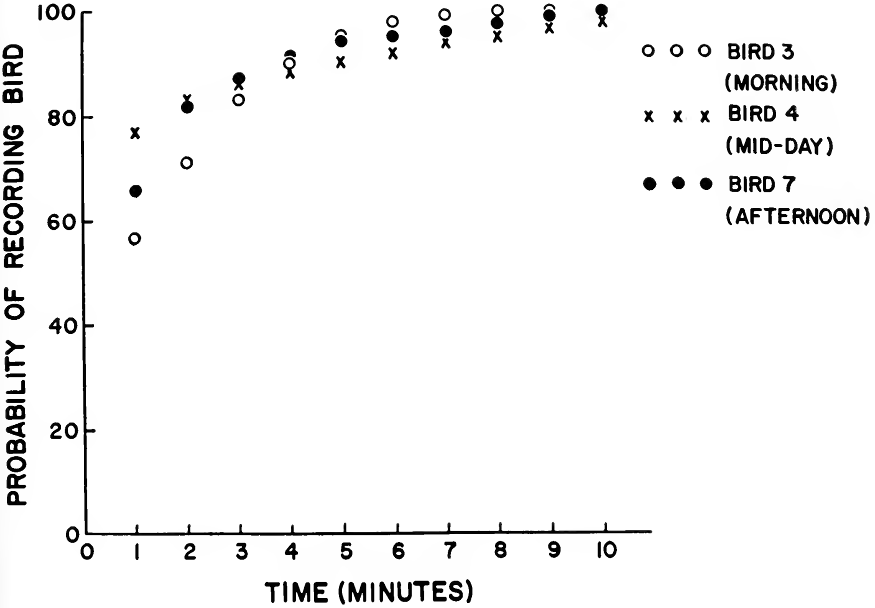

FIG. 2. The probability of recording a bird as singing as a function of the length of time that an observer is within hearing range of the bird. See Appendix for estimation procedures.

birds must not have been recorded even though we located the fields in which they resided. From the estimates of the probability of recording a bird in Figure 2 we can get some idea as to how accurate our census was. A singing male grassquit can be heard from 75 to 100 feet away. If we assume that our walking speed through the fields was between one and two feet per second, it follows that an observer was within hearing range of each bird for from one to three minutes if the field where the bird resided was actually located. Taking a very liberal estimate of the population size we assume that each bird was in hearing range for only one minute and thus, from the lowest estimated probability of recording a bird when it is within hear-range for one minute (From Bird No. 3, Fig. 2), we estimate that only 55 per cent of the male birds were recorded by being heard. Thus, a liberal estimate of population size is about 300 male birds (or approximately 600 birds, total). This estimate may still be too low since there may have been first-year male birds which were not singing. Assuming there may be as many as one non-singing male for each singing male we can boost the total estimated population size to about 1,200. Finally, there were the birds in the fields that we did not locate and assuming that we may have not found as much as 20–25 per cent of the suitable habitat, we reach a figure of 1,500 birds. It should be realized that in arriving at this estimate of population size we took the extremes of all estimation parameters so as to give an absolute upper limit. At the other end of the scale we could assume that we observed all of the male grassquits on the island. Taking the two extremes we can state fairly confidently that there were between 400 and 1,500 Yellow-faced Grassquits on the island at the time of our census.

SOCIAL BEHAVIOR OF THE YELLOW-FACED GRASSQUIT

In Jamaica, the Yellow-faced Grassquit is strictly territorial. Nine territories in optimal habitat measured in June–July, 1968, near Treasure Beach, Jamaica, averaged only 0.25 acres each and aggressive encounters between males on adjacent territories were frequent. Although Jamaican grassquits never occur in flocks, individuals of both sexes are known to aggregate occasionally at artificial feeding stations and when this happens males seem to spend more time fighting than feeding.

Skutch (1954) describes the Yellow-faced Grassquit in Costa Rica as lacking "that pugnacious jealousy so prominent and characteristic in many members of the finch family" and as "a most pacific bird. I have never noted any fighting or discord among them." However, males do defend a small area in the immediate vicinity of the nest from which other males of the same species are expelled. Skutch describes this defense as follows: "all the territorial male does is fly mildly in the direction of the intruder who retreats without necessity of conflict." Grassquits which are not nesting are normally found in large feeding flocks which often contain thirty to forty individuals, with both sexes represented. Pulliam (1970) noticed no signs of aggression within flocks but did note occasional conflicts between grassquits and other seed-eating finch species during a three-week field study during the breeding season in 1969 near Turrialba, Costa Rica.

The contrast between the highly social behavior of Costa Rican grassquits and the strictly territorial behavior of the Jamaican grassquits is typical of the differences in social behavior of a number of passerine bird species from Costa Rica and Jamaica. Pulliam (1970) compared the social behavior of all resident bird species of the families Fringillidae, Thraupidae, and Icteridae for which data could be found for Jamaica and Costa Rica. He found that 18 of the 26 Costa Rican species showed some form of social tolerance (family groups or flocking) compared to only two of the 11 Jamaican species. [The definition of "no social tolerance" is that at all times of the year individuals are either alone or in the company of a single adult of the opposite sex and/or juvenile birds up until a short time after fledging.] This is consistent with the supposition that continuously distributed species are more likely to be

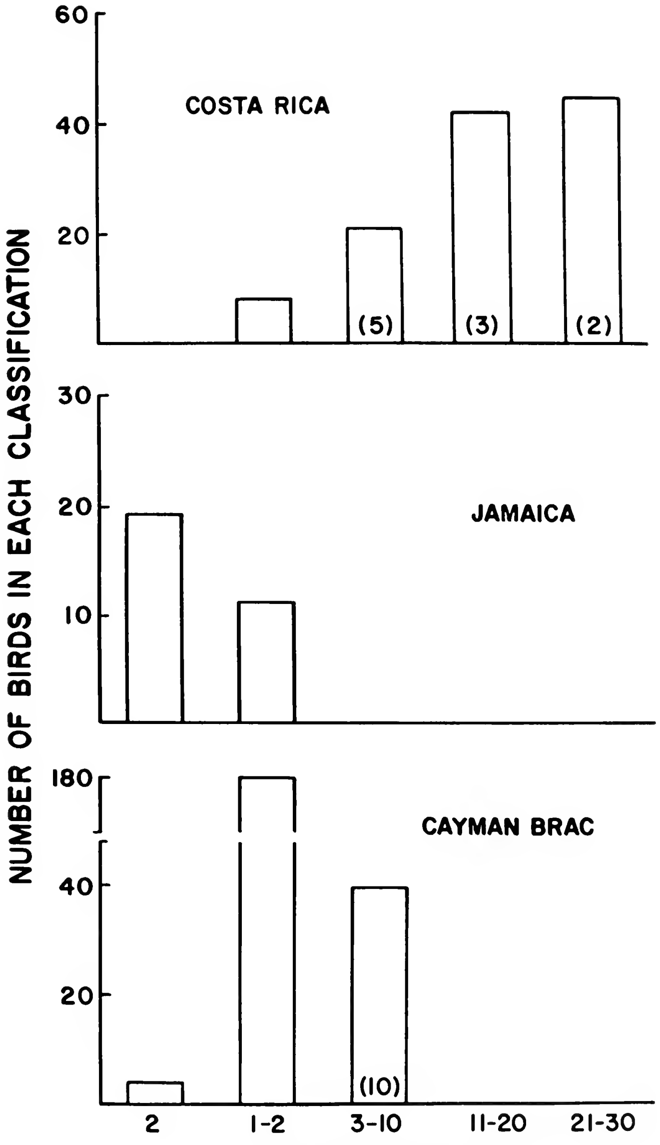

FIG. 3. The sizes of groups of grassquits observed for three different populations.

genetically polymorphic, and thus aggressive, since Jamaican birds seem to be more continuous in their distributions than Costa Rican birds.

The social behavior observed for grassquits on Cayman Brac can best be described as intermediate between the social behavior of Jamaican and Costa Rican grassquits. Adult males were typically seen singing from trees and shrubs on the edges of grassy fields. The frequency of singing appeared to increase in the presence of other adult male birds and dueting between birds on adjacent territories was frequently observed. However, chases between adult male grassquits were observed only on two occasions, whereas they were very frequent in Jamaican grassquits (Pulliam, 1970). On several occasions adult male birds were seen to sit on the same limb within a few inches or feet of each other and sing without any subsequent displacement. On at least two such occasions the birds flew together to the ground where they fed in close proximity to one another.

Figure 3 shows the group sizes observed for Cayman Brac grassquits as compared to group sizes observed by Pulliam (1970) in Jamaica and on the Central American mainland. In each case all observations during a two-week study period are recorded. However, the Cayman Brac data were collected in November–December, 1969 while the Jamaican and Costa Rican data were collected in April–May, 1968. The possibility that the observed differences are due to seasonal change will be discussed later. A total of ten groups in the category of three to ten birds (Fig. 2) were observed on Cayman Brac. These groups ranged in size from three to six and, therefore, some could be family groups. In some of these groups, one or more of the birds was identified as an immature. The category 2♂ indicates that two males were seen together and that there was a subsequent chase and displacement. While this was the most frequent category in Jamaica (perhaps because of conspicuousness), no such interactions were observed in Costa Rica and only two were observed on Cayman Brac.

HABITAT UTILIZATION

Slud (1964) describes the habitat of the Yellow-faced Grassquit in Costa Rica as follows: "it inhabits fields, plantations, pastures, clearings, roadsides, an deforested areas in general." According to Wetmore (1927) and Wetmore and Swales (1931), the grassquit in Puerto Rico is found entirely in open pastures, cultivated fields, hedges, or scanty growth of bushes. In Jamaica, grassquits are commonly found in pastures, gardens, roadsides, and plantations (Pulliam, 1970). The common denominators of grassquit habitats seem to be incomplete canopy cover and the presence of grasses.

The grassquits on Cayman Brac were found mainly along roadsides and in or near grassy fields. There were no grassquits recorded in the coconut palm plantations on the north side of the island where there were very few grasses. However, there were grassquits in the smaller coconut palm plantations on the south side of the island where there were abundant grasses.

A large number of grassquits were found in trees and shrubs in or near grassy fields (see Fig. 1). Grassquits observed in trees were almost without exception males and only in a few instances appeared to be feeding. When the grassquits did feed in the trees they seemed to be gleaning much in the manner of a wood warbler. Skutch (1954) and Slud (1964) report the same behavior occurs in Costa Rican grassquits when food is scarce even though the normal diet consists only of the seeds of grasses.

DISCUSSION

We have argued that the maintenance of the social behavior of Costa Rican grassquits is dependent on the patchiness of their distribution which limits both effective population size and gene flow between populations and thus reduces the genetic diversity within subpopulations. If this interpretation is correct, we would expect that populations of grassquits on small isolated islands would, like the mainland grassquits, exhibit decreased heterozygosity, which would, in turn, limit the expression of selfish traits. Our census of the grassquits of Cayman Brac, indicates that there are between 400 and 1,500 grassquits on the island. A population of this size should be sufficiently large to prevent the loss of genetic diversity through random drift as might occur in smaller populations (see Crow and Kimura, 1970).

Our observations on the sociality of the Cayman Brac grassquits indicates that they are intermediate between the highly territorial Jamaican grassquits and the very social Costa Rican grassquits. However, the observations on the Cayman Brac birds were restricted to a short period in the autumn of 1969 as compared to extensive observations of the Jamaican and Costa Rican birds during all months of the year. Thus, the behavior of the Cayman Brac birds may only reflect a seasonal lull in territoriality at the end of the breeding season. However, the tolerance occasionally observed between adult male birds has not been reported from Jamaica. In Jamaica the birds breed in all months of the year, so some post-breeding males should always be in evidence.

It is clear that three further steps need to be taken to substantiate our prepared explanation: (1.) The Cayman Brac population should be studied at other times of the year to assure there are no seasonal variations in the social organization of the population; (2.) A general survey of the frequency of various forms of social organization in birds as a function of island size and isolation should be conducted; and (3.) Data specifically relating the degree of genetic variability in birds to the size and isolation of islands should be gathered.

SUMMARY

The Yellow-faced Grassquit (*Tiaris olivacea*) is discontinuously distributed and highly social in Costa Rica. In Jamaica its distribution is continuous and it is aggressively territorial. On Cayman Brac we estimate that grassquit population consists of 400–1,500 individuals which seem intermediate between Costa Rican and Jamaican grassquits in their social organization. We speculate that aggressive behavior of the sort we have characterized as "selfish" cannot arise except under conditions of considerable genetic variability.

ACKNOWLEDGMENTS

This work was supported by grants-in-aid from Sigma Xi, the Chapman Fund of the American Museum of Natural History, and NIMH 04453. We thank Kathy Gilbert, Marye Haskins and Erika, Gretchen, Lisa, and Martha Klopfer for their assistance in the field.

APPENDIX

We estimate the probability of recording the given bird as a function of the length of time (m) that an observer is within hearing distance of the bird. First, consider the probability of recording a bird given that the observer arrived within hearing distance during an interval for which the bird was silent for exactly L seconds, where $L > m$. If the observer arrives in the first $L–m$ seconds of the interval then the bird will not be recorded. However, if the observer arrives in the last m seconds of the interval, he will record the bird. Thus the probability of not recording the bird, given that the observer arrived during an interval for which the bird was silent for L seconds ($L > m$) is $(L–m)/L$. Of course, if the observer arrives within hearing distance of the bird during an interval for which the bird is silent for a period of time less than m seconds, then the observer will always record the bird.

The estimated probability that a bird will be silent for exactly L seconds is given by $(n_L \cdot L)/T$, where n_L is the number of times that the bird is observed to be silent for exactly L and T is the total length of time for which the birds' songs are recorded. Thus, the probability that a bird will not be recorded is the product of the probability that the observer arrives during a period for which the bird is silent for exactly L seconds (which is $(n_L \cdot L/T)$ and the probability that the bird will not be recorded given that the observer arrived during such a period (which is $(L–m)/L$) summed over all observed values of L greater than m, which reduces to

$$\frac{1}{T}\sum_{L>m} n_L \cdot (L-m) \; . \qquad 1)$$

These values were calculated for the three birds for which data were available. The values plotted in Figure 1 are for the probability of recording a bird as a function of the length of time that an observer is within hearing distance of the bird. The values for the probability of recording the bird are, of course, simply one minus the probability of not recording the bird which is calculated with Formula 1. Notice that the values are very similar for the three birds indicating rather little variance in the probability of recording a bird. This probability does not approach one until after about nine or ten minutes but after one minute is already about 0.65. Bird No. 4, which was watched in mid-day, does not indicate a lower probability of being recorded despite the lower average number of calls per half-hour period in the mid-day (as shown in Table 1.). Though there were fewer calls, they were more evenly spaced in time than was the case for the other two birds.

LITERATURE CITED

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics. Harper and Row, New York.

Hamilton, W. O. 1964. The genetical evolution of social behavior. J. Theoret. Biol., 7:1–16.

Klopfer, P. H. 1969. Instincts and chromosomes: what is an innate act? Amer. Naturalist, 103:556–560.

Pulliam, H. R. 1970. Comparative feeding ecology of a tropical grassland finch (*Tiaris olivacea*). Ph.D. dissertation, Duke University, Durham, N. C. Ecology, in press.

Skutch, A. F. 1954. Life Histories of Central American Birds. Pacific Coast Avifauna, 31.

Slud, P. 1964. The Birds of Costa Rica: Ecology and Distribution. Bull. Amer. Mus. Nat. Hist., 128.

Soulé, M. 1971. The gene flow-variation hypothesis. Taxon, in press.

Wetmore, A. 1927. The birds of Puerto Rico and Virgin Islands. Scientific Survey of Porto Rico and the Virgin Islands, 9:245–406.

Wetmore, A., and B. H. Swales. 1931. The birds of Haiti and the Dominican Republic. U.S. Natl. Mus. Bull., 155:1–483.

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GENERAL NOTES

Further notes on the Pinnated Bittern in Mexico and Central America.—Since the description of the Mexican form of the Pinnated Bittern, *Botaurus pinnatus caribaeus* (Dickerman, Wilson Bull., 73:333–335, 1961), 17 additional specimens have been collected in Mexico and Central America that substantiate the color characters used to describe *caribaeus* and add to our knowledge of the species' range. One of these from Costa Rica was previously reported by Slud (Bull. Amer. Mus. Nat. Hist., 128:43–44, 1964). Slud (p. 44) questioned the validity of the Mexican form *caribaeus*, but apparently misunderstood the characters of the latter race. Wing and tail length, stressed by Slud, were not utilized as characters, and the bill of the Costa Rican bird matches South American *pinnatus*, as it should. Slud's statement that his bird "approaches the description of *caribaeus* in general appearance" may be discounted, as he saw no specimens of that form. Actually, in coloration, the specimen is typical of the nominate race. Some of the 11 recent Mexican specimens are worn and faded; however, fresh-plumaged Mexican birds are definitely paler, less ochraceous than fresh-plumaged Central or South American specimens (see list of specimens examined below). This is most dramatic in the color of the auriculars, which are sandy buff in *caribaeus* in contrast to ochraceous buff in *pinnatus*. In series, ventrally, *caribaeus* is whiter, less buffy. The auriculars of the juvenile *caribaeus* from Tabasco (Dickerman, ibid.:334) are richer than are those of adults, and thus approximate the color of the auriculars in the nominate form. A second juvenile *caribaeus* beginning the first prebasic molt was taken 14 August near Lerdo de Tejada, Veracruz.

The exposed culmen of *caribaeus* averages slightly longer than the exposed culmen of *pinnatus*. The measurements are: seven female *caribaeus* 84–91 mean (87.4); nine female *pinnatus* 78–87 (82.9); ten male *caribaeus* 87–96 (91.9); thirteen male pinnatus 82–104 (89.5).

Additional Specimens Examined.—Botaurus pinnatus caribaeus: Veracruz: 2 mi. W. Tecolutla (3); 2 mi. E, 2 mi. S Tlacotalpan (2); Ingenio San Cristobal [= near Cosamaloapan] (1); Lerdo de Tejada (5). Tabasco: 14 mi. S. Villahermosa (1); Yucatan: 2 mi. S Progreso (1).

Botaurus pinnatus pinnatus: Costa Rica: Finca Taboga, Departmento de Guanacaste (1); Nicaragua: 11 mi. S San Carlos, Departmento de Rio San Juan (1); El Salvador: Laguna Jocotal, Departmento de San Miguel (1).

The specimens from Yucatan and El Salvador are the first record of the species from those areas.

I wish to thank Dr. Thomas R. Howell, University of California, Los Angeles and Dr. George H. Lowery, Jr., Louisiana State University, for permission to examine recently taken specimens in those respective collections. Scientific collecting permits were provided by the Departmento de Conservacion de la Fauna Silvestre, Secretaria de Agricultura y Ganaderia of the Mexican Government.—Robert W. Dickerman, *Department of Microbiology, Cornell University Medical School, New York, New York, 18 May 1971.*

Chronology of hatching by laying sequence in Canada Geese.—Prince, et al. (Auk, 86:762–763, 1969) found a high correlation between the sequence of laying and the order of hatching in artificially incubated Mallard (*Anas platyrhynchos*) eggs. There is no evidence of this same correlation in the Canada Goose (*Branta canadensis*). During

TABLE 1

CORRELATION OF LAYING, PIPPING, AND EMERGENCE SEQUENCE

Comparison	Number of Eggs	Correlation Coefficient (r)	Percent Variation Explained (R)
Laying Sequence vs. Pipping	110	0.32**	10
Laying Sequence vs. Emergence	109	0.20	4
Pipping vs. Emergence	80	0.69**	47

(** $p \leq 0.01$)

a nesting study of Canada Geese conducted in the spring of 1971 on Marshy Point near Clarkleigh, Manitoba, Canada, we made observations on the order of pipping and order of emergence compared to the order of laying.

Nest searches were made during the egg-laying period in April. Nests containing one egg were visited every other day and each new egg marked with a soft-lead pencil. After the completion of the clutch, these nests were periodically revisted to check for destruction. Hatching time was predicted by using a 28-day incubation period (Brakhage, J. Wildl. Mgmt., 29:761, 1965).

We visited nests two days prior to the predicted hatching day and subsequent checks were conducted every 12 hours to determine hatching progress. When emergence was imminent, nests were inspected every four to six hours. Only those nests in which the exact pipping and emergence sequence was known, those which contained a minimum clutch of four eggs, and those in which at least 70 per cent of the original clutch hatched successfully were included in the analysis.

A significant simple correlation coefficient was found between the pipping sequence and the emergence of the goslings and between laying sequence and pipping sequence. No significant correlation was found between laying sequence and emergence (Table 1).

Prince (op. cit.) found that 80 per cent of the variation in hatching sequence was explained by laying sequence; only four per cent of the variation in gosling emergence was explained by laying sequence. The results of the two studies suggest possible species differences and/or possible differences between natural and artificial incubation environments.

The average time required for a gosling to emerge once an egg was pipped was about 24 hours, agreeing with Collias and Jahn (Auk, 76:494, 1959), Brakhage (op. cit.:762), and MacInnes (J. Wildl. Mgmt., 26:251, 1962). The elapsed time between pipping and emergence (range of 15–30 hrs.) was less than the 8 to 36 hour range reported by Kossack (Amer. Midland Naturalist, 43:645, 1950).

If the last egg hatched between daylight and early afternoon, the female left the nest with the brood the following morning. However, if the last egg hatched in the late afternoon or during the night, the female remained on the nest with the brood the following day and did not lead them away until the morning of the second day. The only variation in this behavior occurred when three females were frightened by us and the dry goslings followed. The gander was never observed brooding dry goslings off of the nest while the female was still incubating the remainder of the clutch as reported by Kossack (ibid.).

The hatchability of the eggs was 89 per cent; well within the normal range found for Canada Geese (Brakhage, op. cit.:767). One dead gosling was found in a nest after brood departure, and there were no desertions. The air temperature during the 15 day period that the hatching checks were made averaged 48.2°F and ranged from a minimum of 26° to a maximum of 70°. No precipitation fell during the hatching period and we believe the study had no measurable effect on nesting success, hatching, or gosling mortality.

This is a contribution of the Massachusetts Cooperative Wildlife Research Unit (supported by the U.S. Bureau of Sport Fisheries and Wildlife, the Massachusetts Division of Fisheries and Game, the University of Massachusetts, and the Wildlife Management Institute), the Massachusetts Agricultural Experiment Station and the Delta Waterfowl Research Station. Thanks are due the owners of East Meadows Ranch for facilities provided.—James A. Cooper and Jon R. Hickin, *Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, Massachusetts 01002, 6 July 1971.*

Spring migration of Swainson's Hawk and Turkey Vulture through Veracruz, Mexico.—At 15:40 hours, 22 March 1970, on Highway 180, 9 km west of Cardel, Veracruz we observed a massive migration of Swainson's Hawks (*Buteo swainsoni*) and Turkey Vultures (*Cathartes aura*) heading generally north-northwest. The hawks, apparently all in typical adult plumage, were in loosely formed flocks of 75 to 200 birds flying approximately 50 to 300 m above the ground. In 30 minutes we conservatively estimated that 1,600 hawks passed overhead.

An approximately equal number of Turkey Vultures were migrating at the same time; they tended to segregate into homogeneous flocks traveling at lower altitudes and wheeling and turning more than did the Swainson's Hawks. At 16:10 we continued south toward Veracruz and observed flocks of migrating birds along the coastal plain to 28 km south of Tamarindo. The weather was warm and overcast.

On 23 March, another overcast day, we encountered along the same route hundreds of migrating birds 14 km south of Tamarindo. Again the Swainson's Hawks tended to be higher than the vultures, although the vultures outnumbered the hawks. As soon as we started up the mountains west of Tamarindo into heavy clouds, we no longer saw migrating flocks.

On 26 March which was mainly overcast with a few short breaks of sunlight and a strong wind off the Gulf of Mexico, we encountered migrating birds on Highway 180 12 km north of Vega de Alatorre at about noon. From there to Tecolutla we observed thousands of vultures. Often they were just above the tops of the palms and other trees bordering the Gulf, but we saw none over the water itself. Hawks were few, although about 27 were over Puente Nautla at 12:13. The stratification of species was still evident. Our northernmost observation was 32 km south of Poza Rica at 15:00.

The spectacular migration of both species through Central America has been noted by many authors. In Veracruz Swainson's Hawk migrations have been reported by Loetscher (Auk, 72:14–54, 1955) near Las Vigas and Jalapa. Sutton and Pettingill (Auk, 59:1–34, 1942) witnessed migrating Swainson's Hawks near Gomez Farias, Tamaulipas, in April. Turkey Vulture spring migration in Veracruz was reported by Wetmore (Proc. U. S. Natl. Mus., 93:215–340, 1943) and Bussjaeger et al. (Condor, 69:425–426, 1967). Heretofore the extensive occurrence of both species migrating together this far north has not been reported. Monroe (Ornithol. Monogr. No. 7:1–458, 1968) reported the two species together in Honduras. Dickey and van Rossem (Field Mus. Nat. Hist., Zool. Ser. No. 23:1–609, 1938) noted migrating flocks of Turkey Vultures and Swainson's Hawks in El Salvador in the fall. They stated that hawks and vultures were "migrating as an integral part of the flight," but they did not indicate whether the species were stratified by altitude.

Swainson's Hawk normally migrates at great heights (Monroe, ibid.; Skutch, Northwest Sci., 19:80–89, 1945), however, on overcast days they are forced to fly much lower (Skutch, ibid.). The overcast weather coupled with the jutting mountains could have funneled the hawks we observed toward the coastline. This idea is supported by Loetscher's observations of migrating Swainson's Hawks in the vicinity of Jalapa and Las Vigas on 5 April 1939. The weather at that time (4 and 5 April 1939) was mostly fair and clear in the mountains (Loetscher, pers. comm.) and on the coastal plain at Tejeria, west of the city of Veracruz (U. S. Weather Bureau records).

On 23 March 1970 the coastal plain was overcast; at Jalapa (elevation 1,400 m) we were in the midst of the clouds, and at Las Vigas (2,450 m) we were above the clouds. Since we observed migrating birds only on the coastal plain, this observation apparently was an example of local weather conditions and topographic features affecting the migration of these birds.—JAMES R. PURDUE, CHARLES C. CARPENTER, DALE L. MARCELLINI, *University of Oklahoma, Norman, Oklahoma,* AND ROBERT F. CLARKE, *Kansas State Teachers College, Emporia, Kansas, 16 June 1971.*

An unusual nest of the Sandhill Crane.—On 7 May 1969 while conducting research on Sandhill Cranes (*Grus canadensis tabida*) at Malheur National Wildlife Refuge, Harney County, Oregon I discovered an unusual crane nest. The nest consisted of two mounds of vegetation with an egg on each mound. One had the appearance of a normal nest, while the other consisted of a small accumulation of broad-fruited bur-reed (*Sparganium eurycarpum*). The second mound was situated 73 centimeters south of the normal structure.

The larger mound had the following measurements: basal diameter 110 × 138 cm; crown diameter 69 × 50 cm; bowl diameter 22 × 25 cm; bowl depth 2.9 cm and nest height above water 11.9 cm. The nest was in 17.8 cm of water and the egg which measured 102.8 × 61.1 mm, was being incubated. The small mound had no definable crown or bowl. It was 3.5 cm above water level in 10.5 cm of water. The egg measured 99.6 × 60.9 mm and had not been incubated.

When I disturbed the incubating bird it showed little interest in the nests; however, a crane was observed incubating on 8 May. Re-examination of the nest in early June revealed both eggs had been destroyed by a raccoon (*Procyon lotor*).

Of 394 Sandhill Crane nests I have inspected on Malheur NWR, this is the first nest observed where the eggs were not deposited on a single mound. I have seen several sites where two mounds had been constructed, but only one was ever utilized.—CARROLL D. LITTLEFIELD, *Department of Biological Sciences, University of Arizona, Tucson, Arizona 85721, 16 August 1971.*

Variability of tail molt in the Burrowing Owl.—Mayr and Mayr (Auk, 71: 172–178, 1954) described simultaneous tail molt in one museum specimen of the Burrowing Owl (*Speotyto cunicularia hypugaea*) as well as in other small owls. However, Thomsen (Condor, 73:177–192, 1971) in her study of a population of *S. c. hypugaea* in California found simultaneous tail molt to be "not apparent." Coulombe (Condor, 73:162–176, 1971) did not study tail molt. This note documents the occurrence of simultaneous or nearly simultaneous tail molt in a captive Burrowing Owl (*S. c. floridana*) and in a natural population of this subspecies.

Fig. 1. Burrowing Owl in nearly simultaneous tail molt (dorsal view).

The captive, an adult female, was kept in a behavioral observation room at the University of South Florida. The bird was under a light-dark cycle set one month ahead of the light cycle outside (i.e. the owl was subjected to March's day length in February, etc;). Between 27 March and 9 May, 1970, the captive was viewed through the observation room window and was not handled. When viewed on 9 May, the owl appeared to have a normal tail but by 11 May, all rectrices had been lost. Examination (Fig. 1) revealed 12 new tail feathers, 3 still in sheath and the remainder partially unsheathed. Judging from the length of the central rectrices, molt must have been in progress before 9 May. On 2 June, no sheathing was seen near the base of the feathers and growth was completed. Wing molt had commenced on 15 March and two primaries were in molt on 11 May. Based on the size relationships of the tail feathers (Fig. 1), the nearly simultaneous molt had a centrifugal order of replacement. The right six rectrices were slightly irregular in order with rectrix 2 being the longest, followed in order by rectrix 1, 3, 4, 6 and 5.

The advanced light-dark cycle of the captive owl and the lack of a mate might explain its early molt compared to molt in a natural population of 37 Burrowing Owls in the vicinity of the University. Most owls in the natural population were observed at least twice a week. Eight of these birds were observed to undergo a simultaneous tail molt. Four owls were seen with all new rectrices in sheath and equally long, while the other four were seen with new rectrices partially unsheathed but appearing to be of equal length (unlike Fig. 1). By 6 August, the new tails were between one-third and one-half developed. At the start of simultaneous molt, the eight birds (4 females, 3 males, and one unsexed) either had no young or had flying young at least 11 weeks old. Each bird had begun wing molt before the onset of tail molt. The flight of owls lacking functional tails seemed unimpaired except for the takeoffs which were slow and wobbly when compared to takeoffs with normal length rectrices. The effect of simultaneous tail molt on aerial foraging was not observed.

The other 29 owls did not undergo a simultaneous tail molt during the summer of 1970. Some of them were known to have undergone a gradual tail molt. Two were seen to begin gradual tail molt by loss of the central rectrices first when their young were 30 days old. It is interesting to note that the simultaneous tail molt in the field occurred after the young had reached some measure of independence and that a majority of the wild, breeding population did not undergo a simultaneous or nearly simultaneous tail molt.

These results supplement Mayr and Mayr's (loc. cit.) finding of a simultaneous tail molt in a museum specimen of *S. cunicularia.* Burrowing Owls can successfully secure insects on the ground without flying. If these owls can capture a sufficient number of prey on the ground, then the short period of complete tail loss may only represent a slight hindrance to foraging activities of the species.

The Department of Zoology, University of South Florida provided support for the work. Noel Snyder and Andrew J. Meyerriecks provided helpful comments on the manuscript.—William D. Courser, *Department of Zoology, University of South Florida, Tampa, Florida 33620, 9 June 1971.*

Another record of a short incubation period for the Robin.—Taft's note (Audubon Field Notes, 24:652, 1970) on the possible 7- or 8-day incubation period for a Robin (*Turdus migratorius*) prompts me to add a verifying observation made by one of my students, Ruth Ellen Sands, in 1956 in Athens, Ohio. She found a nest with 2 eggs on 20 April. On 22 April there were three eggs, the third having been laid between noon of 21 April and noon of 22 April. The three eggs hatched during the day on 30 April, from 8 to 8½ days after the laying of the last egg. All three young left the nest on 16 May, 2 in the morning and one around supper time.—Henri C. Seibert, *Department of Zoology, Ohio University, Athens, Ohio 45701, 10 June 1971.*

Discovery of the nest of the Kauai Akepa.—The Hawaiian Islands are inhabited by a unique family of birds—the Hawaiian Honeycreepers (family Drepanididae). Of the twenty-two full species of drepanidids, eight are already extinct and eight others currently considered to be in danger of extinction (Fisher, Simon, and Vincent, Wildlife in danger. New York, 1969). The six remaining species have at least one race each in danger of extinction.

The Akepa (*Loxops coccinea*) has distinct subspecies on four of Hawaii's main islands: *Loxops coccinea caeruleirostris* on Kauai; *L. c. rufa* on Oahu; *L. c. ochracea* on Maui; and *L. c. coccinea* on Hawaii. The species is fairly common only in the Alakai Swamp region of Kauai, less common at Kokee State Park on Kauai; it is extinct on Oahu, and rare on both Maui and Hawaii.

The nest, eggs, and nestlings have not been described previously for any of the subspecies of Akepa. Perkins (Aves. *in* Fauna Hawaiiensis 1 (4):365–466, 1903) wrote: "On one occasion I saw a pair of the Maui species building their nest high up in a tall ohia, near the extremity of a horizontal branch. Both sexes kept coming to the ground for material and were carrying off the wooly down or 'pulu' of some stunted tree-ferns, probably as a lining for the nest. This was so well concealed that even with glasses

FIG. 1. The exterior of an Akepa nest to show method of nest attachment.

I was unable to make out the details of structure with any certainty, and the eggs and unfledged young I have not seen." I have found no other references to the nests of any subspecies of Akepa.

I discovered the first Kauai Akepa nest in Kokee State Park on 9 March 1969, while conducting a study of the breeding biology of four more common species of drepanidids (Amakihi (*L. virens*), Anianiau (*L. parva*), Apapane (*Himatione sanguinea*), and Iiwi (*Vestaria coccinea*)). The Akepa is not common in the Kokee area but I have seen as many as five in one day of field work there. The nest was in the terminal crown of a non-blooming ohia tree (*Metrosideros*), 30.5 feet above the ground. The top of the tree was too thin to support my weight but I was able to see into the nest by using a mirror attached to the end of a six-foot pole. The nest was empty and appeared incomplete in that one side was still thin. After checking the nest I concealed myself in the underbrush beneath the tree. I then saw one bird fly to the nest, hop in and remain for two or three seconds, after which it flew down to within 15 feet of me. I could plainly see that it was an Akepa. It gave repeated call notes and then flew back to the nest.

I watched both the male and female Akepa adding material to the nest. Between 8:30 and 10:30 on 11 March, each added material eight times. The male often sang from a tall neighboring ohia tree as the female was adding to the nest. His song was a high trill, higher in pitch and shorter in duration than the song of the Anianiau. The male also uttered a variety of whisper songs, similar to those of the Amakihi.

I observed courtship feeding on several occasions, usually on a branch a short distance from the nest but once on a branch only three feet from the ground. The female solicited feeding by crouching slightly, depressing and quivering her wings, and giving a vocalization similar to that of a fledgling begging for food.

A pair of Apapane were building in a neighboring ohia tree 40 feet from the Akepa nest. On several occasions the Apapane flew to the Akepa nest, pulled loose nesting material, and added it to their own nest. This stealing was usually done during the absence of the Akepa but on 14 March an Apapane flew to the nest while the Akepa were present. The male Akepa gave the alarm call and chased the Apapane from the nest

FIG. 2. The Akepa nest is lined with soft bark fragments.

and through several nearby trees, but in less than 15 minutes the Apapane returned and, in the absence of the Akepa, again took material from the nest. The Akepa were still adding material on 18 March. On 27 March I found half of an egg shell on a branch about a foot below the nest. The shell fragment looked very much like the eggs of the other drepanidids—white with irregularly shaped brown markings. The lining had been torn out of the nest and neither adult was near. I continued to observe the nest until 4 April but never saw the Akepa near it again.

The construction of the Akepa nest differs from that of the Apapane in that fewer twigs and coarse materials are employed, the Akepa nest being composed largely of mosses. Construction is less compact so that from the ground the nest appears quite large. Measurements were as follows: rim thickness, ¾ to 1½ inches; outside diameter, 3¼ to 4½ inches; measurement from the top rim to the bottom of the nest, 4½ inches; inside diameter of the nest cup, 1¾ to 2½ inches; depth of the nest cup, 1¾ inches.

In 1970 I found two inaccessible Akepa nests, the first on 26 March and the second on 11 April. I estimated their heights to be approximately 40 feet above the ground. Both were in the terminal crowns of non-blooming ohia trees. The first nest was under construction when I found it and I observed courtship feeding in this pair. The second probably contained eggs because the female spent periods of 15 to 20 minutes in the nest.

On 29 March 1970 I found an accessible Akepa nest 37.5 feet above the ground in the terminal crown of a non-blooming ohia tree. The nest appeared to be complete when I found it. The first egg was laid in this nest on 2 April, the second on 3 April. The eggs measured 16.6 × 13.3 mm and 16.6 × 13.1 mm. They had a whitish background with irregularly shaped dark brown markings scattered over the entire surface, but more concentrated at the large end of the egg. On 4 March the nest lining had been pulled up, burying the two eggs. I observed the nest until 6 April when it was apparent that it had been deserted. I broke one of the eggs to see the yolk. It was yellow, as in the eggs of the Amakihi and Anianiau, as opposed to orange as in Apapane and Iiwi eggs.

Travel funds for this study were provided in part by grants from the Chapman Memorial Fund, the Eastern Bird-Banding Association, and by National Science Foundation Grant GB-5612, awarded to Andrew J. Berger.—C. ROBERT EDDINGER, *Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, 6 May 1971.*

Mobbing of a Fish Crow by passerines.—Mobbing of hawks, crows, and other large birds by passerines is a common behavior seen during the breeding period. Often the factors evoking this aggressiveness are difficult to determine, and there are few published papers relative to the effectiveness of mobbing by small passerines. The following account regarding a Fish Crow (*Corvus ossifragus*) and several passerines gives information on cause and effectiveness of this incident of mobbing behavior. The observations were made at Winter Park, Seminole County, Florida.

In late afternoon of 15 May 1971, a cloudy day, loud distress calls of Mockingbirds (*Mimus polyglottos*) and Red-winged Blackbirds (*Agelaius phoeniceus*) attracted my attention. About 250 feet away in a pine-palmetto habitat bordered by a drainage ditch, three Mockingbirds and at least three Red-winged Blackbirds were vigorously mobbing an unmarked Fish Crow. The passerines directed their beaks at the crow's body, and the most frequent area hit was the back. After about three minutes the crow flew to and perched in one of four closely-spaced pine trees located about 25 feet from the mobbing area. The passerines then perched in the pines but continuously gave raucous calls. In less than two minutes the crow, followed by the passerines, flew from the trees and returned to the area. The mobbing resumed. A calling Blue Jay (*Cyanocitta cristata*) flew to the scene and participated with the Mockingbirds and Red-winged Blackbirds. Again the birds returned to the pines; the crow was panting. Initially I had the impression that the crow accidently came in contact with the passerines and was trying to escape. During the second mobbing incident it seemed clear the crow was not trying to escape since it kept returning to the same area. After two more similar mobbing bouts, the crow, while hovering somewhat, succeeded in its efforts and took a squealing, well-feathered bird from a nest. The distress calls of the passerines became louder. The crow immediately flew away with the young bird dangling from its beak. One Mockingbird continued to chase the crow as both birds flew out of sight beyond a distance of 1000 feet in an area of several large pine trees. The Mockingbird shortly returned to the mobbing area. I am not sure if the nestling was a Mockingbird or Red-winged Blackbird. Active nests of both species were found in the mobbing area. After about five minutes later, much to my surprise, a crow, presumably the same bird since it came from the direction where the other crow made its exit, returned to the area and the mobbing behavior resumed. This crow began hovering in the same area as before as the calling passerines mobbed the intruder. The crow was undoubtedly after another nestling. During these hovering movements a sudden heavy rain began. The crow flew away and the passerines dispersed.—WALTER KINGSLEY TAYLOR, *Department of Biology, Florida Technological University, Orlando, Florida 32816, 24 May 1971.*

Vesper Sparrow nests abandoned after snow.—During the period 8–10 June 1970, three Vesper Sparrow (*Pooecetes gramineus*) nests, each with four eggs, were found on a small watershed study site 14 miles west of Saratoga, Wyoming. The nests were located under partially dead sagebrush plants on an upland sagebrush site at about 7,850 feet elevation. On 11–12 June 1970, an unseasonable snowstorm, preceded by a one-half-inch rain, deposited 4 to 6 inches of snow on the nesting area. Accompanying this storm was a cold air mass that substantially lowered both daytime and nighttime air temperatures. Temperature extremes for the 10 successive days before, during, and after this storm were: 6 June, 40°–60° F.; 7 June, 40°–65°; 8 June, 44°–68°; 9 June 44°–56°; 10 June, 35°–46°; 11 June, 31°–36°; 12 June, 31°–46°; 13 June, 33°–69°; 14 June, 39°–58°; and 15 June, 44°–58°. The nests were visited again on 22 June, and all were found abandoned. Upon examination, the now spoiled but still intact eggs were found to have been fertile, with absorption of the yolk sacs well advanced. Since the adult birds continued to incubate, both during and after previous visits to their nests, I believe that abandonment was caused by the accumulated snow at the nest sites. Frequent visits to the nesting area in the following weeks did not reveal any attempts to reuse the abandoned nests.—MAX H. SCHROEDER, *Bureau of Sport Fisheries and Wildlife, Denver Wildlife Research Center, Denver, Colorado, 9 April 1971.*

Records of the Scarlet Ibis and Red-breasted Blackbird in Ecuador.—In their book, The Species of Birds of South America (Acad. Nat. Sci., Livingston Publ. Co., 1966), Meyer-de Schauensee and Eisenmann did not include Ecuador in the stated range of the Scarlet Ibis (*Eudocimus ruber*) or the Red-breasted Blackbird (*Leistes militaris*). This fact leads me to place on record my observations of these species made in 1964 at Limon Cocha (Oriente Province), Ecuador, near the junction of the Rio Napo and Rio Jivino:

Scarlet Ibis.—One seen on 7 May at less than 50 feet in trees at the edge of the lake. Palmer (Handbook of North American Birds, Vol. 1, Yale Univ. Press, p. 530, 1962) stated that the plumage sequence in this ibis is "almost entirely unknown." The bird I saw was a mosaic of gray and scarlet patches, the arrangement reminiscent of that in some blue-and-white immature Little Blue Herons (*Florida caerulea*).

Red-breasted Blackbird.—Small numbers were seen in a pasture from 25 April into early May. Of 5 specimens collected, 2 are now in the Museum of Zoology at Louisiana State University, the others at Florida State University.—HENRY M. STEVENSON, *Department of Biological Sciences, Florida State University, Tallahassee, Fla., 32306, 26 July 1971.*

PUBLICATION NOTES AND NOTICES

DIE VÖGEL DES BODENSEEGEBIETES. By H. Jacoby, G. Knötsch, and S. Schuster. Schweizerische Gesellschaft für Vogelkunde und Vogelschutz, Winterthur, Switzerland, 1970: 6 × 9 in., 260 pp., 26 photos, plus graphs, maps. Swiss Francs 18.50.

"The Birds of the Lake Constance Region" summarizes many years of ornithological research around that large lake on the border of northern Switzerland and southern Germany. This report was compiled by three workers with the cooperation of many other individuals, and the whole was sponsored by the Swiss Society for Bird Study and Bird Protection. It provides an excellent example of how intensive bird study in one small region can be summarized, and it pictures the birds in another continent but one with similar vegetation, agriculture, and human uses of the landscape to that found in eastern North America.—JAMES T. TANNER.

ORNITHOLOGICAL NEWS

The Chairman of the Program Committee for the Annual Meeting is Dr. Elden W. Martin, Department of Biology, Bowling Green State University, Bowling Green, Ohio 43402. Members and others who desire to present papers at the meeting may contact Dr. Martin at any time even though the official call for papers has not appeared.

At each Annual Meeting a Committee on Resolutions is appointed, and certain resolutions are adopted by the membership. Frequently this Committee is handicapped by a lack of information about matters on which it would be appropriate that the Society take a formal stand. Any member, whether intending to be at the Meeting or not, who knows of a conservation matter upon which he thinks a formal resolution of the Society would be helpful, should send particulars to the Secretary in advance of the Meeting.

Two new Patrons of the Society are Olin Sewall Pettingill, Jr. and Paul A. Stewart.

E. Alexander Bergstrom has retired as editor of *Bird-Banding* after 21 years at the post. The new editor is David W. Johnston of the University of Florida.

Ralph J. Raitt has retired as editor of *The Condor.* The new editor is Francis S. L. Williamson of the Chesapeake Bay Center for Environmental Studies.

The annual meeting of The Eastern Bird Banding Association will be held at Ithaca, New York. 21–23 April 1972. The annual meeting of the Western Bird Banding Association will be held at Sunriver, Oregon on 10–11 June 1972.

The Terra Alta Biological Station of West Virginia University announces a special early session, May 15 to 9 June. Courses in ornithology, herpetology, and plant taxonomy will be offered. The early dates are to coincide with the height of seasonal activity in the fields concerned. Inquiries should be directed to Robert L. Birch, Department of Biology, West Virginia University, Morgantown, West Virginia 26506.

CONSERVATION SECTION

BIRD DAMAGE TO CORN IN THE UNITED STATES IN 1970

CHARLES P. STONE, DONALD F. MOTT, JEROME F. BESSER
AND JOHN W. DE GRAZIO

Accurate assessments of agricultural losses to birds are difficult to obtain, but are fundamental in evaluating the necessity for, and effectiveness of, damage control. Some estimates of statewide losses have been made, but most extensive surveys to date have had little empirical basis, cannot be compared statistically, and were subject to many biases.

The results of the first nationwide survey of bird damage to corn are reported in this

TABLE 1

DAMAGE PATTERNS IN 24 MAJOR CORN-PRODUCING STATES IN 1970

State	Corn acreage (thousands)	Counties		Fields		Corn ears	
		Number surveyed	% with damage	Number surveyed	% with damage	Number examined	% with damage
Alabama	545	36	16.67	61	9.84	1,152	1.04
Florida	322	19	0.00	79	0.00	1,365	0.00
Georgia	1,426	61	4.92	105	2.86	2,641	0.57
Illinois	10,066	78	15.38	188	7.44	6,848	0.45
Indiana	5,027	79	16.46	147	10.88	5,277	1.06
Iowa	9,990	89	1.12	197	1.02	6,897	0.03
Kansas	1,285	38	7.89	112	3.57	3,267	0.15
Kentucky	988	56	33.93	110	18.18	3,043	2.50
Maryland	484	19	57.89	92	19.57	2,538	3.55
Michigan	1,444	37	45.95	116	25.00	3,891	4.81
Minnesota	4,594	49	20.41	158	8.86	7,623	1.08
Mississippi	248	43	37.21	73	28.77	1,305	5.21
Missouri	2,837	63	6.35	150	3.33	4,100	0.27
Nebraska	4,897	60	5.00	169	1.78	5,374	0.13
New York	279	29	62.07	75	41.33	2,698	6.92
North Carolina	1,345	61	11.48	143	4.90	4,709	0.28
Ohio	3,014	60	31.67	133	19.55	4,684	2.82
Pennsylvania	943	37	64.86	121	34.71	3,844	8.32
South Carolina	402	27	40.74	95	16.84	2,262	2.17
South Dakota	2,496	39	33.33	105	18.10	2,606	1.42
Tennessee	569	38	34.21	91	19.78	2,246	1.60
Texas	531	35	8.57	128	4.69	3,070	0.68
Virginia	458	46	21.74	73	12.33	2,294	2.53
Wisconsin	1,794	46	32.61	133	15.04	4,896	2.45
Totals and means	55,984	1,145	21.92	2,854	15.60	88,630	1.82

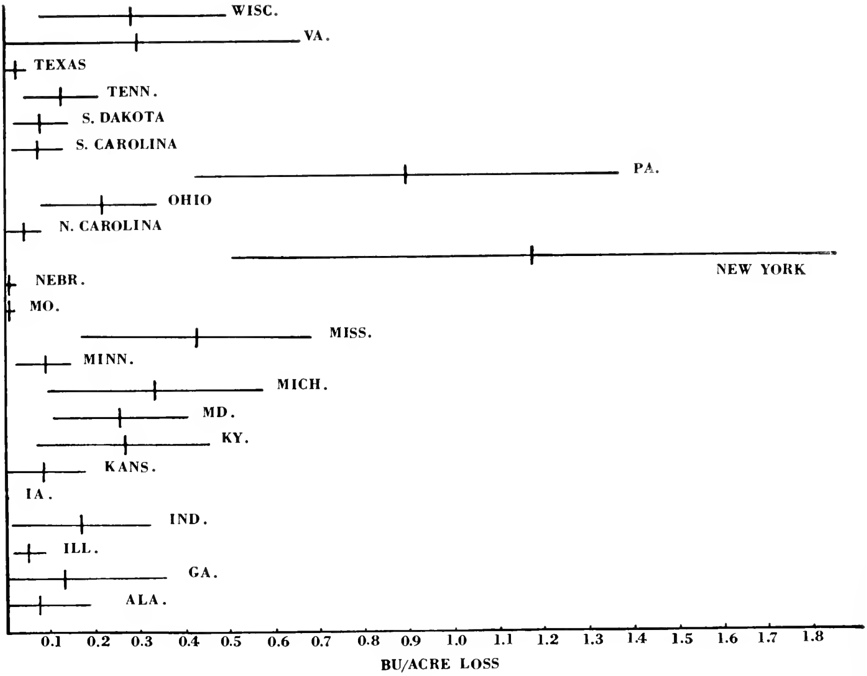

Fig. 1. State corn losses to birds in 1970 (mean bu/acre loss and 95 per cent confidence limits).

paper. The data were collected in a similar manner in each state, and a statistical approach permitted establishment of confidence limits on damage estimates. Valid comparisons of data from the various states are thus possible for the first time. The approach also permitted the mapping of damage according to presence or absence in the counties surveyed. For the states with which we are most familiar, the pattern appears realistic, and for other states it is revealing, but merits further study.

METHODS

The 1970 bird damage survey was conducted under an interagency agreement between the Bureau of Sport Fisheries and Wildlife and the Statistical Reporting Service (SRS) of the U.S. Department of Agriculture. Enumerators employed by the USDA to conduct the annual Objective Yield Survey for corn, were introduced to bird damage in different stages of corn maturity through a slide series and handouts prepared by the authors.

The sampling frame employed by the SRS during their final pre-harvest survey was used to estimate bird damage. Enumerators were asked to complete an additional form relating to bird damage for the fields normally surveyed. Fields were randomly chosen and two 15-foot units of two rows each were randomly established in each field. Enumerators recorded the number of ears of corn with kernels in the first row in each unit. They also measured the average length of damaged and undamaged kernel rows to the nearest 0.1 inch for each damaged ear in the first row of each unit. Bureau personnel

TABLE 2

ESTIMATED STATE CORN LOSS TO BIRDS IN 1970

State	Mean bu/acre loss ± S.E. (t_{05})	Mean bushel loss ± S.E. (t_{05})	Mean dollar loss[1]
Alabama	0.0774 ± 0.1132	42,183 ± 61,694	$ 63,275
Florida	0.0000 ± 0.0000	—	—
Georgia	0.1296 ± 0.2351	184,810 ± 335,253	277,215
Illinois	0.0540 ± 0.0363	543,564 ± 365,396	815,346
Indiana	0.1716 ± 0.1607	862,633 ± 807,839	1,293,950
Iowa	0.0018 ± 0.0027	17,982 ± 26,973	26,973
Kansas	0.0811 ± 0.0969	104,214 ± 124,517	156,321
Kentucky	0.2651 ± 0.1941	261,919 ± 191,771	392,879
Maryland	0.2542 ± 0.1492	123,033 ± 72,213	184,550
Michigan	0.3356 ± 0.2400	484,606 ± 346,560	726,909
Minnesota	0.0896 ± 0.0678	411,622 ± 311,473	617,433
Mississippi	0.4253 ± 0.2584	105,474 ± 64,083	158,211
Missouri	0.0114 ± 0.0141	32,342 ± 40,002	48,513
Nebraska	0.0140 ± 0.0165	68,558 ± 80,801	102,837
New York	1.1791 ± 0.6761	328,969 ± 188,632	493,454
North Carolina	0.0426 ± 0.0386	57,297 ± 51,917	85,946
Ohio	0.2180 ± 0.1373	657,052 ± 413,822	985,578
Pennsylvania	0.8957 ± 0.4732	844,645 ± 446,228	1,266,968
South Carolina	0.0750 ± 0.0577	30,150 ± 23,195	45,225
South Dakota	0.0812 ± 0.0606	202,675 ± 151,258	304,013
Tennessee	0.1271 ± 0.0868	72,320 ± 49,389	108,480
Texas	0.0257 ± 0.0255	13,647 ± 13,541	20,471
Virginia	0.2983 ± 0.3559	136,621 ± 163,002	204,932
Wisconsin	0.2861 ± 0.2086	513,263 ± 374,228	769,895

[1] At $1.50/bushel.

converted the length data to weight of corn lost (in grams) through use of the mathematically generated table developed by De Grazio et al. (J. Wildl. Mgmt., 33:988–994, 1969). It is possible that the table underestimates damage somewhat, and this is being checked at present. Confidence limits were established at the 95 per cent level for bushel-per-acre losses in each state and for total bushel losses for the 24 states surveyed. The data for each state were weighted according to corn acreage grown in order to calculate the overall mean and confidence interval (Cochran, Sampling Techniques, 1953). The 24 states surveyed accounted for 98 per cent of the acreage harvested and for 97.5 per cent of the corn produced in the United States in 1970, according to the SRS.

RESULTS AND DISCUSSION

The estimated mean of the direct corn loss to birds in the 24 states was 0.1112 ± 0.1880 bu/acre, or 6,225,421 ± 10,524,992 bu (95 per cent confidence limits). At $1.50/bu, the dollar loss amounted to $9,338,132 ± 15,787,488. Based on USDA production figures, birds accounted for 0.16 ± 0.26 per cent of the total corn crop in the 24 states in 1970.

Corn damage according to numbers of counties and fields surveyed and ears damaged

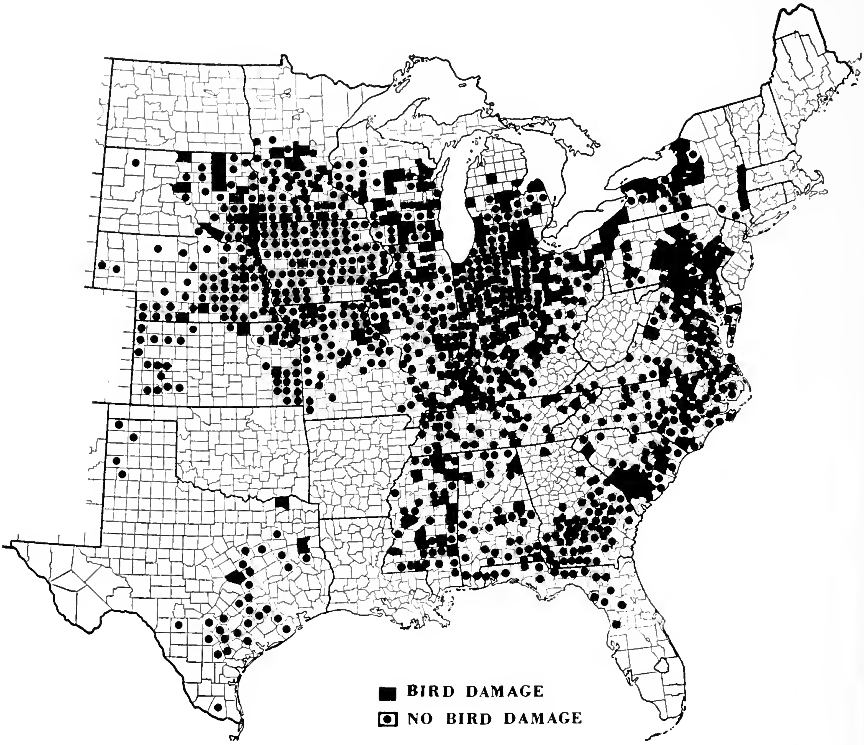

FIG. 2. Distribution of bird damage to corn in 1970 by counties.

in each state is summarized in Table 1. Kentucky, Maryland, Michigan, Mississippi, New York, Ohio, Pennsylvania, and South Carolina showed higher than average damage by all three analyses. These states also suffered relatively high bushel-per-acre losses, although the confidence intervals overlapped considerably with those of other states (Fig. 1). It is evident, however, that bushel-per-acre losses were particularly high in New York and Pennsylvania and comparatively low in Texas, North Carolina, Nebraska, Missouri, Iowa, and Illinois.

The greatest economic losses, determined by a combination of considerable acreages of corn and relatively high bushel-per-acre losses, occurred in Illinois, Indiana, Michigan, Minnesota, Ohio, Pennsylvania, and Wisconsin (Table 2). However, high bushel-per-acre losses in states with relatively low acreages of corn (such as New York) are of obvious importance to the growers involved. The low bushel-per-acre losses in Iowa and Illinois, which together accounted for 35.8 per cent of the corn acreage in the 24 states, are noteworthy.

Counties that contained at least one survey field, and those in which at least some bird damage occurred in 1970, are shown in Figure 2. Probably damage in 1970 was lessened by the rapid corn maturation and early harvest, which resulted in part from an infestation of southern leaf blight.

SUMMARY

The first nationwide survey of bird damage to corn was conducted in 1970; 24 states producing over 97 per cent of the U.S. corn crop were sampled. The total direct loss to birds was estimated to be 6,225,421 bushels ± 10,524,992 bushels (95 per cent confidence limits). New York and Pennsylvania suffered the high losses per acre, and Indiana, Illinois, Wisconsin, Ohio, Pennsylvania, Michigan, and Minnesota showed high total losses.

ACKNOWLEDGMENTS

We wish to thank John L. Oldemeyer of this Center for statistical advice, and Ann H. Jones, also of this Center, for editorial comments.

BUREAU OF SPORT FISHERIES AND WILDLIFE, DENVER WILDLIFE RESEARCH CENTER, DENVER, COLORADO 80225, 22 OCTOBER 1971.

PUBLICATION NOTES AND NOTICES

A NATURAL HISTORY OF NEW YORK CITY. Revised and abridged edition. By John Kieran. Published for The American Museum of Natural History by The Natural History Press, Garden City, New York, 1971: 4½ × 7¼ in., paper covered, viii + 308 pp. $2.95.

This is a revised and updated edition of the original book published in 1959 (and favorably reviewed in *The Wilson Bulletin*, 72:298, 1960). Mr. Kieran tells not only a great deal about the natural history of his city, but also how to see often inconspicuous plants and animals. His enthusiasm for his subject should arouse many New Yorkers to seek it for themselves. They will be amazed to find how much wildlife remains in spite of environmental decay. The illustrations that graced the original edition have unfortunately been deleted from this one.—P. S.

ECOLOGY OF COLORADO MOUNTAINS TO ARIZONA DESERTS. By Helen Moenke. Museum Pictorial No. 20, Denver Museum of Natural History, Denver, Colorado, 1971: 6 × 9 in., paper covered, 96 pp., many col. and bl. and wh. photos. $2.50.

This booklet is accurately self-described as "An interpretive study of the ecology of plants and animals exhibited in life zone habitat groups in the Walter C. Mead Ecological Hall of the Denver Museum of Natural History." Based on these exhibits, the text discusses ecological relationships in sequence from the alpine tops of Colorado's Rocky Mountains down through the life zones to the Sonoran deserts of Arizona. Photographs of these superlative exhibits and of plants and animals in nature are included. The booklet is edited by Alfred M. Bailey, and therefore is up to the high standards of previous Museum Pictorials. It will help travelers in Colorado to see behind the scenery.—P. S.

ORITHOLOGICAL LITERATURE

An Approach to the Study of Ecological Relationships Among Grassland Birds. By John A. Wiens. American Ornithologists' Union Ornithological Monographs, No. 8, 1969: 6¾ × 10 in., 93 pp., 30 figs., 17 tables. $2.50.

The urge to quantify has recently made its way to one of the last strongholds of descriptive ornithology, the study of breeding biology. This monograph presents three years of quantitative data on the ecology of seven species regularly breeding in Wisconsin grasslands: Bobolink, Eastern Meadowlark, Western Meadlowlark, Savannah Sparrow, Grasshopper Sparrow, Henslow's Sparrow, and Vesper Sparrow.

As Wiens states his goals, they ". . . were to develop and test a method for describing and analyzing habitats which would be useful in elucidating ecological relationships among grassland birds." His methodology consists of habitat description—using vegetation type, coverage and height, vertical light penetration, substrate and topographic descriptions; vegetation sampling via the point method; demarkation of the territories of birds present; and recording habitat utilization by continuous tape recorded observations of the birds present.

In addition to the development of an efficient and adequate means of habitat analysis, several important relationships among the inhabitants are delineated. Their territories varied throughout the season as well as yearly, but only the Eastern and Western Meadowlarks had mutually exclusive territories. While the territories of all species had many physiognomic aspects in common, the territory of each species was somehow distinctive. Bobolinks preferred dense tall vegetation with its associated deep litter and low light penetration, while Vesper Sparrows preferred short, sparse vegetation with little litter and high light penetration. Differences among the species also appeared in the frequencies and sites of performance for daily activities. Wiens found evidence of a dominance relationship among the species in the study which, together with their ecological differences, tended to reduce direct competition sufficiently to allow cooccupancy of this relatively homogeneous environment.

This is an excellent paper for the novice ecologist to peruse. It clearly presents methodology in detail and its application in daily field work is easily followed. More than most modern field studies, this monograph also pauses to theorize a bit. What were the theoretical considerations which prompted Wiens to undertake this study? What were the problems in the development of his methodology and the consequent changes they wrought from 1964 to 1966? The graphic representations throughout are clear and easily understood. Such inclusions make this monograph particularly exemplary to the conduct of scientific research.

Alternatively, these same inclusions engender much of the criticism I might make of this paper. Ofter Wiens is less than concise in the presentation of his ideas. In the development of his methodology, I found myself wishing he would simply state exactly what he did, and stop. Yet the comparison between sampling methods and their relative value and efficiency is instructive. Several of his points on theoretical ecological considerations are well taken, but often overly verbose. On pages one and two, Wiens theorizes that his bird species chose this grassland habitat on the basis of specific features of the habitat rather than on the presence of ultimate limiting factors imposed on them there; and regardless of the species, it remains constant in selecting the physiognomy of this habitat. The point is well taken, but supported by an excess of examples. On page five, he overstates the point, though a good one, that ecologists in their use of arbitrary categorization of a community for ease of analysis, often neglect to put the whole back together again.

Again in paragraphs two, three, and four on page 12, Wiens makes several good points, but is unnecessarily complex in their statement. I had the feeling here that he was holding up his side of an argument against imagined opposition. This is more the tone of a dissertation than of a monograph.

Yet in following the format of an instructional monograph, Wiens occasionally assumes too much knowledge on the part of his reader. In such a "standard operating procedure" for grassland habitat description with regard to birds, more references (see pages 17 and 18) might have been included, particularly basic ones. So long as diversity values are discussed on page 81, a brief inclusion of the parameters included in this index would be more instructive and meaningful: how large were the survey units; how were they selected; are the diversity values based on unit area?

Of lesser import are occasional lapses in organization or presentation. The last paragraph on page five would have adhered to the paper better had a topic sentence introduced the ideal approach to the study of animal habitats—through the animal itself. The map symbols used on page 32 are not explained until page 48; although readers are referred to page 48 for explanation, this arrangement is inconvenient. The brief comments on range included species by species on pages 34 to 41, as well as information on site preference, might better have been included in the discussion beginning on page 81 where Wiens discusses these subjects in detail. On page 37, much of paragraph one seems of historical import but irrelevant to the present paper, as do the brief behavioral comments later on that page.

From time to time I encountered seeming omissions in the full development of an idea. On page 44, the Western Meadowlark is listed as one of the species that arrives early on territory, yet in Table 7 on page 46, the species isn't included until 15–25 May.

I would have found useful a comparison of Tables 11 and 13. And I would have found interesting further development of the idea that "The utilization of a habitat by a species is to a large degree dependent upon the relative frequencies of various activities in the total activity repertoire of the species." These frequencies determine the utilization import or dominance, but which utilizations dictate a preference for the habitat selected? The most dominant utilization need not be the most determining one.

I found the greatest strength of this monograph to be in its theoretical approach to the description of vertebrate habitats as is well stated on page 13, and the subsequent parameters of habitat measurement as outlined in Table 2. The description and comparison of territory characteristics, given between pages 44 and 64, are very well done and constitute the life force of this paper.—D. JEAN TATE.

BIRDS OF ISLA GRANDE (TIERRA DEL FUEGO). By Philip S. Humphrey, David Bridge, Percival W. Reynolds, and Roger Tory Peterson. Preliminary Smithsonian Manual. Published and distributed for the Smithsonian Institution by the University of Kansas Museum of Natural History, 1970: 8½ × 11 in., viii + 411 pp., 8 maps, 21 pls. by Jack R. Schroeder. $7.00.

The southernmost part of South America, formed by the Straits of Magellan and Tierra del Fuego together with adjacent archipelagos and islands, has long been subject to ornithological observations. Scattered reports have been published since 1830 but there has not been any complete work on the avifauna of this region. The present book, which deals with the northern part of the Fuegian region (the "Isla Grande"), has been written in order to help overcome this lack. It is unfortunate that the archipelagos and islands off Isla Grande were left out, because it would have been logical to treat the whole Fuegian region in one volume. On the other hand, knowledge of the distribution of birds on the many southern islands is so sparse that the authors were justified in omitting them. Wisely they were modest, avoiding guesses and hypothetical statements.

The book is meant to facilitate field identification and to be a reference for data on seasonal and geographic distribution and on ecology. Providing this much information has created a book that weighs about two pounds; while it is excellent at the desk, it is most uncomfortable in the field. It would have been better to publish this work in two parts—one on distribution and species accounts, and the other a guide to the species, with field marks, habits, and habitats for each. As it is, one wonders if anyone would not hesitate to carry this book in the field. It would be lamentable not to take the book, because it is really full of information.

The authors have included almost everything that has been published about the birds of Isla Grande, an immense task. The unpublished manuscript of the late Percival W. Reynolds was an important source of information, and for this reason Reynolds is listed as a co-author. The work is divided into several sections—"History of Ornithological Exploration," "Geography and Environments," "Avifauna of Isla Grande," "Species Accounts," and "Field Identification." The most important section is that of the species accounts, each of which has subsections on distribution and status, habits, reproduction, vocalization, general notes, description, weight, and specimens known to have been collected. The maps show details of different parts of the island and the plates show most of the birds found in Fuegia.

I found no errors worth mentioning in the species accounts, but I would like to offer some comments. The term "nonbreeding resident" does not fit species which actually breed in Fuegia, such as *Eudyptes crestatus, Diomedea melanophrys, D. chrysostoma*, and *Macronectes giganteus*, but species which do not breed in the region, such as *Daption capensis* and *Fulmarus glacialis.* Subspecies are not mentioned, but in certain cases it would have been well to call attention to little known forms, such as *Milvago chimango fuegensis* (Johnson and Behn, Supl. Aves. de Chile, p. 353, 1957). *Gallinago stricklandi* breeds in bushy or wooded damp areas, not marshes, like the habitat of *G. media, Philohela,* and *Scolopax*; during migration, however, the species appears in grasslands. In regard to certain species of terns, I think it would be sensible not to accept any sight records. There are several similar species along the coast of Argentina, such as *Sterna hirundinacea* (both southern and Brazilian populations, with different breeding cycles), *S. hirundo* (in the southern summer appearing in great numbers as far as Santa Cruz), *S. vittata* (wintering in Buenos Aires and Uruguay), perhaps *S. paradisea*, in addition to which both *S. forsteri* and *S dougallii* can be expected; the different plumages of these birds are apt to be confusing. Species which certainly appear or can be expected to occur in the area of Isla Grande are, for example, *Phoebetria fusca* (recorded off Cape Horn), *Pachyptila turtur* (breeds on Beauchéne Islets, southwest of the Falkland Islands), *Phalacrocorax bougainvillii* (breeds in Chubut, Argentina, and has been reported from the Straits of Magellan), and *Larus belcheri* (breeds in southernmost Buenos Aires, occurs regularly as far as Santa Cruz, and has been recorded from Yellow Island, east of Hoste Island, Tierra del Fuego). *Bartramia longicauda*, which has been reported as far south as the South Shetland Islands, can also be expected in the Fuegian region, as can some other North American migrants, such as *Aphriza virgata* and *Larus pipixcan.*

In the section on field identification, the description and field marks of each species are placed opposite the illustration. The passerines are not in systematic order but are grouped according to habits and habitat. Plate 17, for example, shows "Ground-dwelling

Furnariidae," Plate 18 shows "Flycatchers. Forest zone species" and "Open ground or ground species," Plate 19 shows "Open country birds," Plate 20 "Forest birds," and Plate 21 "Finches." This arrangement is somewhat confusing and ought to have been checked. *Ceryle torquata* and *Curaeus curaeus* are not exactly forest birds, *Tachycineta leucopyga* is a tree swallow, *Sicalis lebruni* and *Melanodera melanodera* ought to have been placed with the ground birds, and *Troglodytes aedon* placed with the forest birds. Confusion of another kind exists in the plates where *Turdus falklandii* and *Scytalopus magellanicus* ("forest birds") are shown amid grass on the ground, true ground-dwellers such as *Sicalis lebruni* and *Phrygilus unicolor* are on branches, and *Zonotrichia capensis*, a typical "brush-bird," on the ground.

These negative remarks are insignificant in comparison with the great value of this manual. Certainly the book will encourage the collecting of more data on the natural history of Fuegian birds. It is to be hoped that the authors will complete this work with a volume on the remaining parts of the region.—CLAES C. OLROG.

THE COTURNIX QUAIL; ANATOMY AND HISTOLOGY. By Theodore C. Fitzgerald. Iowa State University Press, Ames, 1970: 10⅛ × 7 in., xix + 306 pp., 157 text-figs. $7.95.

At present, books presenting detailed information on the anatomy of a bird are so scarce and so necessary that any such book could be a major contribution. Where the subject of such a text is a species used in genetic and physiological investigations, the potential value is enhanced. Regrettably, this text does not achieve this potential. Dr. Fitzgerald made a "valiant fight to finish the manuscript" despite his ill health; that he did so is a tribute to the man and the scientist. Undoubtedly, had he lived to shepherd the book through all of the prepublication stages, many of the errors and deficiencies which mark the text might have been corrected. However, the non-textual portion of the work was prepared by his colleagues and, as frequently happens in such cases, they could not provide the expertise, knowledge, or personal attention and care which the author would undoubtedly have exercised, regardless of their intentions or their competence in their own fields of interest.

The book is attractive; the format and type are exceptionally easy to read. The absence of typographical errors is gratifying as is the intention to aid the reader by including large numbers of illustrations. The organization, with a few exceptions, follows a traditional pattern. I do question the logic of a chapter sequence which runs: "Osteology"—"Arthrology"—"*Angiology*"—"Myology" (italics mine); Angiology seems to fit closer to the chapter on "Splanchnology." Also questionable is the placement of the chapter on "Integument" as the final rather than as the first chapter.

A strong feature of the book is the detailed section on arthrology; nowhere else to my knowledge is so much information available on the joints of birds. The promised, but essentially absent, comparisons between the Coturnix, mammals, and other birds used in research could have been most useful had they been included. While there is an extensive Bibliography there is a paucity of literature citations in the text; the resultant absence of any significant documentation of many factual statements is disturbing especially in a text oriented toward researchers. The various organ systems are unevenly emphasized. Extensive coverage is given to osteology, myology, angiology, and, to some degree, neurology, but only five pages are given over to the endocrine system, and four to the integument. The text also promises, by title, to cover "histology"; with comparatively few exceptions, it does not, leaving a significant void in coverage of functionally important histological aspects of many organs and tissues.

While much of the information presented is accurate, there are some disturbing and notable exceptions, some but certainly not all of which are discussed below.

Illustrations, while numerous, are quite inadequate and thus the reader must carefully study the labels to compensate for deficiencies in the legends. Sometimes the same view is labeled differently in different figures (e.g. Figs. 3.1 and 3.5), or major structures are left unidentified (e.g. several illustrations in chapters 2–5). There are instances where structures are discussed in detail in the text (e.g. middle cardiac vein, p. 63) but are nowhere illustrated. Finally, there are structures illustrated which in no way correspond to the text description (e.g. Mm. quadratus femoris, ischiofemoralis, biceps femoris and some instances of M. gracilis); in other instances illustrations are cited as supportive of text descriptions when other, uncited, illustrations depict more clearly, if still inadequately, the described structure (e.g., M. caudofemoralis). Many illustrations appear to be a cross between diagrammatic representations and a faithful reproduction without being identified as either; Figs. 3.26 and 3.27, which depict the renal portal system, appear to be faithful reproductions, but are instead, diagrammatic. If the reader accepts these figures as an accurate representation, he could construct a completely inaccurate pattern of possibilities of blood flow within this system. The renal portal valve in Figs. 3.26 and 3.27 is oriented backwards and a vein labeled "internal iliac" in Fig. 3.25 is, in Fig. 3.27, identified as "afferent renal"; Akester (J. Anat., 98:865–876, 1964) identifies this vein as the caudal renal portal.

The section on arthrology contains inconsistencies in identification of the "types" of joints described; compare the classification of the humeroscapulo-coracoid, coxofemoral, and costosternal articulations. The vertebral intercentral articulation (rightfully limited to the cervical vertebrae) is classed as an amphiarthrosis (p. 39) despite the stated presence of a joint capsule composed of "fibrous and synovial layers" (pp. 39–40). Further, to refer to the action at these intercentral articulations as "hinge and gliding," while possibly descriptive, is to me an improper and misleading use of terms which have a more precise and restricted arthrological application. Also questionable is the statement that the nasofrontal articulation produces a "gliding movement." The generally accepted action at this articulation is that of a "hinge" (Fisher, H. I., Wilson Bull. 67: 175–188, 1955; Bock, W. J., J. Morphol. 114:1–42, 1964).

Perhaps the most disconcerting aspect of this work arises from the nomenclature employed by the author. The problem of anatomical nomenclature is not new and nowhere is it more acute than in avian anatomy. Unfortunately, while birds are vertebrates, and thus conform to a basic vertebrate body plan in which many structures are unquestionably homologous, the question of homology is in no way firmly established between many similar structures of birds and mammals. Birds are not mammals, they have not evolved from mammals, and the only relationship they have to mammals is that both had a reptile-like ancestor. They have evolved independently for more than 150 million years. To expect that the morphology of two such divergent organisms would be amenable to an identical system of nomenclature universally denies the unique character of birds. Yet, repeatedly the author—unintentionally, I am sure—does so, and I felt that this was an anatomical treatise on that most aberrant of creatures, "The Feathered Mammal." In those instances where there was no possibility of equivalence of terminology, the author, as did Chamberlain whose work (1943, Mich. State Coll. Agr. Exp. Sta.) served as Fitzgerald's authority for nomenclature of avian limb musculature, ignored completely the body of literature on avian morphology which has established a *de facto* even if not a *de jure* nomenclature. The resultant effect is one that can only lead to utter confusion for those who unwittingly accept most of the terminology in this text as authoritative and thus follow it in their publications, or who attempt to compare information presented here with that available on other avian species. In many cases they will find that they do not speak the same language. It is my opinion that this text provides the strongest argument available for formulation and promulgation, at the earliest possible time, of a Nomina Anatomica Avium. The following selected examples illustrate this viewpoint.

One may find some argument for the use of the term "stifle joint" to designate the femori-tibiotarsal (= knee) joint of birds; one could for sake of convenience overlook the term "Ossa faciei" (misspelled in the text as "Ossa facici") though the presence of a "face" is questionable in birds. Perhaps one might accept use of the term "diaphragm" so long as it were pointed out that this term implies something less in function and structure than a similarly named structure in mammals. However, completely unacceptable to me is the term "hock" to refer to the tibiotarsal-metatarsal joint in birds. While the hock of mammals and its analogue in birds are both "inter-tarsal" joints, structurally, here the comparison ends. Similarly, it does not seem accurate to employ terms such as "jejeunum," "ileum," and especially "descending colon," nor to use mammalian names for vessels supplying structures of the avian intestinal tract. Disturbing also are osteological references such as "lumbosacral bone" for the synsacrum; the author does give "synsacrum" as a synonym but he uses the term "lumbosacral bone." Also undesirable is use of the term "urostyle" for "pygostyle" even if used interchangeably as was done in the text.

There is a wealth of literature on avian anatomy to which one can refer for "names." While admittedly there are two sets of myological terminologies extant, (Hudson, Amer. Midl. Nat. 18:1–108, 1937 and Fisher, Amer. Midl. Nat. 35:545–727, 1946), most American workers select one and include a synonymy with the other in their work. These terminologies have been established over a long period of time as the result of the classical works of Gadow, Fürbringer, Garrod, Shufeldt, Forbes, and more recently, Hudson et al., Fisher, Berger, Bock, etc. Fitzgerald, however, chose as a basis for his muscle names, the work of Chamberlain (op. cit.) without either researching works on avian-mammalian homologies or investigating the question himself. Far preferable, it would seem to me, would have been a short comment indicating familiarity with the body of literature on avian terminologies, including citations, and a short statement of reasons for rejecting these studies. In this manner, the reader would then have been forewarned that major variations in nomenclature exist which require "translation" or reference back to the "classics." As it stands, however, the resultant confusion to the researcher because of the terminological differences suggests that extreme caution should be exercised in accepting the data on the myology. A few examples of the problems which can arise because of these terminological differences are cited below.

There are serious inconsistencies and inaccuracies in descriptions, terminology, and illustration of a large number of the muscles in the hind limb. The muscles identified by Fitzgerald as Mm. biceps femoris, semimembranosus, and semitendinosus are not the same muscles given these names in the ornithological literature. M. semitendinosus of Fitzgerald is M. biceps femoris of Hudson, M. semimembranosus is M. semitendinosus of Hudson and M. gracilis of Fitzgerald is M. semimembranosus of Hudson. The muscle identified as M. biceps femoris by Fitzgerald is *apparently* the caudal portion of M. tensor fascia lata although Fig. 4.10 is the only place it is illustrated; in all other illustrations the muscle is simply referred to as M. tensor fascia lata. Equal confusion results in the identification of other muscles (e.g. M. quadratus femoris, compare description on p. 158 with illustration on Fig. 4.21). M. quadratus femoris is supposedly

M. ischiofemoralis of Hudson but it appears more probable that it is, in reality, pars iliofemoralis of M. piriformis. I cannot overlook the fact that Fitzgerald uses the name "M. pectineus" for "M. ambiens"; this muscle has long been recognized to be without *any* apparent homologue in mammals.

The digital flexor muscles of the hind limb of the bird are unique in their arrangement and differ from those of the mammal. It is thus a gross oversimplification to simply arrange these muscles into a group of superficial and a group of deep digital flexors. Neither is there any justification for departing from the *universally* accepted nomenclature for the five major digital flexors by introducing completely new names for them. Finally, virtually no attention is paid to the frequently functionally important tarsometatarsal muscles. The names given to, and the general descriptions provided for, the few such muscles described are insufficient to be of any value at all.

Undoubtedly there is information of value in the text, but it is obvious that if other sections are as disturbing as those reviewed in detail, a great deal of care must be used in relying on this book as an authoritative reference. *Perhaps*, in company with a broad knowledge of the literature of avian anatomy, the text can be useful. It might serve as a possible point of departure for the most general information on the anatomy of the Common Coturnix; but it is neither an accurate or a reliable compendium for use by an investigator. The text is the only one available on the Coturnix, and for that reason one might wish to purchase it. I suggest extreme caution in reliance upon it as an authoritative text.—ROBERT D. KLEMM.

A FIELD GUIDE TO AUSTRALIAN BIRDS. NON-PASSERINES. By Peter Slater and others. Livingston Publishing Co., Wynnewood, Pennsylvania, 1970: 5¼ × 7½ in., xxxii + 428 pp., 43 col. and 21 bl. and wh. pls., 47 figs. $10.00.

Although the name of Peter Slater figures prominently on the first page of this book, he is responsible only for the illustrations and for the text for one order, the Falconiformes. The text for the remaining 18 orders has been written by seven bird experts, six of whom are professional ornithologists employed by the Wildlife Section of the Commonwealth Scientific and Industrial Research Organization (CSIRO).

This book, which is the first of a two part issue, is designed to help in identifying any non-passerine bird that may occur in the Australian region. It contains a visual index for quick identification, a so-called check list, and a section of 131 pages which includes the plates, on which are shown every non-passerine found within the stipulated area, together with the name and the key markings of each species. The second section of 282 pages contains the notes on each species and distribution maps, with appropriate cross references to the illustrations in the first section. The final pages contain indexes of common and scientific names.

This is one of the most comprehensive field guides ever to be prepared on Australian avifauna. It incorporates most of the features that have appeared in other modern guides, and with such a galaxy of talent the text should be nearly perfect. In general, the typesetting and printing are good, but some letters are faint or even missing, and the black and white illustration of the Giant Petrel on Plate 3 is badly spotted.

The colored plates are somewhat garish, possibly owing to heavy inking in the printing. The Gang-gang Cockatoos on Plate 53 are almost as black as the black cockatoos. Although printing on blue paper outlines the white parts of the plumages, it is not conducive to clarity. It is stated that the "illustrations are intended to be an aid to identification, not works of art," and this aim has been achieved, helped by the large size of the image of each bird depicted.

Some of the plates, however, can be misleading. On Plate 2, the albatross heads, while not being drawn to scale, show variation in size. The bill of the Wandering Albatross is almost 20 per cent larger instead of being that much smaller than that of the Royal Albatross; the Sooty Albatross and the Light-mantled Albatross are similar to the other species instead of being much smaller. The identification key on Figures 15 and 16 shows the opposite sizes to the plates and gives the correct comparison of these species.

The only other group that I checked was the genus *Pachyptila*, which is identified almost solely by the size and shape of the bills. On figure 21 there are two drawings of the bill of the Dove Prion, and although the range of width of the bill of this species is said (p. 165) to be 11 to 14 mm., the drawings are 14 and 19 mm.

The paintings of the Cattle Egret in breeding plumage on Plates 13 to 15 show considerable variation in the same plumage state. The adult Swamp Harrier, on Plate 22, does not show the white patch on the rump, which is diagnostic; this field mark is not even mentioned in the accompanying key although it is referred to in the text on page 250. The black and white drawing of the Malleefowl on Plate 28 is described as "upperparts attractively patterned," with no mention of color. On Plate 59, the title is given as Horsfield Brown Cuckoo, which is corrected on page 384 to Horsfield Bronze Cuckoo.

This book clearly reflects the chaotic state of the nomenclature of Australian birds, due to the lack of an accepted check-list. From the taxonomy used, including vernaculars, it would appear that the ornithologists within the CSIRO Wildlife Section do not accept the "CSIRO Index of Bird Names" which was prepared by one of their members. It is stated that the "text is arranged in systematic order, following the CSIRO Index—we have taken the liberty of departing from the order in a few places." The first liberty taken is to alter the sequence of one of the orders. The order of grebes—Podicipediformes—was placed in the Index *after* Procellariiformes and Pelecaniformes. Instead of now placing it *before* these two orders, to follow modern taxonomy, in the book it is placed *between* them. Many liberties have been taken in switching the sequence in which genera and species were placed. Even the sequence of families has been changed, and in one instance a new family, Arenariidae, has been introduced.

It is at the species level, however, that most changes have taken place. The Oriental Dotterel, *Charadrius veredus*, becomes a subspecies of Caspian Plover, *C. asiaticus veredus*; the Spur-winged Plover, *Vanellus novaehollandiae*, is lumped with the Masked Plover, *V. miles novaehollandiae*; the White-tailed Black Cockatoo, *Calyptorhynchus baudini*, becomes Yellow-tailed Black Cockatoo, *C. funereus baudinii*; the Red-sided Parrot, *Eclectus pectoralis*, is changed to Eclectus Parrot, *E. roratus*; the Cattle Egret, *Bubulcus ibis*, becomes *Ardeola ibis*; the Golden Bronze Cuckoo, *Chrysococcyx plagosus*, is made a subspecies of Shining Bronze Cuckoo, *C. lucidus plagosus*, and there are many other changes. Each author has acted as his own taxonomist.

The vernacular names have been altered to an even greater extent. This particularly applies to the Psittaciformes, Falconiformes, and Procellariiformes. No alternative names are shown, and the only clue to other works is through the scientific names, many of which are altered. This book is stated to be for beginners as well as for serious students, and it is essential that they be able to refer to other works on birds. This particularly applies to the current record-selling book, "What Bird is That," which has been on the market since 1931, and brought up to date with each edition.

This guide could become a popular book on Australian birds. Unfortunately, the number of pages in the two parts, some 800–900, will make it very bulky for a field guide.—Roy P. Cooper.

EVOLUTION OF DIVING ADAPTATIONS IN THE STIFFTAIL DUCKS. By Robert J. Raikow. University of California Publications in Zoology, vol. 94, Berkeley, 1970: 10¼ × 6¾ in., vi + 52 pp., 32 figs., 16 tables. $2.50.

This study is mainly a functional-anatomical comparison of the tails and hind limbs of four species of duck. Three of these—the Black-headed Duck, Ruddy Duck, and Musk Duck—belong to the stifftail tribe, Oxyurini. The fourth species, the Mallard, is used as a representative of the ancestral surface feeding stock from which the Oxyurini presumably evolved. These species (each representing a different genus) were selected because of their availability and supposed approximation to an evolutionary sequence in which increasing efficiency in underwater swimming is achieved at the expense of terrestrial locomotion.

After an introduction and a materials and methods section, four pages are devoted to a summary of locomotor habits. Unfortunately almost all of this information seems to have been taken from the literature and is lacking in details and preciseness.

The next section compares the tails of the four species. Tail vertebrae counts and measurements are given and the tail muscles are described. For both the tail skeleton and its muscles, ratios are used for interspecific comparisons (different tail lengths are expressed as a per cent of "trunk length" while the separate muscle weights are expressed as a per cent of total caudal muscle weight).

In the section on the hind limb, the approach is similar to that employed for the tail. Relative proportions of the pelves and hind limbs are presented. Interesting differences in the knee joints are noted. Finally the hind limb muscles are described and their mechanical advantages and relative weights used in functional comparisons.

The data collected are employed to formulate both systematic and functional conclusions. The new anatomical evidence substantiates the earlier presumption that the three stifftails represent an evolutionary sequence. At the beginning of this sequence, the Black-headed Duck serves as a connecting link between the surface feeders and the more advanced stifftails. Raikow summarizes the functional modifications in the sequence as follows: "Various modifications of the osteology and myology of the hind limb and tail have occurred which improve the efficiency of an adducted leg posture in diving, and the use of the tail as an underwater rudder. These include lengthening of the tail and enlargement of the caudal levator muscles, narrowing of the pelvis and elongation of the postacetabular portion, enlargement of the area of origin of leg muscles from the knee area, reduction of the size of thigh muscles and increase in shank muscles correlated with the change from walking to swimming. Changes in the line of action of certain thigh muscles improve their effectiveness as fixators of the thigh during diving. An increase in the mechanical advantage of many muscles may be associated with the need for strength of action rather than speed, in swimming as compared to walking."

Raikow's approach is traditional and follows the general philosophy and techniques pioneered in avian anatomy by Alden Miller (1937) in his study of the Hawaiian Goose. Recently some of these techniques have been seriously questioned. Walter Bock has been particularily vigorous in exposing errors. For instance, muscle weights, volumes or ratios derived therefrom are not necessarily accurate indices of the force producing capabilities of muscles. Rather other parameters, particularly those involving fiber length and arrangement, must be considered. Likewise, the use of mechanical advantages to differentiate between muscles which generate force at the expense of speed versus muscles which produce speed at the expense of force is probably incorrect. Rather, Bock advocates the use of "free-body diagrams" (1968). Raikow's functional interpretations unfortunately place heavy reliance on both the mechanical advantages and relative weights of muscles.

If Walter Bock's recommendations are followed, many of the widely accepted "ground rules" of avian functional anatomy will have to be modified. Regrettably, there is still no study of a scope comparable to Raikow's which attempts to incorporate the new theoretical aspects of functional anatomy into an operational framework. Hopefully such a study will appear in the near future.

As it stands, Raikow's study contains a wealth of interesting information. His efforts should be commended even if his functional conclusions must be viewed with some skepticism.—LOWELL SPRING.

PORTRAITS OF TROPICAL BIRDS. By John S. Dunning. Livingston Publ. Co., Wynnewood, Penna., 1970: 8¾ × 11¼ in., xx + 153 pp., 72 color pls., $20.00.

Beautiful color photographs of 72 species of the most striking neotropical birds dominate this book. The photographer-author has commented on each species and family in a single short paragraph, usually to identify the habitat and something of the bird's behavior. It is a handsome book and will stimulate enthusiasm for tropical birds in most readers.

Dunning describes how he captured wild birds in nets and even includes plans for constructing the portable enclosure in which he photographed them in the field with electronic flash. The enclosure is supplied with vegetation and perches appropriate to the bird's habitat, the bird is introduced to the cage, photographed in what appears to be a natural setting, and then released. One-third of the plates are of tanagers, and an eighth are of antbirds; the remaining plates illustrate representatives of 21 other families. Even the colors of unfeathered areas are sometimes striking; e.g., eleven species have vivid red eyes!—STEPHEN M. RUSSELL.

THE PINE BARRENS. A PRELIMINARY ECOLOGICAL INVENTORY. By Jack McCormick. Research Report No. 2, New Jersey State Museum, Trenton, New Jersey, 1970: 6 × 9 in., 103 pp., 9 maps, one table, 23 halftones. $2.75.

The New Jersey Pine Barrens constitute the most extensive (approximately 2000 square miles) wildland tract on the Atlantic seaboard. Although close to the densely populated metropolitan areas of Philadelphia and Camden, it is sparsely settled and has no major industries. Due to its infertile and droughty soil, it is, with the exception of its blueberry and cranberry culture, unattractive to agriculture. Mostly forested, it is interlaced with slow meandering streams and spotted with bogs. Its geological history is complex, but its most interesting feature is its flora, which has, in addition to common plants, a considerable number of rare ones. The Barrens are the northern limit of many southern species and the southern limit of some northern ones. Twenty-four species of plants, including two found only here, have been originally described from the Pine Barrens. Bird life here is relatively poor compared with other areas in the state.

The New Jersey Audubon Society, the Pine Barrens Conservationists, and other citizens' groups became concerned about threats to the preservation of the Pine Barrens. They enlisted the cooperation of the National Park Service in an endeavor to have the Barrens designated a National Landmark, thereby putting a brake on the threats of real estate developments, possible expansion of the blueberry and cranberry growing, and the establishment of a jet airport which would gobble up 51 square miles at one fell swoop.

The National Park Service made a grant to the Academy of Natural Sciences of Philadelphia for a study of the natural resources of the area. Jack McCormick of the Academy staff made the survey, and his report, entitled "A Study of the Significance of the Pine Barrens of New Jersey" was issued in January, 1968. The present publication is a summary of that report.

It concisely summarizes the past industrial background of the region, and lists its plants and animals. Two areas in the region which have varied habitats are studied in considerable detail. The value of the area, not only for the preservation of its native wildlife, open space conservation, recreation, hunting and fishing, and water supply, but also as a scientific laboratory for the study of its unique ecosystem is stressed. The Pine Barrens have generated much scientific debate, and this work points out that there is much yet to be learned. It is refreshing to have the challenges to our understanding so well delineated. An excellent bibliography will help all who wish to learn more about this fascinating region.—ERNEST A. CHOATE.

PUBLICATION NOTES AND NOTICES

CHECK-LIST OF BIRDS OF THE WORLD. Volume XIII. By Raymond A. Paynter, Jr. and Robert W. Storer. Museum of Comparative Zoology, Harvard University, Cambridge, Mass., 1970: 6½ × 9¼ in., xiv + 443 pp. $15.00.

This volume treats the buntings and American sparrows, Plush-capped Finch, cardinal-grosbeaks, tanagers, and the Swallow-Tanager, all united under the family Emberizidae. These birds have been separated from the carduelines and *Fringilla* by the wood warblers, Hawaiian honeycreepers, vireos, and icterids (already treated in Check-list, Vol. 14). Of the fifteen volumes in this indispensable series, volumes 8 and 11 remain to be published.—P. S.

This issue of *The Wilson Bulletin* was published on 29 March 1972

SUGGESTIONS TO AUTHORS

Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, with at least one inch margins, and on one side only of good quality white paper. Tables should be typed on separate sheets, and should be designed to fit the normal page width, i.e., narrow and deep rather than wide and shallow. Before preparing these, carefully consider whether the material is best presented in tabular form. 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.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107. He will notify the printer.

The permanent mailing address of the Wilson Ornithological Society is: c/o The MUSEUM of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

PLAN TO ATTEND THE 1972 ANNUAL MEETING

The 1972 meeting of the Wilson Ornithological Society will be at Cape May, New Jersey from Thursday, 15 June to Sunday, 18 June 1972. The meeting is being sponsored jointly by the Academy of Natural Sciences of Philadelphia, the Delaware Valley Ornithological Club, the New Jersey Audubon Society and the Urner Ornithological Club of New Jersey. The chairman of the local committee for arrangements is Dr. Ernest A. Choate, Cape May Point, New Jersey 08212. Information concerning accommodations, transportation, and a call for papers will be sent to all members with advance registration forms. Cape May, being a summer resort, has a large number and variety of restaurants and lodging accommodations. Headquarters will be at the Colonial Hotel and Motor Lodge, Central Beach Front, Cape May.

The Cape May region has been a center of ornithological interest since the time of Alexander Wilson and John James Audubon. The list of birds recorded here began with them and is still growing. The last new bird was a Skua sighted about five miles off shore on 16 June 1969 bringing Cape May's cumulative list up to 354. A special feature of the area is the Stone Harbor Heronry, one of the largest breeding colonies in the United States of Common, Snowy, and Cattle Egrets, Louisiana, Little Blue, Black-crowned Night, and Yellow-crowned Night Herons as well as thousands of Glossy Ibis. The largest breeding colony of Laughing Gulls on the continent is on a nearby salt marsh. Close by on the sand flats breed Black Skimmers, Common and Least Terns interspersed with an occasional Gull-billed Tern. Off shore the sight of a Sooty Shearwater, Cory's Shearwater, Wilson's Petrel, or a jaeger is a possibility. A walk in the woods may turn up a Black and White Warbler, Redstart, Kentucky, Prothonotory, or Hooded Warbler. Near the Cape May Point Lighthouse the notes of the Chuck-wills-widow and the Whip-poor-will are occasionally accompanied by the call of a rail and the hoot of the Great Horned Owl.

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The Wilson Ornithological Society

Founded December 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

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The Josselyn Van Tyne Memorial Library

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University 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

STUDIES OF THE BROWN PELICAN

RALPH W. SCHREIBER AND ROBERT W. RISEBROUGH

I. STATUS OF BROWN PELICAN POPULATIONS IN THE UNITED STATES.

THE American Ornithologists' Union Check-list of North American Birds (1957: 29) records the following distribution for *Pelecanus occidentalis*, the Brown Pelican:

> "From southern British Columbia south along the Pacific coast to Chiloe Island, southern Chile, casually to Tierra del Fuego, including the Pearl Islands, in the Gulf of Panama, and the Galapagos Islands, and from North Carolina and the Gulf coast of the United States southward through the West Indies including the Netherlands West Indies, to British Guiana, casually to extreme northern Brasil."

Since the mid-1950's the Brown Pelican population has declined in much of its northern range. In Louisiana no pelicans bred between 1961 and 1970; in 1971 several semi-captive birds introduced from Florida to Grand Terre Island, Louisiana nested there successfully (Evenden, 1968, 1969; Joanen and Neal, 1971). In Texas the breeding population is reduced to a few pairs (H. Hildebrand, in litt.); in California and northwestern Baja California, Mexico, a sizable population persists but breeding has been largely unsuccessful since 1968 (Schreiber and DeLong, 1969; Jehl, 1969; Gress, 1970; Risebrough, Sibley, and Kirven, 1971).

This paper briefly discusses the past and present status of the Brown Pelican in the United States. It must be emphasized that there are few data concerning the status of the species throughout the country at any time in this century. Documentation of population declines is therefore difficult. The available information, however, provides a useful background for interpretation of the present status of the species and for formulation of a conservation policy.

There is now considerable evidence linking reproductive failures of fish-eating birds to chemical pollutants in the environment. As yet no monitoring programs have been devised to measure the rates of accumulation of the known persistent pollutants in coastal waters, or to determine whether steady state concentrations have been established, with input from all sources balanced by degradation and deposition in sediments. Continued accumulation would clearly pose a threat to the remaining populations of Brown Pelicans; moreover, the long term effects of current levels of pollution are unknown.

NORTH CAROLINA

In North Carolina the first nesting record of Brown Pelicans was in 1929, when Birsch found 14 pairs breeding on Royal Shoal (Wray and Davis, 1959). Wind and tide destroyed the shoal the next year and North Carolina nesting was not reported again until 1947 when Wolff found 30 nests and 33 young on Shell Castle Island, Ocracoke Inlet (Wray and Davis, op. cit.). This is the northernmost breeding record for the Brown Pelican on the East coast. The maximum number of young recorded at Shell Castle Island was in 1959, when H. T. Davis banded 116 nestlings. Between 1960 and 1967 the number of young banded fluctuated between 11 in 1966 and 100 in 1965 (Davis, pers. comm.). No detailed observations were made in 1968 and 1969, but R. H. Steiner visited the island in July 1970 and counted 31 nestlings and 9 nests with eggs (Steiner, in litt.). No young remained on the island on 19 August and fewer than 30 young may have fledged in 1970 (Steiner, in litt.).

SOUTH CAROLINA

In South Carolina, there are few data and those available are in need of close scrutiny. Apparently, three colonies have existed in recent years. In the 1940's, a small colony was present on Egg Bank, Beaufort County (Mason, 1945); the other colonies are in the Cape Romain National Wildlife Refuge and on Deveaux Bank south of Charleston.

At the Cape Romain National Wildlife Refuge information on Brown Pelicans has varied with the assigned priorities and individual interests of refuge managers. The available data are therefore not sufficient to determine population trends. Mr. Travis McDanial, Refuge Manager at Cape Romain NWR from 1968 through 1970, has kindly provided us with the following information: since the establishment of the refuge in 1932 the pelican colony has been on at least five different islands, including Bird Bank, Bulls Bay, noted as an egg collection site in Anderson and Hickey (1970: 26). Exact numbers are not available, but distinct yearly fluctuations in productivity are indicated. In 1949 to 1953, 500 to 900 young fledged each year. In 1954–56 only 250 to 500 young fledged per year. In 1957–60 the breeding population increased and from 1,200 to 1,500 young fledged each year. The estimated population remained stable in 1961 but productivity was higher and 1,800 young fledged. In 1962 the population declined and only 500 young fledged that year and in 1963. In 1964, 800 young fledged; production reached its highest level on record in 1965 when 2,000 young fledged. Approximately 500 young fledged in 1966 and 1967.

Accurate records are available for 1968–70. McDanial estimated that 500 young fledged in 1968. In April 1969 he counted 1,016 nests. After periodic visits to the colony through the summer he estimated that 900 young fledged.

In May 1970, McDanial counted 627 nests and estimated that 500 to 600 young fledged (McDanial, pers. comm.). Although total production was lower in 1970 than in 1969, it is essentially the same as that reported for 1962–1964 and 1966–1968. Since historical population fluctuations are apparent at Cape Romain, it would seem worthwhile documenting future population trends in detail.

On the Deveaux Bank, T. A. Beckett III believes that the breeding population has undergone an apparent 90 per cent decline in the last decade. Beckett (1966: 94) reported 5,000 breeding pairs in unspecified "former years" and in the early 1960's 7,000 to 10,000 young fledged per year (1966: 99). In 1964 Beckett (op. cit.) noted high nestling mortality and in 1965 estimated only 600 breeding pairs. In 1970 Beckett counted 485 nests (in litt.). The reasons for the decline are not documented but Beckett notes (pers. comm.) that almost three-fourths of the Deveaux Bank has washed away in the last 10 years.

GEORGIA

Although in 1898 T. D. Perry collected pelican eggs "on beach" in Chatham Co., Georgia, Burleigh (1958) states that Brown Pelicans are not known to have nested in the state. Explanation of this apparent discrepancy at this time is impossible.

GULF STATES

In 1918 T. Gilbert Pearson (1918) estimated the adult pelican population between Corpus Christi, Texas and Key West, Florida as 65,000 birds. This same region in 1971 has fewer than 5,500 nests and probably not more than 12,000 birds (Hildebrand, in litt.; Joanen and Neal, 1971; Fogarty, in litt.).

In Alabama, Imhoff (1962) noted that Brown Pelicans possibly bred prior to 1900 but none have done so there since. He listed the species as "abundant throughout the year" but notes that in 1956–57 the local non-breeding population declined sharply. No recovery has occurred to date (Imhoff, pers. comm.).

LOUISIANA

The state bird of Louisiana is the Brown Pelican, yet no wild birds have bred there since 1961. Bailey and Wright (1931) indicate that thousands of birds nested on the mud lump islands at the mouth of the Mississippi River and in 1918 Bailey (in Bailey and Wright, op. cit.) estimated 1,200 pairs nesting on Grand Gosier Island. Oberholser (1938) listed Brown Pelicans as an abundant permanent resident in Louisiana, and during a survey of the coast in June 1933 estimated at least 5,500 nests with young and a population of at least 14,000 adults. He found no breeding on Grand Gosier Island in 1933

(p. 35). McIlhenny (1943) did not mention Brown Pelicans in a paper on major changes in the bird life of southern Louisiana. Lowery (1960) makes no mention of a decrease in numbers of pelicans in the state and notes that he "once" found approximately 5,000 adults with eggs and young on East Timbalier Island (p. 113), where Oberholser found none in 1933. These shifts of breeding locations exemplify the problems encountered in documenting an historical account of pelican nesting populations.

Brown Pelicans were not mentioned in the nesting season reports from the Central Southern Region of *Audubon Field Notes* between 1950 and 1955. However, in 1956 several observers noted large numbers of dead adults washed up on beaches and Imhoff believed a severe mid-June storm may have caused high mortality among young birds in the large colony on North Island of the Chandeleurs (Newman, 1956). On 27 June 1957, Hurricane Audrey had disastrous effects on many nesting species of birds in Louisiana, but no mention was made of Brown Pelicans (Newman, 1957). In 1957–1958 wintering Brown Pelicans were "alarmingly" scarce along the entire northern Gulf, and were entirely absent in many areas (Newman, 1958*a*). On 7 July 1958 "thousands" of adults and young of all ages were present on North Island (Newman, 1958*b*). Again, few birds were seen during the fall and winter, and the first speculation as to what happened to the species appeared in *Audubon Field Notes* (Newman, 1959*a*, 1959*b*). Between 1956 and 1960 the total coastal Christmas Bird Count estimates of Brown Pelicans decreased from 995 to 366, to 41, to 14, to four individuals. On North Island in 1960 only about 200 pairs were reported nesting (Imhoff, 1960). On 21 June 1961, van Tets (1965: in litt.) observed ca. 200 pairs and 100 chicks with white down and developing primaries on North Island. In June 1962 no nests were present on the island and during a survey of the area only six adults were observed (Stewart, 1962).

A propagation program was begun in the state in 1968 and over 170 nestlings were imported from Florida during 1968, 1969, and 1970. In March 1971 some of the 1968 imports nested on a shell island in Barataria Bay near Grand Terre (Joanen and Neal, 1971). Few wild pelicans occur elsewhere in Louisiana or the northern Gulf region.

TEXAS

In Texas fewer than ten pairs of Brown Pelicans nested in 1969 or 1970 (Hildebrand, in litt.). Pearson (1921) estimated the total Texas Brown Pelican population at approximately 5,000 birds. Little information is available about the dramatic decline in nesting, but reports in *Audubon Field Notes* for the South Texas Region between 1950 and 1963 reveal some interesting observations. "Brown Pelicans that had a somewhat-below-normal nesting season last year had a repeat this year with hundreds of adults having been killed by the freeze" of 29 January–3 February, 1951 (Goldman, 1951). In 1952 "Brown Pelicans which decreased in numbers at the time of the freeze early in 1951, had a much improved season this year" (Goldman and Watson, 1952). Between 1953 and 1959 pelicans are not mentioned, but in 1960 pelicans "made a comeback at Galveston" (Webster, 1960). This last comment apparently refers to the effects of Hurricane Audrey in June 1957, or to other unidentified factors. For 1961 and 1962 no mention appears of Brown Pelicans, but in 1963 only 18 young were produced in Texas (Webster, 1963).

In 1967 four pairs are known to have produced four young in Corpus Christi Bay and Hildebrand believes a few pairs bred in Texas each year from 1964–1966 as well (Hildebrand, in litt.). In 1968, four young fledged from two nests on Carroll Island in the Second-chain of Islands. In 1969 the only observed nesting was reported on an unnamed spoil island on Long Reef in Aransas Bay, five nests produced seven young (Hildebrand, in litt.).

In 1970 Emily Payne recorded observations on the few remaining pelicans in Texas and Hildebrand supplied the following information (in litt.): one or two birds overwintered along the coast and numbers increased in March to a peak in mid-June of 105 Brown Pelicans concentrating in Corpus Christi Bay. Only eight "subadults" were seen. Three pairs and at least ten eggs were noted on Carroll Island but the birds abandoned the site between 3 April and the end of the month. The cause of the desertion was apparently not human molestation. Several pairs nested in May on "Pelican Island" in Corpus Christi Bay (the same island used in 1969) and in early July four nests contained 9 healthy young.

The status of the Brown Pelican in eastern Mexico, the Caribbean, or Central America, past or present, is essentially unrecorded. Pelicans are reported to have nested and apparently still nest in scattered colonies in the Mexican states of Veracruz, Yucatan, and Quintana Roo; nesting also occurs in Panama, British Honduras, Colombia, Venezuela, Trinidad, Tobago, the Lesser and Greater Antilles, and the Bahamas (A.O.U., 1957; Murphy, 1936; Wetmore, 1945, 1965; Hildebrand, pers. comm.). Probably none of the colonies contain more than a few hundred pairs. The precise locations of most colonies is unknown and the ranges of the subspecies are uncertain (Palmer, 1962; Voous, 1957). The need for more information on the Brown Pelicans in these areas is obvious.

CALIFORNIA

Historic breeding records for Brown Pelicans in California were summarized by Schreiber and DeLong (1969) who noted that no nesting occurred in the state in 1968, except on Anacapa Island, where sites active in early April had been abandoned by mid-May. In the early 1900's, colonies of up to a few hundred pairs existed in at least five locations and several thousand pairs were present on Los Coronados, Baja California, Mexico, and on Anacapa Island. In 1958, large numbers were still present on Los Coronados. On Anacapa in 1964 perhaps 1,000 pairs bred successfully. In 1969 Anacapa was visited by Risebrough et al. (1971) who summarized the nesting attempts for the summer and noted that a minimum of 1,272 nests were built, more than 75 per cent received eggs, and no more than four young fledged. Gress (1970) working on Anacapa Island in 1970 found from over 500 nests constructed, only one young fledged. Schreiber and Gress (unpubl. observ.) noted aberrant nesting behavior in the Anacapa pelicans in 1970 and Risebrough et al. (in prep.) present data on shell thickness and chemical residue analyses.

The status of the Brown Pelican in the Gulf of California of western Mexico is poorly understood but the Section of Pesticide-Wildlife Ecology, Bureau of Sport Fisheries and Wildlife, Denver, Colorado is presently carrying on extensive investigations of the biology of the pelicans in the Gulf. Information on the pelicans in Peru is available but is beyond the scope of this discussion.

FLORIDA

In Florida the available historical information on the Brown Pelican status was summarized by Howell (1932). Little accurate information on the total population is available, but the species has been abundant in the state since the first bird observations were recorded. Williams and Martin (1968; 1970) present data based on aerial surveys and visits to colonies in 1968, 1969, and 1970 indicating that the Florida breeding population has remained essentially stable with 6,705, 6,133, and 7,690 nests counted in those years respectively. The conclusion by Blus (1970) that the Florida east coast population was declining based on data supplied in 1969 by Williams (pers. comm. to Blus) appears to have been premature in light of the 1970 survey by Williams and Martin (1970).

II. STUDIES OF THE BROWN PELICAN IN FLORIDA.

In summarizing the available information on the natural history of Brown Pelicans, Palmer (1962) indicates the dearth of knowledge about their biology. One of us (R.W.S.) began a detailed study of Brown Pelicans in Florida in January 1969 with efforts being concentrated in the largest colony in the state, on Tarpon Key in Boca Ciega Bay, St. Petersburg, at the mouth of Tampa Bay.

The pelicans nest on Tarpon Key from two to 25 feet above the high tide

TABLE 1

BROWN PELICAN HATCHING SUCCESS, TARPON KEY, BOCA CIEGA BAY, ST. PETERSBURG, FLORIDA, 1969 AND 1970

		1969		1970	
		Nests checked weekly	Nests checked more frequently	Nests checked weekly	Nests checked more frequently
No. Nests Observed		13	63	25	37
Eggs Laid		37	142	64	77
Eggs/Nest		2.85	2.25	2.56	2.08
Eggs Hatched	no.	31	80	45	22
	%	84	56	70	29
Eggs Destroyed	no.	3	45	8	50
	%	8	32	13	65
Eggs Addled	no.	3	17	10	2
	%	8	12	16	3
Eggs Crushed	no.	0	0	1	3
	%			2	4

line in black mangrove (*Avicennia nitida*) primarily surrounding the central lagoon of the key. The colony is subdivided into distinct areas relatively isolated from each other and one "subcolony" could be surveyed without disturbing others. In 1969 13 nests were checked weekly and 63 nests were checked more frequently, as often as thrice weekly in March, April, and May.

In 1970, over 100 nests were selected for study. However, while Schreiber was on Anacapa Island in California during the last week of April, the colony was disturbed at least once. We are unable to explain otherwise the egg loss from certain areas of the colony and thus have limited analysis to 25 nests checked weekly and 37 nests checked more frequently from 19 March till mid-August. Nest building and laying began in early March and continued through mid-May in both years and nest checks began when the first nest was found. Most nests were found and marked before egg deposition began and were checked periodically thereafter.

CLUTCH SIZE

In 1969 the 13 nests checked only weekly contained slightly larger clutches than the 63 more frequently checked nests; in 1970, the same pattern emerged (Table 1). The lowered clutch size in the nests which were more frequently checked may reflect reduced laying by disturbed birds. On 30 April 1969 Schreiber surveyed 250 nests which had never been disturbed and counted 728 eggs and/or small nestlings, or 2.91 eggs per nest. A similar survey of 193 nests on 6 May 1970 showed 537 eggs and/or small nestlings, or 2.73

eggs per nest. Three eggs per clutch was the maximum found. Bent (1922: 297) states that three or often two eggs constitute a full clutch of the Brown Pelican. He also found four or five eggs in a set but believed these were from two different females. Anderson and Hickey (1970) analyzed 236 sets in oological collections and found the mean clutch size was 2.95 eggs.

HATCHING SUCCESS

Hatching success in both years was higher in nests checked less frequently (Table 1). Total hatching success was lower in 1970 than in 1969 (Table 1). In nests checked weekly, 84 and 70 per cent of the eggs laid hatched in 1969 and 1970 respectively. In nests checked more frequently, 56 and 29 per cent of the eggs laid hatched in 1969 and 1970 respectively.

Causes for failure to hatch were assigned to three categories: 1) "addled"—eggs remaining in nests after other eggs of the clutch had hatched. These either were infertile or contained a dead embryo. In 1969, 20 of 179 eggs laid (11 per cent) were addled; in 1970, 12 of 141 eggs laid (9 per cent) were found addled. 2) "destroyed"—eggs noted as laid but missing on subsequent nest checks. Some of these eggs were found broken below nests; others just disappeared between visits. In both years the more frequently disturbed nests suffered distinctly higher egg loss and many more eggs were destroyed in 1970 than in 1969 (Table 1). 3) "crushed"—eggs obviously thin shelled and crushed in the nest. In 1969, no crushed eggs were found among the 179 eggs laid in marked nests. During 1970, 4 (3 per cent) of 141 eggs laid in marked nests were crushed.

In both 1969 and 1970 the two major known causes of "destroyed" eggs were egg breakage by flushing adult pelicans and egg breakage by predators. Pelicans incubate with their totipalmate feet surrounding the clutch. When its flight distance is "trespassed" by a human intruder an incubating adult will flush and the force exerted to become airborne is often sufficient to break the egg shell. To avoid this cause of egg destruction, nesting pelicans must be approached slowly and in full view so they can step off the eggs before flying.

Fish Crow (*Corvus ossifragus*) predation was the most serious known cause of egg loss. When undisturbed, one partner of a pair of pelicans remains on the nest throughout incubation, and crows do not molest the nest. However, when disturbed, pelicans leave their nests and either circle overhead or land on the water nearby. During March, April, and May, as many as 50 Fish Crows spend the daylight hours on Tarpon Key. Frequently within seconds after pelicans were disturbed, crows would land on nests, peck holes in the eggs, and eat the contents.

Because of the high level of mortality in pelican colonies accompanying

TABLE 2

BROWN PELICAN EGGSHELL THICKNESS FROM FLORIDA IN 1969 AND 1970

Colony	Date	No.	Mean thickness ± 95% confidence limit range	Per cent change*
Tarpon Key Boca Ciega Bay St. Petersburg	1969	14	0.506 ± 0.022 (0.55–0.42)	9
	1970	21	0.509 ± 0.024 (0.58–0.39)	9
Hemp Key Charlotte Harbor	1970	20	0.518 ± 0.024 (0.61–0.43)	7
Hall Island Cocoa Beach	1970	22	0.501 ± 0.013 (0.56–0.46)	10
Rio Del Mar Vero Beach	1970	10	0.502 ± 0.018 (0.53–0.46)	10
All Florida		87	0.508 ± 0.009 (0.61–0.39)	9

* Pre-1943 Florida eggs: 0.557 ± 0.004 mm, n = 172 (Anderson and Hickey, 1970).

human visitation from accidental breakage of eggs, predation on eggs and young by other birds, temperature stress on eggs and naked nestlings (Bartholomew and Dawson, 1954; Schreiber, unpubl. observ.), and possible disruption of adult nesting behavior, we strongly recommend that human visits to pelican colonies be curtailed.

EGGSHELL THICKNESS AND CHEMICAL RESIDUE ANALYSES

In 1969 and 1970, R. W. S. collected eggs from four colonies in Florida for chlorinated hydrocarbon residue analyses. From Tarpon Key in 1969, 17 eggs were collected: one egg each from 11 three-egg clutches in April and May, one three-egg clutch on 15 April, and one three-egg clutch on 31 May. In 1970, 20 eggs from this colony were collected: one egg each from 20 three-egg clutches, two on 30 March, 16 on 5 April, and 2 on 19 April. Fifty-three eggs were collected from other colonies in 1970: ten from the Rio Mar Island colony in Vero Beach on 27 March; twenty from Hemp Key, Charlotte Harbor on 16 April; and two from the Fort Pierce colony and 18 from the Cocoa Beach Colony on 21 April. All these eggs were one of three in a clutch and almost all were fresh or in early stages of incubation.

To prevent contamination, eggs were wrapped with aluminum foil in the

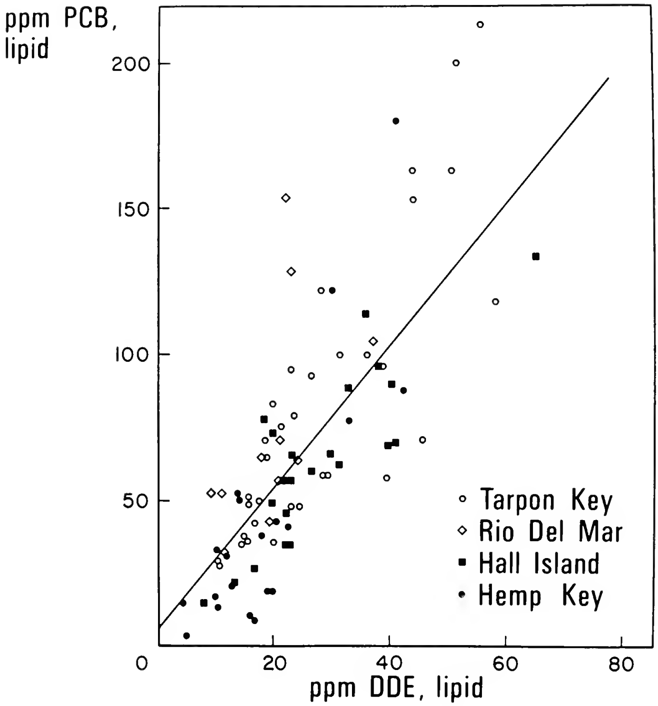

Fig. 1. Relationship between concentration of DDE and PCB in eggs of Florida Brown Pelicans obtained in 1969 and 1970 ($r = 0.701$, $p < 0.01$).

field and frozen within six hours after collection. Eggs remained frozen during air shipment to the Laboratory of the Institute of Marine Resources, University of California, Berkeley. The analytical techniques employed for measuring chlorinated hydrocarbons, including the polychlorinated biphenyls, have been described by Risebrough, Florant, and Berger (1970) and Risebrough (in press). Eggshells were measured by D. W. Anderson as described in Anderson and Hickey (1970).

Eggshell thickness.—No statistical differences were apparent between the thickness means for four colonies (Table 2). The 87 eggs collected in Florida in 1969 and 1970 averaged 9 per cent thinner than 172 eggs collected prior to 1943 (Anderson and Hickey, 1970). It must be pointed out that the thickness data presented for 1970 from the Tarpon Key colony, and undoubtedly from all colonies as well, represent a maximum thickness for the colony. Eggs were collected from three-egg clutches, which evidently had not lost eggs due to shell collapse. There is therefore a greater probability that one- and two-egg clutches, which were not sampled, have lost eggs due to excessive thinning.

TABLE 3

DDT COMPOUNDS AND POLYCHLORINATED BIPHENYLS IN BROWN PELICAN EGGS, FLORIDA 1969 AND 1970.

Concentrations in ppm of the yolk lipid and wet weight contents. Mean values with 95% confidence limits.

	Tarpon Key Boca Ciega Bay St. Petersburg		Hemp Key Charlotte Hbr.	Hall Island Cocoa Beach	Rio Del Mar Vero Beach	All Florida
	1969	1970	1970	1970	1970	
Number of eggs	14	21	20	22	10	87
p,p′-DDE lipid	37.2± 21.5	26.4± 12.0	18.3± 8.6	27.8± 12.3	20.6± 14.1	26.0± 5.6
p.p′-DDD lipid	12.8± 7.4	6.6± 3.0	4.5± 2.1	2.9± 1.3	4.0± 2.9	5.9± 1.3
p,p′-DDT lipid	6.0± 3.5	3.2± 1.5	1.1± 0.5	1.4± 0.6	1.0± 0.7	2.5± 0.5
Total DDT lipid	56.0± 32.3	36.2± 16.5	23.9± 11.2	32.1± 14.2	25.7± 18.4	34.3± 7.4
wet	2.90± 0.83	1.68± 0.38	1.19± 0.35	1.45± 0.24	1.42± 0.42	1.67± 0.22
PCB lipid	120.0± 69.3	68.9± 31.4	44.6± 20.9	63.8± 28.3	77.4± 55.4	71.2± 15.3
wet	6.21± 2.62	3.69± 0.38	2.20± 1.03	2.88± 0.53	4.20± 1.34	3.61± 1.99

Remaining eggs in those clutches were more likely thinner shelled than the average. On 16 May 1970 a shell-less egg composed of only membrane and albumen was found. None of the four thin shelled and crushed eggs found in the 62 nests on the Tarpon Key colony (see Table 1) were included in this analysis. These results regarding eggshell thinning are essentially the same as described by Blus (1970).

Chlorinated Hydrocarbon Residues.—Concentrations of the DDT compounds, p,p′-DDE, p,p′-DDD (TDE), and p,p′-DDT, and of the polychlorinated biphenyls (PCB) in the 87 Florida Brown Pelican eggs are presented in Table 3. Pollutant concentrations in eggs may be expressed as parts per million (ppm) of the wet weight, including the shell; as ppm of the wet weight of the contents (consisting of the yolk, albumen, and embryo): or as ppm of the yolk lipid. In Table 3 concentrations are expressed as both ppm of the wet contents and of the yolk lipid. In order to compare wet weight concentrations among eggs which may have lost moisture it is necessary to apply correction factors (Mulhern and Reichel, 1970). As wet weight of the contents was determined by subtracting the weight of the dried shell from the weight of the fresh egg measured at the time of collection, a correction factor was not necessary.

Chlorinated hydrocarbons are associated with the lipids in the yolk rather than with albumen or shell. The lipid content of the 87 Florida Brown Pelican eggs averages 4.4 g per egg or 5.0 per cent of the wet weight contents. The percentage of lipid in eggs of the White Pelican (*Pelecanus erythrorhynchos*) and the Double-crested Cormorant (*Phalacrocorax auritus*) are on the order of 4.2 and 4.4 per cent respectively (Anderson et al., 1969) and average 6.5 per cent in the egg contents of American Kestrels (*Falco sparverius*) (Wiemeyer and Porter, 1970). Fresh eggs of the Common Murre (*Uria aalge*) from California contained 13.7 per cent lipid (Gress et al., 1971). Concentrations of chlorinated hydrocarbons expressed on a wet weight basis only might appear to be higher in eggs of species such as the Common Murre, with greater amounts of lipid than in eggs of other species with lower amounts of lipid. Concentrations in tissue such as breast muscle and brain should always be expressed as ppm of both wet weight and lipid weight.

Yolk materials laid down in ova are derived from lipids and other components of the blood. Presumably chlorinated hydrocarbons codeposited with the yolk lipid are in physiological equilibrium with the chlorinated hydrocarbons associated with the blood lipids and these in turn are in physiological equilibrium with the chlorinated hydrocarbons at sites such as the membranes of the shell gland where the egg shell is deposited. Although many different physiological and biochemical factors can be expected to modify these relationships somewhat, the model appears to represent adequately the sequence of events in the deposition of chlorinated hydrocarbons in the egg. Therefore, we prefer to relate parameters such as eggshell changes to chlorinated hydrocarbon concentrations in the yolk lipid, rather than in whole yolk, albumen, or total egg contents.

In the Florida Brown Pelican eggs, as in most environmental samples, p,p′-DDE is the most abundant of the DDT compounds. PCB, a class of compounds with varying chlorine content, is about twice as abundant as the DDT compounds (Table 3). The eggs obtained in 1969 from Tarpon Key were also analyzed for dieldrin and endrin. Mean concentrations of dieldrin in yolk lipid was 4.17 ppm with a range from 8.1 to 0.38 ppm. Mean concentrations of endrin in the yolk lipid was 0.12 ppm with a range from 0.37 to 0.02 ppm.

DDT concentrations in Florida pelican eggs, with an arithmetic mean of

34 ppm in yolk lipid, are higher than those in pelican eggs from Jamaica ($\bar{x} = 5.5$, $n = 4$), Panama ($\bar{x} = 11.7$, $n = 6$), Venezuela ($\bar{x} = 1.0$, $n = 4$) and Peru ($\bar{x} = 9.1$, $n = 5$); but are much lower than in eggs of California Brown Pelicans. The arithmetic mean of DDT concentration in the yolk lipid of 65 eggs, the majority of them thin shelled and crushed, from Anacapa Island, California, was 1,223 ppm. The excessively high residues in California eggs are believed to derive from the effluent of a DDT manufacturing plant in Los Angeles (Risebrough et al., in prep.).

PCB concentrations are also higher in Florida than in the Caribbean and lower than in the coastal waters of California (Risebrough et al., in prep.).

There is a highly significant linear correlation ($r = 0.701$, $p < 0.01$) between the concentration of PCB and concentration of DDE in the yolk lipid of the Florida eggs (Figure 1). Thus, birds with high PCB also tend to have high DDE. A similar correlation exists between PCB and DDE in California Brown Pelicans but in the west coast ecosystems DDE is more abundant than is PCB. We interpret this to mean that these compounds move in similar ways through marine food chains. The sources of DDT compounds in Florida coastal waters include aerial fallout from global sources (Tarrant and Tatton, 1968; Risebrough et al., 1968), aerial fallout from local application, and local runoff in water. The relative importance of each source has not been determined. A study of the effects upon south Florida wildlife of the "eradication program" for the mosquito *Aedes aegypti* concluded that "there was little reason to suspect immediate and widespread damage to wildlife" from the DDT spraying. Although many songbirds were analyzed for DDT residues in this study, possible accumulation in marine food webs was not considered (Lehner et al., 1967).

Since several pollutants may occur together in environmental samples, it is frequently difficult to determine which is causing an effect such as a reduction in eggshell thickness. The correlation between DDE concentration and shell thinning of the Florida Brown Pelicans is highly significant ($r = -0.579$, $p < 0.01$). However, as PCB is also highly correlated with DDE, the correlation between thickness and PCB is also significant ($r = -0.499$, $p < 0.01$). Experimental studies have shown that DDE induces shell thinning in Mallard Ducks (*Anas platyrhynchos*) (Heath et al., 1969), American Kestrels (Wiemeyer and Porter, 1970), Japanese Quail (*Coturnix coturnix*) (Stickel and Rhodes, 1970), and Ring Doves (*Streptopelia risoria*) (Peakall, 1970), but PCB does not affect shell thickness in Mallard Ducks (Heath et al., in press), Bobwhite Quail (*Colinus virginianus*), and Ring Doves (Peakall, 1971). The relative contributions of the various pollutants to shell thinning in the Brown Pelican is further discussed by Risebrough et al. (in prep.).

Very low concentrations of DDE are correlated with significant thinning of eggshells of the Brown Pelican and the relationship is linear from zero concentrations of DDE (Risebrough et al., in prep.). Physiological mechanisms proposed to explain the effect of DDE on egg shell thickness must take this into account. Our data are inconsistent with the theory that inhibition of soluble carbonic anhydrase in the shell gland is responsible for shell thinning. In all systems examined thus far, carbonic anhydrase is present in excess of physiological needs (Dvorchik et al., 1971). Inhibition of a small fraction of the soluble enzyme by low concentrations of DDE would not be expected to produce a physiological effect, whereas our observations indicate that small amounts of DDE are associated with a reduction of shell thickness.

Our data are consistent with a theory that postulates inhibition of a finite number of sites in the shell gland membrane associated with transport of calcium ions or diffusion of bicarbonate ions. The enzyme inhibited could be an ATP-ase associated with calcium transport or a membrane-bound carbonic anhydrase (Risebrough, Davis, and Anderson, 1970).

Thinning of Brown Pelican eggshells below about 0.45 mm (20 per cent reduction) usually causes them to break during incubation (Risebrough et al., in prep.). The mean reduction of 9 per cent in the Florida eggs has not yet been observed to have an effect on population stability. Moreover, there is no clear evidence to indicate that thinning of this magnitude interferes with water retention or gas exchange. It may, however, increase the probability of accidental breakage. The data in Table 1 show that a substantial number of eggs are lost during incubation. Mysterious disappearance of eggs of the Peregrine Falcon (*Falco peregrinus*) (Ratcliffe, 1970) and of American Kestrels (Porter and Wiemeyer, 1969) coincided with shell thinning in those species. In evolutionary terms, any significant deviation from normality might be considered a selective disadvantage lowering the reproductive capacity and affecting the long term population stability. In areas such as California and perhaps also Louisiana and Texas where levels of environmental pollution are higher than in Florida, effects on Brown Pelican productivity have been both rapid and dramatic. The species, however, is long-lived and exhibits deferred maturity; effects on the reproductive capacity associated with the present level of shell thinning in Florida will not be evident for many years.

SUMMARY

This paper summarizes the historical status of the Brown Pelican in the United States through 1970; presents data on the effects of human disturbance on clutch size and hatching success for a colony on Tarpon Key, St. Petersburg, Florida in 1969 and 1970; and presents data on eggshell thickness and chlorinated hydrocarbon residues, including polychlorinated biphenyls, for 87 eggs collected from four colonies in Florida in 1969 and 1970. Methods of reporting pollutant residues are reviewed and the relationship between PCB's and DDE in samples is noted. The significance of these levels of contamination and attendant eggshell thinning to the Florida Brown Pelican population is discussed.

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LITERATURE CITED

American Ornithologists' Union. 1957. Check-list of North American Birds. 5th ed. Amer. Ornithologists' Union.

Anderson, D. W., and J. J. Hickey. 1970. Oological data on egg and breeding characteristics of Brown Pelicans. Wilson Bull., 82:14–28.

Anderson, D. W., J. J. Hickey, R. W. Risebrough, D. F. Hughes, and R. E. Christensen. 1969. Significance of chlorinated hydrocarbon residues to breeding pelicans and cormorants. Canadian Field-Naturalist, 83:93–112.

Bailey, A. M., and E. G. Wright. 1931. Birds of southern Louisiana. Wilson Bull., 43: 114–142.

Bartholomew, G. A., Jr., and W. R. Dawson. 1954. Temperature regulation in young pelicans, herons, and gulls. Ecology, 35:466–472.

Beckett, T. A., III. 1966. Deveaux Bank—1964 and 1965. Chat, 30:93–100.

Bent, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U. S. Natl. Mus. Bull., 121.

Blus, L. J. 1970. Measurements of Brown Pelican eggshells from Florida and South Carolina. BioScience, 20:867–869.

Burleigh, T. D. 1958. Georgia birds. Univ. Oklahoma Press, Norman, Oklahoma.

Dvorchik, B. H., M. Istin, and T. H. Maren. 1971. Does DDT inhibit carbonic anhydrase? Science, 172:728–729.

Evenden, F. G. 1968. Report of committee on conservation, 1968. Auk, 85:669–677.

Evenden, F. G. 1969. Report of committee on conservation, 1969. Auk, 86:738–744.

Goldman, L. C. 1951. South Texas Region. Audubon Field Notes, 5:298–300.

Goldman, L. C., and F. G. Watson. 1952. South Texas Region. Audubon Field Notes, 6:289–291.

Gress, F. 1970. Reproductive status of the California Brown Pelican in 1970, with notes on breeding and natural history. California Dept. Fish and Game, Wildlife Management Admin. Report 70-6.

Gress, F., R. W. Risebrough, and F. C. Sibley. 1971. Shell thinning in eggs of Common Murres *Uria aalge* from the Farallon Islands, California. Condor, 73:368–369.

Heath, R. G., J. W. Spann, and J. F. Kreitzer. 1969. Marked DDE impairment of Mallard reproduction in controlled studies. Nature, 224:47–48.

Heath, R. G., J. W. Spann, J. F. Kreitzer, and C. Vance. In press. Effects of polychlorinated biphenyls on birds. Proc. XV Internatl. Ornithol. Congress, The Hague.

Howell, A. H. 1932. Florida bird life. Florida Dept. Game and Fresh Water Fish, Tallahassee, Florida.

Imhoff, T. A. 1960. Central Southern Region. Audubon Field Notes, 14:454–456.

Imhoff, T. A. 1962. Alabama birds. Univ. Alabama Press, University, Alabama.

Jehl, J. R., Jr. 1969. A wonderful bird was the pelican. Oceans, 2:11–19.

Joanen, T., and D. A. Neal. 1971. The return of the Brown Pelican. Louisiana Conservationist, May, June:10–13.

Lehner, P. N., T. O. Boswell, and F. Copeland. 1967. An evaluation of the effects of the *Aedes aegypti* eradication program on wildlife in South Florida. Pesticides Monitoring Journ., 1:29–34.

Lowery, G. H., Jr. 1960. Louisiana birds. 2nd ed. Louisiana State University Press, Baton Rouge, Louisiana.

McIlhenny, E. A. 1943. Major changes in the bird life of southern Louisiana during sixty years. Auk, 60:541–549.

Mason, C. R. 1945. Pelican travels. Bird-Banding, 16:134–143.

Mulhern, B. M., and W. L. Reichel. 1970. The effect of putrefaction of eggs upon residue analysis of DDT and metabolites. Bull. Environ. Contam. Toxicol., 5:222–225.

Murphy, R. C. 1936. Oceanic birds of South America. Vol. 2. Amer. Mus. Nat. Hist., New York.

Newman, R. J. 1956. Central Southern Region. Audubon Field Notes, 10:387–390.

Newman, R. J. 1957. Central Southern Region. Audubon Field Notes, 11:409–413.

Newman, R. J. 1958*a*. Central Southern Region. Audubon Field Notes, 12:284–287.

Newman, R. J. 1958*b*. Central Southern Region. Audubon Field Notes, 12:417–421.

Newman, R. J. 1959*a*. The Changing Seasons. Audubon Field Notes, 13:4–10.

Newman, R. J. 1959*b*. Central Southern Region. Audubon Field Notes, 13:298–302.

Oberholser, H. C. 1938. The bird life of Louisiana. Dept. of Conservation, New Orleans.

Palmer, R. W. 1962. Handbook of North American birds. Vol. 1. Yale University Press, New Haven.

Peakall, D. B. 1970. p,p′-DDT: Effect on calcium metabolism and concentration of estradiol in the blood. Science, 168:592–594.

Peakall, D. B. 1971. Effects of polychlorinated biphenyls (PCB's) on the eggshells of Ring Doves. Bull. Environ. Contam. Toxicol., 6:100–101.

Pearson, T. G. 1918. Report of T. Gilbert Pearson, Secretary. Bird-Lore, 20:455.

Pearson, T. G. 1921. Notes on the bird-life of southeastern Texas. Auk, 38:513–523.

Porter, R. D., and S. N. Wiemeyer. 1969. Dieldrin and DDT: Effects on Sparrow Hawk eggshells and reproduction. Science, 165:199–200.

RATCLIFFE, D. A. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. J. Appl. Ecol., 7:67–115.

RISEBROUGH, R. W. In press. Determination of polychlorinated biphenyls in environmental samples. Proc. of the Symposium on the identification and measurement of environmental pollutants. Ottawa. 1971.

RISEBROUGH, R. W., R. J. HUGGETT, J. J. GRIFFIN, AND E. D. GOLDBERG. 1968. Pesticides: Translantic movements in the northeast trades. Science, 159:1233–1236.

RISEBROUGH, R. W., J. D. DAVIS, AND D. W. ANDERSON. 1970. Effect of various chlorinated hydrocarbons. *In* Gillett, J. W. (Ed.). The biological impact of pesticides in the environment. Environmental Health Series 1, Oregon State Univ., Corvallis, Oregon.

RISEBROUGH, R. W., G. I. FLORANT, AND D. D. BERGER. 1970. Organochlorine pollutants in Peregrines and Merlins migrating through Wisconsin. Canadian Field-Naturalist, 84:247–253.

RISEBROUGH, R. W., F. C. SIBLEY, AND M. N. KIRVEN. 1971. Reproductive failure of the Brown Pelican on Anacapa Island in 1969. Amer. Birds, 25:8–9.

SCHREIBER, R. W., AND R. L. DELONG. 1969. Brown Pelican status in California. Audubon Field Notes, 23:57–59.

STEWART, J., JR. 1962. Central Southern Region. Audubon Field Notes, 16:480–481, 485–486.

STICKEL, L. F., AND L. I. RHODES. 1970. The thin eggshell problem. *In* Gillett, J. W. (Ed.). The biological impact of pesticides in the environment. Environmental Health Series 1, Oregon State University, Corvallis, Oregon.

TARRANT, K. R., AND J. O'G. TATTON. 1968. Organochlorine pesticides in rainwater in the British Isles. Nature, 219:725–726.

VAN TETS, G. F. 1965. A comparative study of some communication patterns in the Pelecaniformes. Ornithol. Monogr. No. 2, American Ornithologists' Union.

VOOUS, K. H. 1957. The birds of Aruba, Curacao, and Bonaire. Studies on the fauna of Curacao and other Caribbean Islands, No. 29.

WEBSTER, F. S., JR. 1960. South Texas Region. Audubon Field Notes, 14:460–465.

WEBSTER, F. S., JR. 1963. South Texas Region. Audubon Field Notes, 17:469–471.

WETMORE, A. 1945. A review of the forms of the Brown Pelican. Auk, 62:577–586.

WETMORE, A. 1965. The birds of the Republic of Panama. Smithsonian Misc. Coll., No. 150.

WIEMEYER, S. N., AND R. D. PORTER. 1970. DDE thins eggshells of captive American Kestrels. Nature, 227:737–738.

WILLIAMS, L. E., JR., AND L. MARTIN. 1968. Nesting status of the Brown Pelican in Florida in 1968. Quart. J. Florida Acad. Sci., 31: 130–140.

WILLIAMS, L. E., JR., AND L. MARTIN. 1970. Nesting populations of Brown Pelicans in Florida. Proc. 24th Annual Conf. S. E. Assoc. Game and Fish Comm.

WRAY, D. L., AND H. T. DAVIS. 1959. Birds of North Carolina. North Carolina Dept. of Agriculture, Raleigh, North Carolina.

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BEHAVIORAL RESPONSES OF MIGRATING BIRDS TO DAYLIGHT AND DARKNESS: A RADAR AND DIRECT VISUAL STUDY

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In spring nearly all the passerine migrants that enter southern Louisiana do so after completing a migration across the Gulf of Mexico, and although most of the birds are considered nocturnal migrants and embark on their crossing at night (Lowery, 1951), they usually arrive on the northern Gulf coast during the daytime (Lowery, 1955; Newman, 1957). The migrants that arrive during the day alight shortly after reaching land and usually initiate another migration the same night, but occasionally the trans-Gulf flights continue to arrive after nightfall (Gauthreaux, 1968, 1971). Because of the timing of these movements, I have been able to examine the landing behavior and the altitudinal and spatial distribution of the same population of migrants aloft during the day and at night.

MATERIALS AND METHODS

This paper is based on radar, direct visual, and acoustic methods which are essentially the same as those given in earlier papers (Gauthreaux, 1969, 1970, 1971). I gathered data from the WSR-57 radar and made telescopic watches at Lake Charles and New Orleans, Louisiana, during spring migration from 1965 to 1967 and accumulated information on the landing behavior of the trans-Gulf migrants on the Louisiana coast from 1958 to 1968 (see Newman, 1958; Newman and Lowery, 1959). Call-notes from migrants aloft were counted during daytime and nighttime telescopic watches throughout the study.

DAYTIME FLOCKING

The data I collected with a telescope and binoculars indicate that the majority of passerines arriving from over the Gulf during the daytime were in compact flocks. Although isolated passerines were frequently recorded, the total number of birds in flocks exceeded the total number of single birds by a factor of three. The aggregations of small and medium sized passerines ranged from two or three individuals to more than 100; the average was 20. The largest flock I saw with the telescope was 175 birds, and the largest flock I recorded with binoculars was 300 birds.

The migrants were in four basic flight formations. About 70 per cent of the flocks were nearly circular or slightly oval in shape. About 30 per cent were in a line formation; in 20 per cent the line was perpendicular to the flight direction, and in the remaining 10 per cent it was parallel to the flight direction. On two occasions the migrants appeared to be randomly spaced,

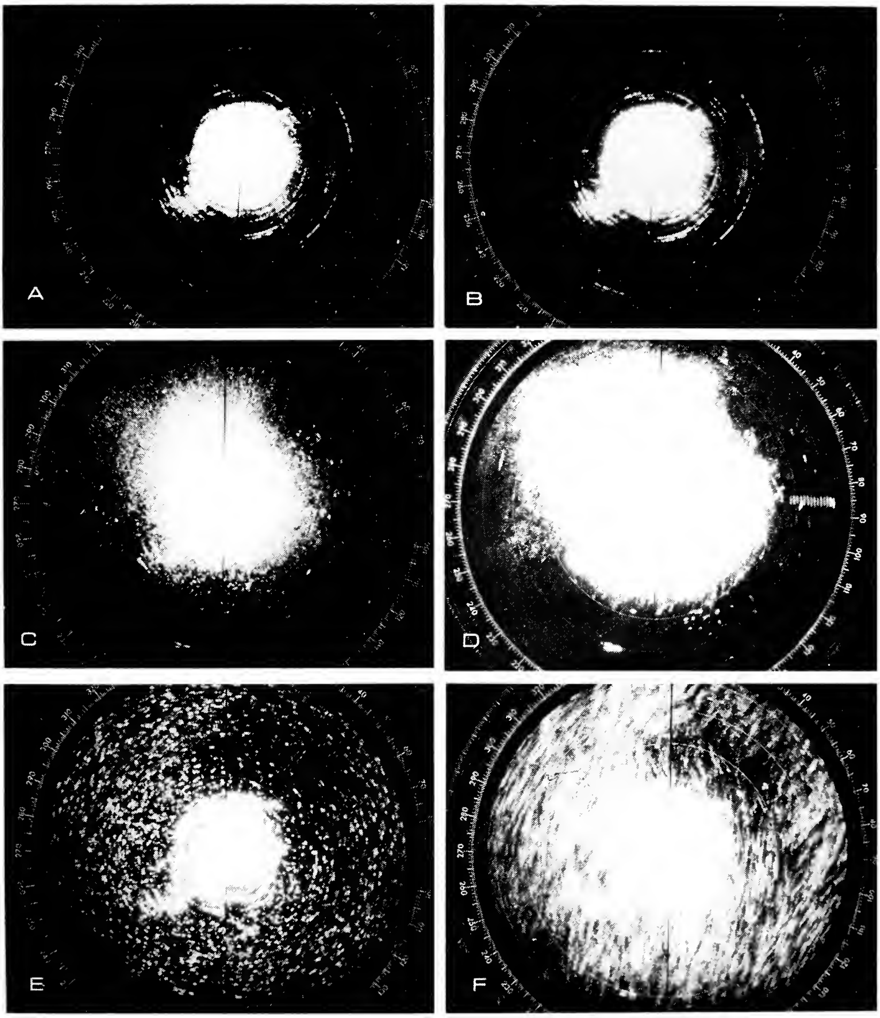

FIG. 1. Photographs of the radar screen at Lake Charles, Louisiana, during spring of 1965. A, C, and E are exposures for a single revolution of the antenna; B, D, and F are five-minute time exposures. A and B—19 March, 23:28 to 23:33 CST, 1° antenna elevation, no migration. C and D—15 May, 20:11 to 20:16 CST, 3° ant. elev., nocturnal migration. E and F—15 May, 18:46 to 18:51 CST, 3° ant. elev., daytime migration.

but this could have resulted from several large flocks joining together. The following example illustrates the compactness of the flocks. On the afternoon of 7 May 1965 two flocks of 30+ and 15+ passerines passed through the field of the vertical telescope when a partial moon was located in the field of view. From each flock 12 and seven birds, respectively, were over the lunar background at the same time.

Figures 1A and 1B show the radar screen (PPI) of the WSR-57 at Lake Charles, Louisiana, when there was no migration. The permanent echoes in the middle of the radar screen are from ground objects in the vicinity of the radar installation and are present in the other radar photographs. The echoes on the PPI from arriving trans-Gulf migrants were coarse bright dots (Figures 1E and 1F). They were strong and persistent and could be tracked for distances of two to six nautical miles. Finer echoes were often distributed among the larger ones, and frequently several coarse echoes coalesced on the radar screen. Although the density of the dot echoes occasionally caused saturation of the PPI (large areas of solid echo coverage), the concentrations were usually such that separate echoes were distinguished and counted.

By employing the radar's attenuation circuits and reducing signal strength, I estimated the relative abundance of different flock sizes. Forty-five per cent contained 12 birds or fewer; 55 per cent contained 13 to 200+ birds, and the median flock size was 19 birds. The earliest that I saw radar echoes from trans-Gulf migrants offshore was 41 minutes before sunrise, and the echo pattern suggested that the birds were already flocked.

LANDING BEHAVIOR

In favorable weather (clear to partly cloudy skies and southerly winds), most flocks of trans-Gulf migrants passed over the first coastal woodlands with only a few birds dropping out and alighting; the majority continued farther inland to the first extensive forests. When rain and adverse winds were present over the Gulf, or the Louisiana coast, or both, many more individuals landed in coastal woodlands. Under these conditions entire flocks often plummeted from great heights into the trees. When viewed through binoculars from one end of a wooded ridge, the migrants looked like large, dark hailstones falling into the trees.

The following sequence of events characterizes the landing behavior of the migrants as diagramed in Figure 2. As a flock high aloft moved over a coastal woodland some of the individuals hesitated, hovered, or flew in broad, shallow spirals while the remaining flock members continued farther inland. The individuals that left the flock then closed their wings and dove nearly straight down. Diving at great speed the migrants occasionally braked their descent by quickly flitting their wings, and just above the trees they abruptly pulled out of the dive producing a distinct whizzing sound. The birds then continued flying rapidly for 10 to 50 feet and landed with a quick flutter of their wings. After alighting the birds often remained motionless for two or three minutes, and then preened for two or three additional minutes. The

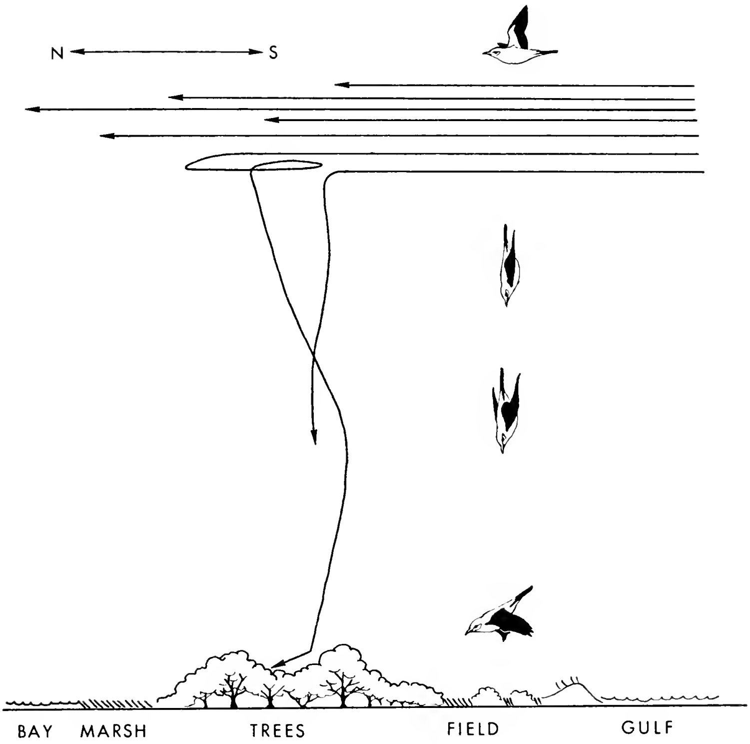

FIG. 2. Daytime landing sequences of trans-Gulf migrants in a coastal woodland. The bird postures figured on the right side are adopted during the landing behavior.

grounded migrants then started to feed, and many of the birds while moving from tree to tree continued in the direction of their migration.

When observed through the vertical telescope certain of the flocks aloft appeared to be aggregations of a single species, and I verified this on those occasions when entire flocks dove into the trees. I recorded the following species in homogeneous species flocks: Eastern Kingbird (*Tyrannus tyrannus*), Catbird (*Dumetella carolinensis*), Wood Thrush (*Hylocichla mustelina*). Red-eyed Vireo (*Vireo olivaceus*), Tennessee Warbler (*Vermivora peregrina*). Yellow Warbler (*Dendroica petechia*). Bay-breasted Warbler (*Dendroica castanea*), Bobolink (*Dolichonyx oryzivorus*). Orchard Oriole (*Icterus spurius*), Baltimore Oriole (*Icterus galbula*). Scarlet Tanager (*Piranga olivacea*), Summer Tanager (*Piranga rubra*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Blue Grosbeak (*Guiraca caerulea*). Indigo Bunting (*Passerina cyanea*), Painted Bunting (*Passerina ciris*). and Dickcissel (*Spiza americana*). In addition, some flocks contained only one sex (e.g.. Baltimore

TABLE 1

ALTITUDE OF DAYTIME MIGRATION AT LAKE CHARLES AND NEW ORLEANS
(Expressed as percentage of total number of dot echoes aloft)

Antenna elevation		Altitudinal zones in feet				
2.5°		*796–1,859*	*1,592–3,718*	*2,388–5,577*	*3,184– 7,437*	*3,980– 9,296*
(N = 4)	$\bar{x}$	8	11	30	36	15
	S.D.	7	3	10	3	14
3.0°		*1,061–2,125*	*2,123–4,251*	*3,184–6,377*	*4,246– 8,503*	*5,307–10,629*
(N = 30)	$\bar{x}$	5	10	29	38	18
	S.D.	6	5	10	11	12
4.0°		*1,593–2,659*	*3,186–5,319*	*4,779–7,979*	*6,373–10,638*	*7,966–13,298*
(N = 9)	$\bar{x}$	5	15	35	35	10
	S.D.	3	8	13	16	10

Oriole, Scarlet Tanager, Rose-breasted Grosbeak, Blue Grosbeak, Indigo Bunting, and Painted Bunting). It was often difficult to detect homogeneous species flocks once the birds landed and fed together in the trees. I did notice frequently that certain species were more abundant in certain portions of a particular woodland and that the relative abundance of a particular species differed markedly among different coastal woodlands. Two species of herons, the Green Heron (*Butorides virescens*) and the Yellow-crowned Night Heron (*Nyctanassa violacea*), showed the same landing behavior as the landbirds, and both of these species were commonly found resting in trees after completing a trans-Gulf migration.

ALTITUDE OF DAYTIME AND NIGHTTIME FLIGHTS

Table 1 gives the altitudinal distribution of the trans-Gulf migrants during their daytime arrival at the latitude of the Lake Charles and New Orleans radar stations (30°N). I gathered the data by counting dot echoes on the radar screen in a 5 × 5 nautical mile area centered at 5, 10, 15, 20, and 25 nautical mile range. The numbers of dot echoes were averaged for each altitudinal stratum and were corrected for increasing beam size and loss of power that follows the fourth power rule (see Eastwood, 1967).

On Lake Charles radar the altitude of the daytime movements averaged approximately 500 feet higher over land than over the Gulf, and flights were frequently 1,000 feet higher over New Orleans than over Lake Charles. The reason is probably that the migrants rather consistently flew above the convective cumulus clouds that formed near the coastline and piled higher as they moved inland with southerly winds. The cumulus over New Orleans

TABLE 2

ALTITUDE OF NIGHTTIME MIGRATION AT NEW ORLEANS
(Expressed as percentage of total number of birds aloft)

Antenna elevation		Altitudinal zones in feet			
2.5°		*796–3,718*	*1,592–5,577*	*2,388–7,437*	*3,184–9,296*
(N = 34)	$\bar{x}$	70	20	8	4
	s.d.	19	13	10	8
		796–1,592	*1,592–2,388*	*2,388–3,184*	*3,184–3,980*
(N = 30)	$\bar{x}$	74	18	7	2
	s.d.	17	14	8	3

were better developed than those over Lake Charles because the former city is farther inland than the latter, and the cloud formations had more time to build up, inducing the birds to fly higher. Whenever cumulus development exceeded 7,000 feet the migrants lowered their altitude. The distribution of the daytime flights was frequently the same as the altitude of the inversion layer aloft, but cumulus rarely develop above the altitude of an inversion. The air just above an inversion is quite stable and flows smoothly, and Raynor (1956) has suggested that migrants might prefer to fly in this zone.

Excluding cirrus overcast, solid overcast covered southern Louisiana on 11 days when trans-Gulf flights arrived. On nine of these days the mean altitude of the overcast base was 2,540 feet (s.d. = 1,160 feet; range = 1,300 to 5,000 feet), and 80 to 95 per cent of the migrants displayed on radar were above the overcast. Only on two days when the base of the overcast was at 7,500 feet and 10,000 feet did most of the migrants fly below the cloud layer. On 30 April 1967 cumulus cloud tops (8/10 coverage) extended up to 3,100 feet and the base of a higher cloud layer (9/10 coverage) was at 10,000 feet. On this afternoon 83 per cent of the migrants passing over the radar station flew between 4,000 and 6,000 feet between the cloud layers. On certain occasions some migrants appeared to be flying in clouds. Three times with binoculars I saw flocks of migrants so close to the base of a cloud that some individuals in the flocks momentarily disappeared into the cloud.

Whenever migrants continued to arrive from over the Gulf and pass over the radar stations near nightfall, their height lowered markedly. The average change from the daytime altitudinal distribution to the nighttime one was approximately 3,000 feet. Table 2 gives the quantity of nocturnal migration per altitudinal stratum expressed as the percentage of the total number of birds aloft. These data are from New Orleans during the spring of 1967, and I gathered them by using the attentuation technique (Gauthreaux, 1970). The data were corrected in the same manner as the daytime data, but they refer to densities of individual birds and not flocks. Seventy per cent of the migrants at night were most frequently between 796 feet and 3,718 feet. Within this zone approximately 75 per cent were between 796 feet and 1,592 feet.

Excluding cirrus overcast, solid overcast over southern Louisiana occurred on 5 nights of migration. The altitudes of the solid cloud layers on three of the nights were 2,800; 8,000; and 9,000 feet, respectively, and the migrants were below the overcast. On the remaining two nights the overcast was at 1,000 and 900 feet, and the migrants were in and above the cloud layer. Call-notes from the migrants on the latter two nights were quite numerous (50 to 100 per minute).

I recorded nocturnal flights at altitudes much higher than usual on 2 May and 4 May 1967. On 2 May, 42 per cent of the migrants were between 5,580 and 7,440 feet; on 4 May, 41 per cent were between 3,720 and 5,580 feet. When these altitudes were compared with the winds aloft (radiosonde-radar tracked balloon) for these nights, the migrants were found to be flying with favorable winds in warmer air above shallow cold fronts and northerly winds that had moved into the area.

CHANGE IN FLOCKING BEHAVIOR AT NIGHTFALL

As the altitude of migration lowered near nightfall another feature of the migration also changed—the flocks characteristic of daytime migration disbanded. On 11 occasions during full moon periods, I observed by moon-watching the breakup of flocks as trans-Gulf migrants continued to arrive over the Louisiana coast near sunset and later. The moon rises before sunset on the days preceding the full moon and it rises at the time of sunset on the date of the full moon. I began the watches while it was still daylight, and the passerine migrants that crossed the moon were still in tight aggregations with up to 10 birds against the moon at one time. As the watches continued and darkness approached the aggregations became looser, and shortly after dark only single birds passed before the lunar background. On five of these occasions thin cirrus cloud veiled the moon and the entire field of the telescope could be used to see the silhouettes of the migrants. Even with the added field of view only *single* landbirds were seen once it was night. After dark the ducks and shorebirds that passed before the moon were clearly grouped into tight flocks.

On the radar screen from the time of sunset to the time of darkness the large dot echoes characteristic of daytime migration changed to a finely stippled echo pattern. The fine dust-like echoes on the PPI of the WSR-57 are typical of nocturnal migration when passerine birds are flying singly in the night

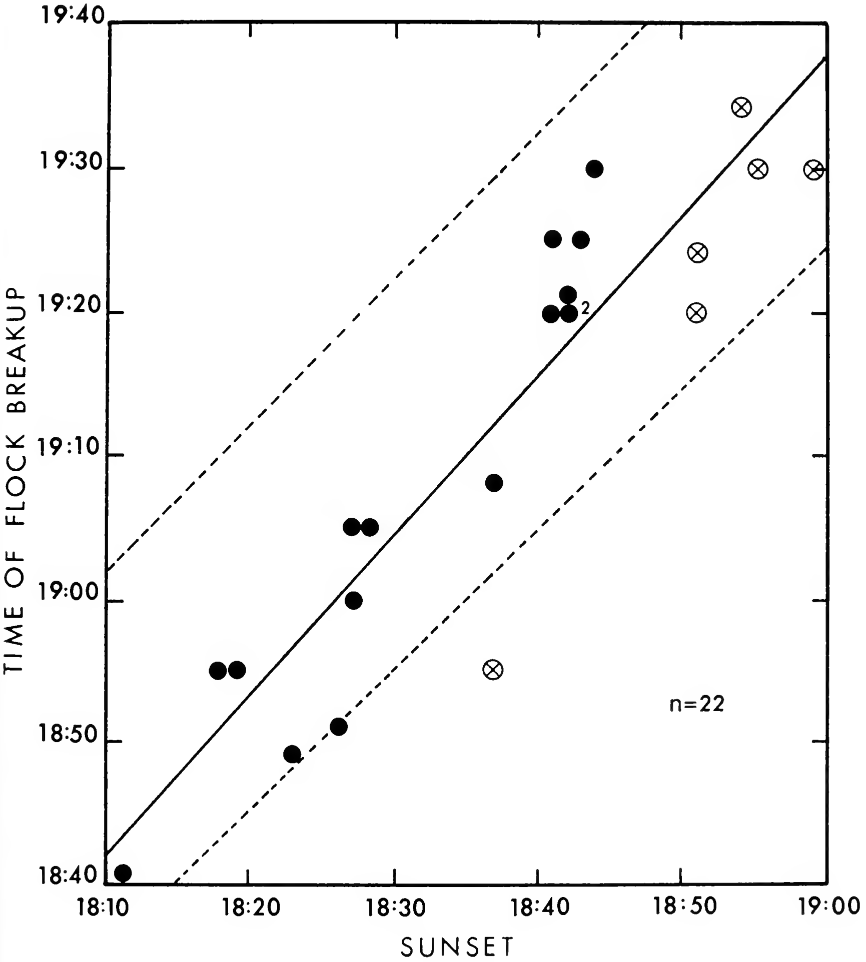

FIG. 3. Scatter diagram showing the time of the breakup of daytime flocks. Upper and lower dashed lines represent the end of nautical and civil twilight, respectively. The solid line is the computed line that best fits the points. The solid circles are points for New Orleans and the crossed circles are points for Lake Charles.

sky (Figs. 1C and 1D). The flock echoes on radar started to disband about 26 to 46 minutes after sunset. The mean time of the start of flock breakup based on 22 cases is 35 minutes after sunset with a standard deviation of 5 minutes. Most of the dot echoes were completely fragmented about 15 minutes later, or after the end of civil twilight and the beginning of nautical twilight. The duration of civil twilight during spring migration at 30°N is 24 to 25 minutes, and it is followed by nautical twilight which lasts for 52 to 59 minutes from 19 March to 19 May. Figure 3 is a scatter diagram showing the time of flock breakup in relation to the time of sunset and the beginning of nautical twilight. The breakup of passerine flocks aloft occurs about the same time as the exodus of grounded trans-Gulf migrants from the woodlands of southern Louisiana (Gauthreaux, 1971), and both events are clearly distinguishable on the radar screen.

CALLING BY MIGRANTS ALOFT

If trans-Gulf migrants flying high overhead during the day called, I did not hear them. However, when migrants were alighting in coastal woodlands during the day, they often gave call-notes. Passerine migrants called infrequently even when flocks aloft were disbanding and migrants were departing from woodlands during the first part of the night under fair skies. In contrast, I counted many call-notes from songbirds early in the evening on overcast nights and when trans-Gulf migrants were arriving after dark and landing. The greatest amount of calling from passerines usually occurred when the radar showed the density of migration to be falling rapidly. Shorebirds and waterfowl normally called frequently after dark and throughout the first half of the night.

DISCUSSION

Lowery (1951) established that nocturnal passerine migrants cross the moon individually as they initiate their trans-Gulf migration from areas south of the Gulf of Mexico. In this paper I have emphasized that these nocturnal migrants arrive from over the Gulf on the northern coast during the daytime in flocks. How single birds over the Gulf manage to congregate into homogeneous, single-species flocks is an intriguing question that is not easily answered. The radar findings of Gehring (1963) on daytime autumn migration in northern Switzerland suggest that the grouping possibly takes place at dawn. He found that the initial phases of diurnal migration occurred about half an hour before sunrise and at that time the radar echoes from the migrants were small and diffuse—an echo pattern characteristic of nocturnal migrants flying indvidually. As the light intensity increased the echoes became larger probably due to a tendency of the birds to form larger flocks. It is possible that nocturnal passerine migrants when forced to continue migrating in daylight over the Gulf of Mexico show the same flocking behavior exhibited by typical diurnal migrants at dawn. The two types of migrants show additional similar behaviors.

Gehring (1963) discovered that the altitude of migration over northern Switzerland decreased until half an hour before sunrise when it increased sharply. He attributed the lowering phase to nocturnal migrants ending their migration and the sharp increase to diurnal migrants. Myres (1964) recorded a late-night descent of nocturnal migrants flying over the southern part of the Norwegian Sea and the northern part of the North Sea, but near dawn the migrants gained altitude quickly. Although my evidence is circumstantial, nocturnal migrants probably show a gain in altitude at dawn over the northern Gulf, for the altitude of daytime migration from over the Gulf is approximately 3,000 feet higher than that typical for nighttime migration in the same area. Unfortunately, at the critical time when the ascent behavior occurs most of the migrants are too far offshore to be detected by coastal radar.

Lowery (1951) and Lowery and Newman (1955) found that most passerines aloft at night migrate singly and are randomly spaced. Nisbet (1963*a*) concluded that "... migration in small groups is a habit widespread in at least three North American families, Parulidae, Turdidae and Emberizidae, as well as in non-passerines." He pointed out that it would be valuable to seek direct visual evidence for the shape and size of groups by observing either when the moon is very low, or when haze or thin clouds cover the moon and a relatively large area of the sky can be examined with a low-power binocular. My telescopic and binocular observations under the latter conditions do not support Nisbet's conclusions. I found that daytime flocks of passerines disband at dusk; shorebirds and waterfowl remain in flocks. The change in echo pattern on the radar screen of the WSR-57 further supports the conclusion that most nocturnal passerine migrants fly individually in the night sky. According to the evidence presented by Eastwood and Rider (1966) some of the echoes on radar at long ranges are probably true groups of nocturnal migrants similar to those found by day; others, and perhaps the majority, are pseudo-groups which are a consequence of the pulse-volume effect (poor radar resolution) particularly with 23- and 10-cm radars. Schaefer (1968) also found by careful analysis of radar signals from migrating birds that the majority of nocturnal migrants over central England fly singly. Furthermore, when passerine migrants initiate their flight from woodlands at the beginning of the night they do so individually and not in groups (Hebrard, 1971).

The altitude of migration lowered during twilight whenever trans-Gulf migrants continued to arrive from over the Gulf near nightfall. Bellrose and Sieh (1960) described a similar phenomenon in flocks of migrating ducks. They recorded a gradual descent of birds from 2,000 or more feet to 500 feet as darkness approached on an overcast afternoon and believed that the ducks were attempting to remain in visual contact with the ground. This behavior should be looked for at other locations where nocturnal migrants are required to fly over 24 hours without landing. The lowering of the altitude at nightfall does not appear to be related to landing, for the number of migrants aloft usually increased after the descent as grounded migrants started their migration. The average altitude of nocturnal migration that I recorded from southern Louisiana is lower than that reported by certain workers (e.g., Lack, 1960; Nisbet, 1963*b*; Bellrose and Graber, 1963), but it is very close to other published figures (e.g., Eastwood and Rider, 1965; Able, 1970; Bellrose, 1971).

During the day the altitude of migration gradually increased as migrants crossed the coastline and moved inland. Similar altitudinal differences over land and sea have been reported by Bergman and Donner (1964) and Eastwood and Rider (1965). The propensity of trans-Gulf migrants to gradually gain altitude after crossing the coast is probably a response to stay above the building cumulus over land. Despite the increase in altitude, most birds landed when they reached the first inland forests. Although my data are few, it appears that migrants fly above overcast during the day when the cloud layer is under 7,000 feet. At night when solid cloud cover is above 3,000 feet, most migrants are below it, but when the overcast is lower most migrants fly in or above the cloud.

Graber (1968) reported that nocturnal migrants normally call more frequently later in the night reaching a peak in the pre-dawn hours. He also found that cloud cover causes a sharp increase in the number of call-notes. In southern Louisiana during the first part of the night, flight calls from passerine migrants aloft were scarce unless the birds were landing or it was overcast. When my radar and telescopic observations revealed that the density of nocturnal migration was declining rapidly, calling by the migrants was greatest. Hebrard (1971) found that nocturnal migrants did not call when they initiated their flights from woodlands in coastal Louisiana. Similarly, I did not hear flight calls when the daytime flocks disbanded at nightfall. Waterfowl and shorebirds called frequently at the beginning of the night even under clear skies. That calling serves some function in flock maintenance cannot be disputed, but it also seems plausible that calling by passerine migrants at night functions in some manner in the landing process. Exactly what that function is will require further investigation.

SUMMARY

I studied the behavior of migrating birds aloft by means of telescopic and binocular observations during the day (open sky overhead) and at night (ceilometer and moon-watching) and with WSR-57 radars in southern Louisiana. Spring passerine migrations across the Gulf of Mexico usually arrived on the northern Gulf coast during the daylight hours, and most of the birds were in tight flocks that averaged about 20 birds. On radar the flocks produced coherent dot echoes, and most occurred at an altitude of 4,000 to 5,000 feet (1,220 to 1,524 meters). When landing the migrants dove nearly

straight down from these altitudes and produced a whizzing sound as they pulled out of the dive just above the trees.

The daytime flocks of passerines disbanded about 30 to 45 minutes after sunset, and the altitude of the migration lowered approximately 3,000 feet (915 meters). At night individual passerines produced fine, dust-like echoes on the radar screen while flocks of waterfowl and shorebirds contributed the scattered dot echoes. Most nocturnal migration occurred between 800 and 1,600 feet (244 to 488 meters). Flight calls from migrants were heard during the day when the birds were landing. Passerine calling at the beginning of the night was primarily associated with landing and overcast. Waterfowl and shorebirds called regularly during the first part of the night even under clear skies. Calling by migrants aloft probably serves to keep individuals of a flock together and functions in the landing of songbird migrants at night.

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LITERATURE CITED

Able, K. P. 1970. A radar study of the altitude of nocturnal passerine migration. Bird-Banding, 41:282–290.

Bellrose, F. C. 1971. The distribution of nocturnal migrants in the air space. Auk, 88:397–424.

Bellrose, F. C., and R. R. Graber. 1963. A radar study of the flight direction of nocturnal migrants. Proc. XIII Internatl. Ornithol. Congr.:362–389.

Bellrose, F. C., and J. G. Sieh. 1960. Massed waterfowl flights in the Mississippi Flyway, 1956 and 1957. Wilson Bull., 72:29–59.

Bergman, G., and K. O. Donner. 1964. An analysis of the spring migration of the Common Scoter and the Long-tailed Duck in southern Finland. Acta Zool. Fennica, 105:3–59.

Eastwood, E. 1967. Radar ornithology. Methuen, London.

Eastwood, E., and G. C. Rider. 1965. Some radar measurements of the altitude of bird flight. Brit. Birds, 58:393–426.

Eastwood, E., and G. C. Rider. 1966. Grouping of nocturnal migrants. Nature, 211: 1143–1146.

Gauthreaux, S. A., Jr. 1968. A quantitative study by radar and telescope of the vernal migration of birds in coastal Louisiana. Unpubl. Ph.D. dissertation, Louisiana State Univ. Baton Rouge. (Univ. Microfilms, Ann Arbor, Michigan. Diss. Abstr., 29:3538-B).

Gauthreaux, S. A., Jr. 1969. A portable ceilometer technique for studying low-level nocturnal migration. Bird-Banding, 40:309–320.

Gauthreaux, S. A., Jr. 1970. Weather radar quantification of bird migration. BioScience, 20:17–20.

GAUTHREAUX, S. A., JR. 1971. A radar and direct visual study of passerine spring migration in southern Louisiana. Auk, 88:343–365.

GEHRING, W. 1963. Radar- und Feldbeobachtungen über den Verlauf des Vogelzuges im Schweizerischen Mittelland: Der tagzug im Herbst. Ornithol. Beob., 60:35–68.

GRABER, R. R. 1968. Nocturnal migration in Illinois—different points of view. Wilson Bull., 80:36–71.

HEBRARD, J. J. 1971. The nightly initiation of passerine migration in spring: A direct visual study. Ibis, 113:8–18.

LACK, D. 1960. The height of bird migration. Brit. Birds, 53:5–10.

LOWERY, G. H., JR. 1951. A quantitative study of the nocturnal migration of birds. Univ. Kansas Publ. Mus. Nat. Hist., 3:361–472.

LOWERY, G. H., JR. 1955. Louisiana birds. Louisiana State Univ. Press, Baton Rouge.

LOWERY, G. H., JR., AND R. J. NEWMAN. 1955. Direct studies of nocturnal bird migration. *In* A. Wolfson (Ed.), Recent studies in avian biology. Univ. Illinois Press, Urbana.

MYRES, M. T. 1964. Dawn ascent and reorientation of Scandinavian thrushes (*Turdus* spp.) migrating at night over the northeastern Atlantic Ocean in autumn. Ibis, 106:7–51.

NEWMAN, R. J. 1957. Spring migration—Central Southern Region. Audubon Field Notes, 11:350–357.

NEWMAN, R. J. 1958. Spring migration—Central Southern Region. Audubon Field Notes, 12:358–359.

NEWMAN, R. J., AND G. H. LOWERY, JR. 1959. The changing seasons—A summary of the 1959 spring migration and its geographic background. Audubon Field Notes, 13:346–352.

NISBET, I. C. T. 1963*a*. Quantitative study of migration with 23-centimetre radar. Ibis, 105:435–460.

NISBET, I. C. T. 1963*b*. Measurements with radar of the height of nocturnal migration over Cape Cod, Massachusetts. Bird-Banding, 34:57–67.

RAYNOR, G. S. 1956. Meteorological variables and the northward movement of nocturnal land bird migrants. Auk, 73:153–175.

SCHAEFER, G. W. 1968. Bird recognition by radar. A study in quantitative radar ornithology. *In*, The problems of birds as pests. Academic Press, London.

DEPARTMENT OF ZOOLOGY, CLEMSON UNIVERSITY, CLEMSON, SOUTH CAROLINA 29631, 29 AUGUST 1971.

ORIENTATION BEHAVIOR OF NIGHT-MIGRATING BIRDS (EUROPEAN ROBINS) DURING LATE AFTERNOON AND EARLY MORNING HOURS

Wolfgang Wiltschko and Hiltrud Höck

It has been shown previously that European Robins (*Erithacus rubecula*) will orient their nocturnal locomotor activity in Kramer cages in their natural migratory direction when exposed outdoors to the natural night sky; and that these directional preferences can be essentially changed by change of the direction of the magnetic field (Wiltschko, Höck, and Merkel, 1971). During these experiments the birds' activity was recorded also during late afternoon and early morning hours. An analysis of this daytime activity, which differs in several respects from orientation during darkness, will be presented in this report. These data are of interest with respect to questions of variation of directional preference between night and day and with respect to the development and deterioration of directional preference before and after nocturnal migratory activity.

MATERIAL AND METHODS

We used the methods previously described by Wiltschko (1968). The orientation cage was octagonal, 1 m in diameter and 35 cm high. It contained 8 radially-positioned perches. Every hop of an experimental bird closed a micro-switch, and caused a signal to be punched into a paper tape which was processed later by a computer. Food and water were offered in the center of the cage.

We installed two of these cages in the open air and covered them with plexiglass. With a pair of Helmholtz coils we made a magnetic field in which the north direction deviated from geographic north by 115° to ESE, although the intensity and inclination remained the same as in the earth's magnetic field (0.47 Gauss, mN = 115°, Incl. 68°) (Fig. 1). We used the earth's magnetic field (0.47 Gauss, mN = 360°, Incl. 68°) as a control.

A grey plastic curtain between the Helmholtz coils and the cage prevented the birds from seeing the coils and the surrounding landmarks. From the center of the cage the birds had a 53° view of the sky, but when the birds moved to the sides of the cage they could actually see a 102° sector of the sky. The test installation was located in the Rhön Mountains, 110 km northeast of Frankfurt a.M.

In both cages the directional preference of European Robins were recorded alternately in the natural magnetic field (Control) and with the direction of the magnetic field artificially turned (Test). We used two different groups of robins, 16 as Test birds and 15 as Controls, in order to avoid the possible transfer of effects from Test to Control conditions.

During the recording period the operator classified sky conditions as "clear" when there was a cloudless sky; as "partly covered" when the sky was partly obscured by clouds or when fog came up during a clear period, and as "overcast" when the sky was completely covered with clouds or when the sun was invisible because of fog during the entire test period.

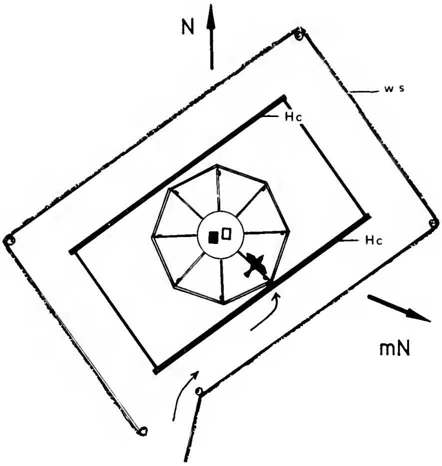

Fig. 1. Ground plan of the test arrangement: N = geographic north; mN = magnetic north when current is switched on; Hc = Helmholtz coils; ws = windscreen.

The tests were made during spring migratory period of 1969, with registration between dusk and 10:00 of the following day, and in autumn 1969 and spring 1970, with registration between 16:00 and 10:00 of the following day. The computer provided for a distinction between evening, night, and morning activity. The directional tendencies (calculated by computer) of the birds in each period are indicated by the mean direction, α_m, and by the concentration term, a_m. The statistical significance of a_m was examined by the Rayleigh Test for directional preference, and differences in mean direction were examined by the Watson and Williams Test (Batschelet, 1965). In the figures the mean directions for single evenings and mornings are represented by triangles on a circle, and the mean direction, α_m, of the test series is shown as a vector originating from the center. The length of this vector represents the concentration a_m, and the two inner circles are the 5 per cent (dotted) and the 1 per cent significance borders of the Rayleigh Test.

RESULTS

The data for night activity, which are reported in detail by Wiltschko et al. (1971), are summarized here briefly as an essential basis for interpreting the records for morning and afternoon activity in the same birds:

In spring 1969 and 1970 the robins under Control conditions showed a significant directional preference ($p < 0.01$) towards 26°, i.e. NNE, whereas the birds under Test conditions showed a significant preference ($p < 0.01$) towards 142°, which is geographic SE, but experimental NNE. In autumn 1969 the Controls showed a mean direction towards 175°, i.e. S, but this direction is not significant ($p > 0.05$). The birds under Test conditions show a significant directional preference ($p < 0.01$) towards 321°, which is experimental SSW. So in spring as well as in autumn the birds during nighttime selected their migratory direction according to the direction of the magnetic field.

Activity recorded during late afternoon and evening.—In spring 1969 and 1970, the mean direction of 16 values under Control conditions (i.e. birds

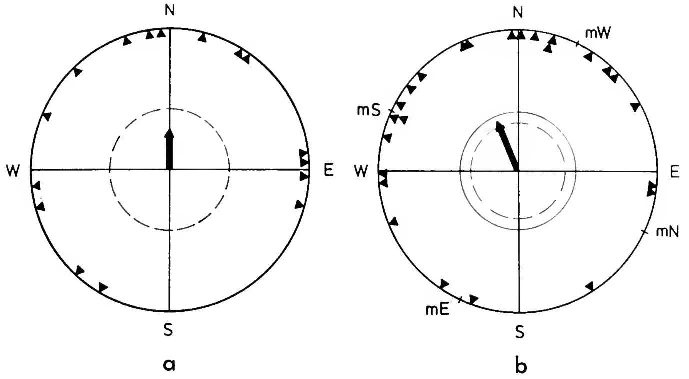

FIG. 2. Mean directions of activity recorded during late afternoon in spring 1969 and 1970: a. Control; b. Test conditions, mN = 115°.

were tested under the natural sky and the earth's magnetic field) pointed towards 360° = N (Fig. 2a), but this direction was not significant ($p > 0.05$). Under Test conditions (birds were tested under natural sky, but had the magnetic field turned by 115° to ESE) the birds showed in 25 evening periods a significant directional preference ($0.05 > p > 0.01$) at 337° which is geographic NNW, but experimental SW (Fig. 2b).

In autumn 1969 the Control experiments showed again a mean direction of 21 values at NNW at 347° (Fig. 3a), but again this directional tendency was not significant ($p > 0.05$); whereas under Test conditions we found for 33 values a significant directional preference ($p < 0.01$) at 331° = geographic NNW = experimental SW (Fig. 3b).

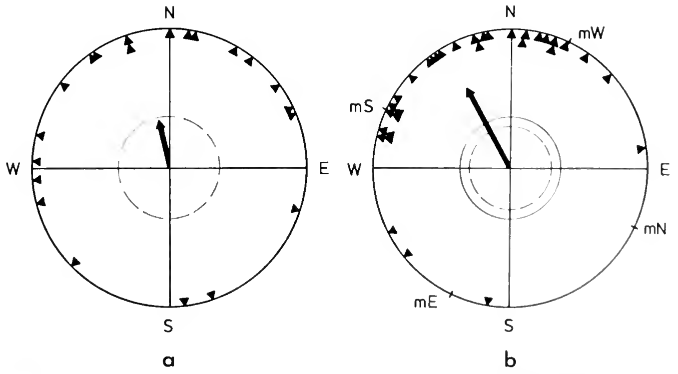

FIG. 3. Mean directions of activity recorded during late afternoon in autumn 1969: a. Control; b. Test conditions, mN = 115°.

TABLE 1

THE EFFECT OF WEATHER CONDITIONS ON DIRECTIONS PREFERRED BY ROBINS DURING EVENING ACTIVITY

	Control			Test		
	n	α_m	p	n	α_m	p
clear:						
spring:	3	29°	—	3	274°	—
autumn:	9	15°	—	16	320°	$(p < 0.01)$
spring and autumn:	12	18°	$(p > 0.05)$	19	313°	$(p < 0.01)$
partly covered:						
spring:	7	320°	—	13	5°	$(0.05 > p > 0.01)$
autumn:	7	10°	—	10	334°	$(p < 0.01)$
spring and autumn:	14	360°	$(p > 0.05)$	23	349°	$(p < 0.01)$
overcast:						
spring:	6	357°	—	9	298°	—
autumn:	5	265°	—	7	353°	—
spring and autumn:	11	305°	$(p > 0.05)$	16	330°	$(p > 0.05)$

The foregoing data show that the mean direction of orientation in robins in evening points towards the geographic NNW sector in both spring and autumn and in either Test or Control conditions. We do not find any statistically significant differences (Watson and Williams Test) in directional preferences between spring and autumn for either Test or Control conditions. We are therefore justified in combining data for spring and autumn, in which case we find a significant directional preference ($p < 0.01$) towards 333° for Test and a significant directional preference ($0.05 > p > 0.01$) towards 352° for Control.

On the other hand the Watson and Williams Test does not allow us to assume that the mean directions of Test and Control experiments originate from different statistical populations: the only difference is that under Test conditions the directional preference is in both seasons more concentrated than under Control conditions.

We may next examine the effect of different weather conditions on directions preferred by the robins, with results summarized in Table 1. Here again we cannot find significant differences between the mean directions for any weather conditions, nor can we, for any weather condition, find a difference between Test and Control.

If we classify the test values of evening activity according to whether the birds showed migratory activity (*Zugunruhe*) during the following night, we obtain the results shown in Table 2. We again cannot find any significant differences.

TABLE 2

DIRECTIONS PREFERRED BY ROBINS DURING EVENING ACTIVITY

	Control			Test		
	n	α_m	p	n	α_m	p
followed by migratory activity:						
spring:	13	10°	$(p > 0.05)$	13	314°	$(0.05 > p > 0.01)$
autumn:	16	347°	$(p > 0.05)$	18	319°	$(p < 0.01)$
spring and autumn:	29	360°	$(p > 0.05)$	31	317°	$(p < 0.01)$
not followed by migratory activity:						
spring:	3	323°	—	12	20°	$(p > 0.05)$
autumn:	5	346°	—	15	348°	$(p < 0.01)$
spring and autumn:	8	342°	$(0.05 > p > 0.01)$	27	357°	$(p < 0.01)$

Activity recorded during the morning hours.—In spring we found a mean direction of 44° = NE for 36 Control values and one of 56° = geographic NE = experimental WNW for 42 Test values. The directional preference was significant for Control $(p < 0.01)$, but not significant for Test $(p > 0.05)$. In autumn the mean direction of 20 Control values pointed towards 307° = NW, the mean direction of 32 Tests towards 311° = geographic NW = experimental SSW. This time the birds' behavior produced a significant directional preference $(p < 0.01)$ under Test conditions, whereas for Control we got random movements $(p > 0.05)$.

But if we now classify these values according to whether the birds had shown migratory activity during the night before, we obtain the results shown in Table 3. It is obvious that the mean direction of morning activity following

TABLE 3

DIRECTIONS PREFERRED BY ROBINS DURING MORNING ACTIVITY

	Control			Test		
	n	α_m	p	n	α_m	p
following migratory activity:						
spring:	30	34°	$(p < 0.01)$	25	128°	$(p > 0.05)$
autumn:	15	232°	$(p > 0.05)$	16	295°	$(0.05 > p > 0.01)$
spring + (autumn + 180°):	45	34°	$(p < 0.01)$	41	120°	$(0.05 > p > 0.01)$
not following migratory activity:						
spring:	6	134°	—	17	22°	$(p < 0.01)$
autumn:	5	320°	—	16	312°	$(p > 0.05)$

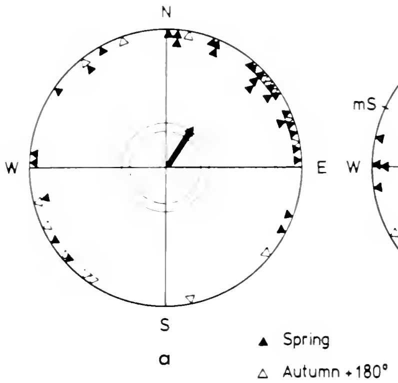

Fig. 4. Mean directions of morning activity when the birds had shown migratory restlessness the night before: dark triangles: data of spring 1969 and 1970: light triangles: data of autumn 1969 turned to the opposite side by adding 180°. a. Control; b. Test conditions. mN = 115°.

nocturnal activity correspond to the mean directions of this nocturnal activity, although the dispersion of data is larger than at night. The Watson and Williams Test does not show a difference between the direction of night activity and morning activity for any set of values. If we assume that the birds return in spring using about the same route they used in autumn and that therefore the migratory directions in spring and autumn lie opposite, we can combine the data of both seasons by turning the autumn data to the opposite side by adding 180°. We now find significant mean directions at 34° = NNE for Con-

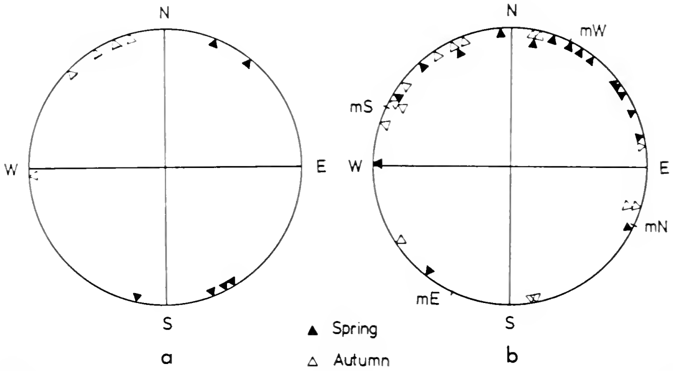

Fig. 5. Mean directions of morning activity not preceded by nocturnal activity: dark triangles: data of spring 1969 and 1970; light triangles: data of autumn 1969. a. Control; b. Test conditions, mN = 115°.

TABLE 4

EFFECT OF WEATHER CONDITIONS ON DIRECTIONS PREFERRED BY ROBINS ON MORNINGS AFTER NIGHTTIME *ZUGUNRUHE*

	Control			Test		
	n	α_m	p	n	α_m	p
clear and partly covered:						
spring:	15	49°	$(0.05 > p > 0.01)$	8	147°	—
autumn:	7	65°	—	4	239°	—
spring + (autumn + 180°):	22	47°	$(p > 0.05)$	12	91°	$(p > 0.05)$
overcast:						
spring:	15	19°	$(0.05 > p > 0.01)$	17	120°	$(p > 0.05)$
autumn:	8	238°	—	12	312°	$(0.05 > p > 0.01)$
spring + (autumn + 180°):	23	24°	$(0.05 > p > 0.01)$	29	127°	$(0.05 > p > 0.01)$

trol (Fig. 4a) ($p < 0.01$) and at 120° = geographic ESE = experimental N for Test (Fig. 4b) ($0.05 > p > 0.01$). The fact that these mean directions in Test and Control originate from different statistical populations is significant with $p < 0.01$.

On the other hand the data of morning activity not preceded by migratory activity show no relation to the directions the same birds selected when they showed migratory restlessness (Fig. 5).

Different weather conditions did not cause significant differences in birds' directional behavior recorded during mornings after *Zugunruhe* (Table 4).

The mean directions of evening, night, and morning activity of single registration periods are given in Tables in the Appendix.

DISCUSSION

When we started to register daytime activity we wanted to find out whether in the migratory season night-migrating birds have a tendency to move in their migratory direction also during the daytime periods before and after darkness. The direction selected during early morning hours corresponds with the migratory direction, but only when the birds were actually restless the night before. The concentration of these directional preferences is lower than the concentration found during nighttime. This may result from both the shorter registration time (3–5 hours, compared with 9–11 hours during nights) and a weaker motivation to keep the migratory course. These findings correspond with those of Mewaldt et al. (1964), who found that pre-dawn migratory restlessness may persist into the post-dawn period. Mewaldt et al.

found these tendencies with *Zonotrichia* only in autumn, whereas our robins showed this behavior also in spring. This may be merely an interspecific difference.

We cannot state exactly whether the directional preference during morning hours depends on the directional preference during night. The fact that in more than 50 per cent of all experiments the birds selected during morning hours a direction deviating more than 45° from the one they had selected the night before indicates that the birds might select their migratory direction anew. This is also supported by the observation that in most experiments there is a period of low activity or no activity between the night activity and the morning activity peak.

The experiments in our Test arrangement give evidence that the selection of the migratory direction is dependent on the magnetic field also during daylight hours. Most data for Test conditions were obtained during "overcast" morning periods when the sun was not visible; but on "partly covered" mornings the birds' orientation behavior might have been influenced by the sun compass. The robins were unable to see the sun itself because of the plastic curtain that concealed the Helmholtz coils and surrounding landmarks, but they may have got information of the sun's position by lighted clouds or lighter parts of the sky. Unfortunately we have only very few values for "partly covered" Test mornings: the seven values obtained in spring cannot be interpreted as evidence for the use of a sun compass, since their mean direction (statistically nonsignificant) corresponds to the migratory direction according to the magnetic field. In autumn the mean direction points towards SW as expected for sun compass orientation, but it is based on only four values. So we need more data to decide under which conditions the birds use the sun compass, and how they select their migratory direction when sun compass and magnetic compass give conflicting information.

The orientation of morning activity following nights without nocturnal restlessness seems to have no relation to the migratory direction.

The activity recorded during late afternoon and evening shows an orientation towards the NNW sector, which seems similar to the "nonsense" orientation of released non-migrating Mallards, described by Matthews (1961). This orientation in robins does not depend on the direction of the magnetic field, does not alter between spring and autumn, and shows no relation to the migratory direction (except in Test in autumn, where by chance this "nonsense" direction and the migratory direction coincide). But this "nonsense" orientation, unlike the one described by Matthews (1963) is independent of the weather condition and seems to persist under total overcast. We do not think that this direction is caused by phototaxis from the setting sun, since (1) the mean is too far north from the sunset point, (2) it persists under total overcast, and (3) the morning activity not preceded by nocturnal activity shows no corresponding eastward direction. A simple explanation could be that the door of the windscreen was in the SE, and so the birds were released from this side into the cage (Fig. 1). NNW is the direction where they try to escape from the operator, and hence may be temporarily fixed in the behavior pattern. In spring as well as in autumn this "nonsense" orientation is much more concentrated under Test conditions. The reason may be that under Test conditions the birds' motivation to prefer this direction is intensified by the fact that it coincides with the axial migratory direction. It is not surprising that the direction opposite to the migratory direction (situation in spring experiments) has a certain prominence for a bird, since we know from the magnetic compass that in the first step the bird perceives only the axial direction of the magnetic field lines (Wiltschko 1971).

Maybe we can interpret the data of morning activity not preceded by nocturnal activity (except for the four values of Control in spring) as an expression of a similar "nonsense" tendency. This tendency is much weaker than in the evening, as might be expected, since the birds had 13–15 hours to forget the procedure of being caught and brought into the registration cage.

SUMMARY

1. The birds' activity during early morning hours is concentrated in migratory direction, but only when the birds showed migratory activity in the night before.
2. When the magnetic field was artificially changed (magnetic north at 115° in ESE), the birds during morning hours selected their migratory direction according to the direction of the magnetic field.
3. The birds' behavior during late afternoon and evening shows a "nonsense orientation" towards the geographic NNW sector in Test (magnetic north in ESE) and Control (earth's magnetic field) in spring as well as in autumn.
4. This "nonsense orientation" seems to persist under clear, partly covered and overcast skies, and might be explained as a temporarily fixed part in the birds' behavior pattern caused by carrying the birds into the cage from the opposite side.

ACKNOWLEDGMENTS

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APPENDIX (TABLES 5–10)

The tables give the mean direction of afternoon and evening-, night-, and morning activity for the single registration periods between 16:00 and 10:00 the following day.

We evaluated every afternoon- and morning activity period in which the bird did more than 50 hops and every night activity period with more than 70 hops.

During spring 1969 afternoon and evening activity was not registered, registration time started at dusk. In a few cases when the entire activity of that night (more than 70 hops) occurred during the first hour, it is considered as evening activity rather than night activity and given as "afternoon" activity in the tables. Also in spring 1969 the morning activity had to be registered separately and could not be registered regularly. The mornings, when no morning activity was registered, are marked as "not reg." in the tables. "Techn. defect" means that the bird showed activity, but this activity could not be evaluated because of a defect in the recording system. The letters refer to weather conditions: cl = clear; pc = partly covered; ov = overcast.

Table 5

Spring 1969, Control

Date	Bird	Afternoon	Night	Morning
5 April	R 3	—	cl 360°	not reg.
6 April	R 3	—	cl 131°	not reg.
9 April	R 3	—	cl 200°	not reg.
11 April	R 3	—	ov 338°	cl 1°
12 April	R 7	—	pc 18°	—
13 April	R 6	—	—	pc 22°
14 April	R 3	pc 105°	—	pc 160°
17 April	R 12	—	ov 358°	—
18 April	R 3	—	—	ov 154°
19 April	R 9	cl 293°	—	cl 193°
20 April	R 12	—	pc 233°	pc 227°
23 April	R 9	—	ov 348°	—
24 April	R 12	—	ov 139°	—
25 April	R 8	—	pc 125°	pc 42°
26 April	R 4	—	ov 326°	pc 23°
27 April	R 10	—	pc 21°	ov 5°
1 May	R 9	—	ov 66°	not reg.
3 May	R 12	—	pc 234°	ov 5°
4 May	R 9	—	ov 38°	pc 56°
6 May	R 12	—	ov 359°	ov 23°
7 May	R 9	—	ov 17°	ov 305°
9 May	R 12	—	pc 235°	ov 87°
10 May	R 9	—	pc 315°	—
11 May	R 12	—	cl 301°	cl 75°
12 May	R 21	—	cl 26°	pc 40°
14 May	R 12	—	ov 267°	pc 256°
16 May	R 12	—	pc 352°	not reg.
20 May	R 12	—	ov 35°	not reg.
21 May	R 15	—	ov 19°	not reg.

TABLE 6

SPRING 1969, TEST

Date	Bird	Afternoon	Night	Morning
4 April	R 2	—	—	cl 218°
5 April	R 2	cl 200°	—	cl 117°
8 April	R 4	—	cl 180°	not reg.
10 April	R 4	—	—	ov 301°
12 April	R 8	—	—	pc 57°
13 April	R 4	pc 357°	—	pc 355°
14 April	R 2	—	pc 116°	—
16 April	R 4	—	—	ov 37°
20 April	R 10	—	cl 171°	pc 205°
21 April	R 8	—	ov 159°	ov 172°
22 April	R 2	—	ov 229°	ov 77°
23 April	R 4	—	ov 186°	ov 153°
24 April	R 10	—	ov 166°	not reg.
25 April	R 7	—	pc 215°	—
26 April	R 9	—	ov 359°	—
27 April	R 12	—	ov 153°	ov 130°
28 April	R 8	—	ov 109°	ov 192°
29 April	R 4	—	ov 102°	ov 282°
30 April	R 10	—	ov 70°	ov 110°
3 May	R 10	—	pc 207°	ov 329°
4 May	R 4	—	ov 215°	pc 151°
5 May	R 19	—	pc 239°	—
6 May	R 10	—	ov 41°	ov 112°
7 May	R 4	—	ov 78°	ov 80°
8 May	R 19	—	ov 194°	—
10 May	R 4	—	pc 71°	ov 95°
12 May	R 4	—	pc 252°	pc 261°
13 May	R 13	—	cl 17°	pc 91°
14 May	R 10	—	pc 7°	—
16 May	R 10	—	pc 39°	not reg.
18 May	R 13	—	pc 89°	not reg.
19 May	R 18	pc 248°	—	ov 31°
21 May	R 13	—	pc 155°	not reg.

TABLE 7

AUTUMN 1969, CONTROL

Date	Bird	Afternoon	Night	Morning
13 September	R 27	cl 64°	cl 181°	pc 75°
14 September	R 22	cl 308°	—	pc 315°
16 September	R 27	ov 265°	ov 218°	ov 249°

TABLE 7

Continued

Date	Bird	Afternoon	Night	Morning
19 September	R 27	cl 53°	pc 20°	pc 349°
20 September	R 22	cl 11°	cl 195°	pc 37°
22 September	R 27	pc 161°	pc 17°	pc 64°
23 September	R 22	cl 225°	techn. defect	techn. defect
24 September	R 27	cl 108°	pc 122°	ov 231°
25 September	R 32	pc 29°	—	ov 335°
27 September	R 22	pc 360°	pc 279°	ov 161°
30 September	R 22	pc 67°	ov 130°	ov 33°
1 October	R 27	pc 273°	pc 347°	ov 310°
2 October	R 32	ov 325°	—	ov 338°
4 October	R 22	cl 327°	pc 194°	ov 49°
7 October	R 22	pc 8°	—	ov 267°
9 October	R 27	cl 37°	pc 30°	ov 259°
11 October	R 32	cl 342°	—	pc 329°
16 October	R 27	ov 284°	ov 118°	pc 235°
23 October	R 27	ov 173°	ov 175°	ov 142°
26 October	R 27	ov 255°	pc 282°	pc 228°
4 November	R 27	pc 342°	ov 186°	pc 190°

TABLE 8

Autumn 1969, Test

Date	Bird	Afternoon	Night	Morning
13 September	R 28	cl 286°	—	pc 108°
15 September	R 26	ov 19°	—	—
16 September	R 28	ov 47°	—	ov 236°
17 September	R 23	—	—	ov 326°
18 September	R 26	cl 34°	—	cl 107°
19 September	R 28	cl 242°	techn. defect	techn. defect
21 September	R 23	—	—	ov 298°
22 September	R 28	pc 19°	pc 257°	pc 237°
23 September	R 26	cl 326°	pc 341°	ov 308°
24 September	R 28	cl 12°	pc 24°	ov 273°
25 September	R 29	pc 328°	ov 328°	ov 311°
28 September	R 28	cl 335°	cl 305°	pc 327°
29 September	R 29	ov 81°	—	ov 81°
30 September	R 26	pc 6°	ov 2°	ov 7°
1 October	R 28	pc 360°	—	ov 12°
2 October	R 29	ov 322°	—	ov 307°
5 October	R 28	cl 5°	pc 16°	ov 23°
6 October	R 29	pc 15°	—	ov 339°

TABLE 8

Continued

Date	Bird	Afternoon	Night	Morning
9 October	R 28	cl 189°	pc 193°	ov 225°
11 October	R 29	cl 230°	—	pc 171°
13 October	R 28	cl 345°	—	ov 9°
15 October	R 34	cl 301°	—	ov 298°
16 October	R 28	ov 350°	—	ov 47°
17 October	R 29	cl 24°	—	ov 169°
19 October	R 28	cl 348°	pc 350°	ov 60°
20 October	R 29	cl 285°	cl 254°	cl 237°
21 October	R 34	cl 283°	pc 343°	ov 275°
22 October	R 28	pc 344°	pc 299°	techn. defect
23 October	R 29	ov 294°	ov 335°	ov 236°
28 October	R 29	pc 283°	pc 240°	pc 169°
29 October	R 28	pc 296°	—	ov 288°
30 October	R 34	pc 297°	ov 278°	ov 294°
1 November	R 28	cl 324°	cl 62°	—
2 November	R 34	—	pc 213°	ov 14°
3 November	R 29	ov 294°	ov 31°	ov 310°
4 November	R 28	pc 312°	—	pc 334°

TABLE 9

SPRING 1970, CONTROL

Date	Bird	Afternoon	Night	Morning
16 April	R 49	—	—	pc 39°
17 April	R 46	pc 263°	pc 47°	pc 237°
18 April	R 43	ov 210°	ov 126°	ov 110°
20 April	R 46	pc 83°	pc 17°	pc 46°
21 April	R 43	pc 14°	ov 46°	ov 69°
22 April	R 49	—	ov 338°	—
23 April	R 46	ov 356°	pc 227°	ov 82°
24 April	R 43	—	pc 100°	ov 21°
26 April	R 46	ov 87°	ov 295°	ov 272°
27 April	R 43	pc 351°	pc 34°	pc 46°
28 April	R 49	—	pc 77°	—
29 April	R 46	pc 254°	pc 332°	ov 331°
30 April	R 43	ov 316°	—	ov 150°
1 May	R 49	—	pc 70°	—
2 May	R 46	—	ov 26°	ov 47°
3 May	R 43	ov 341°	ov 60°	ov 276°
4 May	R 49	—	ov 327°	—
5 May	R 46	pc 222°	pc 71°	pc 71°

TABLE 9

Continued

Date	Bird	Afternoon	Night	Morning
6 May	R 43	—	pc 76°	pc 57°
7 May	R 46	cl 93°	pc 106°	pc 118°
9 May	R 53	cl 35°	pc 183°	pc 53°
10 May	R 43	ov 31°	ov 33°	ov 322°
11 May	R 46	—	pc 116°	ov 66°

TABLE 10

SPRING 1970, TEST

Date	Bird	Afternoon	Night	Morning
17 April	R 44	pc 42°	pc 324°	pc 271°
18 April	R 41	pc 17°	—	ov 26°
19 April	R 40	ov 61°	—	ov 66°
20 April	R 44	pc 1°	pc 101°	pc 113°
21 April	R 41	ov 314°	ov 50°	ov 315°
22 April	R 40	ov 307°	ov 257°	—
23 April	R 44	ov 294°	pc 322°	ov 48°
24 April	R 41	pc 338°	pc 199°	—
25 April	R 40	pc 99°	—	ov 18°
26 April	R 44	ov 214°	ov 176°	ov 326°
27 April	R 41	pc 16°	pc 150°	—
28 April	R 40	pc 7°	—	pc 335°
29 April	R 44	pc 96°	pc 96°	ov 117°
30 April	R 41	ov 293°	—	ov 318°
1 May	R 40	pc 32°	—	pc 53°
2 May	R 44	pc 269°	ov 150°	ov 270°
3 May	R 41	ov 265°	ov 123°	ov 192°
4 May	R 40	cl 336°	—	pc 271°
5 May	R 44	pc 299°	pc 260°	pc 348°
6 May	R 41	—	—	pc 10°
7 May	R 44	—	pc 101°	pc 81°
9 May	R 40	cl 284°	pc 133°	—
11 May	R 44	ov 46°	—	ov 51°
12 May	R 40	ov 148°	—	ov 77°

LITERATURE CITED

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. A.I.B.S., Washington, D.C.

MATTHEWS, G. V. T. 1961. "Nonsense" orientation in Mallard (*Anas platyrhynchos*) and its relation to experiments on bird navigation. Ibis, 103a:211–230.

MATTHEWS, G. V. T. 1963. The astronomical basis of "nonsense" orientation. Proc. 13th Internatl. Ornithol. Cong.: 415–429.

MEWALDT, L. R., M. L. MORTON, AND I. L. BROWN. 1964. Orientation of migratory restlessness in *Zonotrichia*. Condor, 66:377–417.

WILTSCHKO, W. 1968. Über den Einfluß statischer Magnetfelder auf die Zugorientierung der Rotkehlchen (*Erithacus rubecula*). Z. Tierpsychol. 25:537–558.

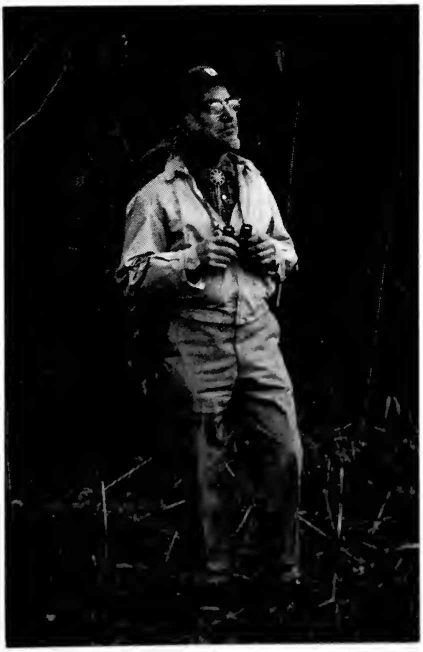
WILTSCHKO, W. 1971. The influence of magnetic total intensity and inclination on directions preferred by migrating European Robins (*Erithacus rubecula*). Proc. of the A.I.B.S. Symposium on Animal Orientation and Navigation. Wallop's Island, Virginia 1970. In press.

WILTSCHKO, W., H. HÖCK, AND F. W. MERKEL. 1971. Outdoor experiments with migrating robins (*Erithacus rubecula*) in artificial magnetic fields. Z. Tierpsychol. 29: 409–415.

ZOOLOGISCHES INSTITUT DER UNIVERSITÄT, 6 FRANKFURT AM MAIN, GERMANY, 2 JUNE 1971.

NEW LIFE MEMBER

A recent addition to the roster of Life Members of the Wilson Society is Robert L. Haines, of Moorestown, New Jersey. Mr. Haines, who has retired from a family paint and glass business, now spends his time in pursuing his ornithological interests, and is active in several organizations concerned with the welfare of the American Indians. He is in fact an adopted member of the Seneca tribe. A graduate of Haverford College, Mr. Haines has carried out serious studies of birds and has published several papers. He has been a member of the Society for 25 years, and is also a member of the AOU, the Cooper Society, The National and New Jersey Audubon Society, and the Delaware Valley Ornithological Club, having served as president of the latter in 1950. He is married and has two children and two grandchildren.



DIURNAL AND SEASONAL ACTIVITIES OF A POST-BREEDING POPULATION OF GULLS IN SOUTHEASTERN ONTARIO

F. Cooke and R. K. Ross

Although the breeding biology of the Herring Gull has been extensively studied, the post-breeding activities are less well understood. The Herring Gull undertakes an explosive post-breeding dispersal with direction influenced to some extent by prevailing winds and by the tendency of the birds to follow waterways or coasts. Gross (1940) noted that few of the gulls banded at Kent Island, New Brunswick moved inland and most moved southward. Poor (1943) reported similar findings from colonies in the Gulf of St. Lawrence. Banding data from gulls breeding around Lake Michigan indicated a predominantly easterly post-breeding movement along the Great Lakes-St. Lawrence system which was attributed to the prevailing winds (Smith, 1959). Young birds tended to disperse more widely than adults. Kadlec and Drury (1968) reported extensive data on the distribution of winter banding recoveries of Herring Gulls in relationship to the areas in which the birds were banded.

Schreiber (1968) carried out a study of gull numbers at Bangor, 35 miles northwest of the Maine coastline. He was able to correlate numbers of birds with cloud cover. Clear days were associated with northwest winds which were thought to drive the gulls towards the coast, while the overcast days usually with little wind allowed numbers to increase as the gulls returned.

In the present study we made daily observations on a flock of gulls which congregate daily on the Kingston (Ontario) City Dump during the fall and early winter. Usually around 95 per cent of this fall flock consisted of Herring Gulls (*Larus argentatus*). During September, however, Ring-billed Gulls (*Larus delawarensis*) comprised up to 40 per cent of the flock but after September, only very small numbers of this species were present. The Great Black-backed Gull (*Larus marinus*), the Glaucous Gull (*Larus hyperboreus*), and the Iceland Gull (*Larus glaucoides*) also occur in extremely small numbers, the last two only late in the fall.

The primary aim of this project was to investigate the factors responsible for the daily fluctuations in flock size and for the eventual disappearance of the flock from the Kingston area in early winter. A study in the Kingston area (see Fig. 1), lying midway between the other major areas where Herring Gulls had been studied, would add to an understanding of the continental dispersion pattern of this species.

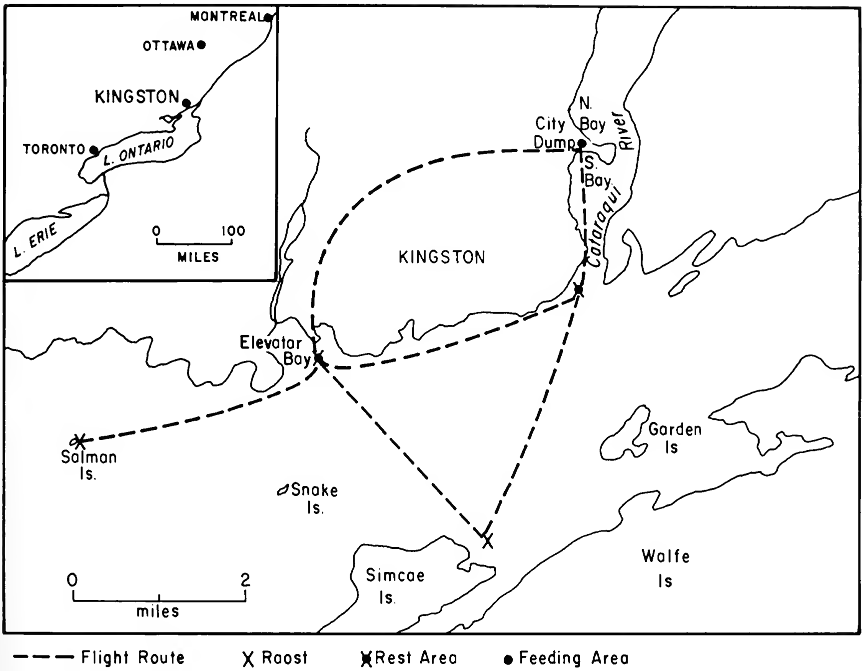


Fig. 1. Map of the Kingston area showing gull flight routes.

METHODS

We made observations from 22 September 1968 to 22 December 1968 and from 22 September 1969 to 10 December 1969. Less regular observations were made in January 1969. In the first season of study we made daily observations at gull concentration areas in the Kingston area. The major area studied was the Kingston City Dump which is the principal feeding site for the gull population. Numbers at this site remained essentially constant between 10:00 and 14:00 each day and we made daily gull counts during this time interval throughout both seasons. With larger flocks, estimates were made.

Weather records were obtained from the Kingston Weather Office, which is located seven miles southwest of the main study area. Weather conditions at 08:00 were used in the tables. The location of the actual roosts in Lake Ontario were found by spotting from the shore and by aerial survey in the late afternoon.

DAILY MOVEMENTS AND BEHAVIOR

The morning feeding flight.—The first of the gulls' daily movements was the flight from the roosting area on Lake Ontario and the islands to the feeding area, i.e. the Kingston City Dump (see Fig. 1). This started just before sunrise and continued over a period of three to four hours. Incoming birds were constantly visible throughout this period, coming in singly or in

TABLE 1

FREQUENCY OF FEEDING IN SAMPLES OF TWO AGE GROUPS OF HERRING GULLS

		Loafing		Feeding	
Date	Time	1st & 2nd	3rd & Adult	1st & 2nd	3rd & Adult
18 November 1969	13:00	40	245	47	80
16 September 1970	13:00	16	188	18	15
17 September 1970	11:30	11	78	6	12
20 October 1970	13:30	32	453	33	67
Total		99	964	104	174

small groups. During the peak movements which occurred in the middle of the period, these groups increased in size (up to 30–40). The groups were not very cohesive and splitting often occurred. The method of flight depended on wind direction and speed although in all cases it was fairly direct with little circling and chasing of one another. Major directions of flight are shown in Figure 1. The easterly route between the Simcoe Island roost and the City Dump was the most used.

Arrival in the feeding area.—On arrival in the dump vicinity, the gulls initially congregated south of the feeding area. They were active at this time. After a build-up in numbers to several hundred, the birds began moving onto the actual dumping area. The first sorties often involved a simple circling of the area and a return to the south bay. This was soon followed by actual landing in the dumping area.

Feeding.—Feeding activity varied throughout the day from a complete cessation to a frenzy of hundreds of birds swirling around the garbage piles. Periods of feeding activity could last for up to half an hour after which most of the birds returned to the loafing areas. There was a tendency to move to water after these sessions and drinking was observed. Schreiber (1967) noted a definite requirement for a supply of fresh water near the feeding area.

The age classes of the Herring Gulls were determined following Dwight (1925). On each of four sample counts it was found that there were a significantly higher proportion of first and second year birds in the feeding groups than were found in the loafing groups (see Table 1). A Chi square value of 534.9 ($P < 0.001$) was obtained. The presence of larger numbers of younger birds on the garbage pile suggests that they spend more time feeding than do older birds. This could be due to lack of dominance and youthful inexperience in food procuring. Drury and Smith (1968) found a definite dominance of adults over younger birds. Immature Herring Gulls were never observed chasing adults with food although the converse was frequently seen. It seems likely that immature birds would have to remain longer on the garbage pits to meet their nutritional requirements and so would tend to be concentrated in this area.

Loafing.—The birds spend much of the time loafing while in the general area of the dump. Loafing gulls stood or sat in groups. Very little preening activity was observed. Regular commuting between feeding and loafing areas occurred. In the early fall loafing groups could be found in the water of the south bay, along its shores, and on the flat open land around the dump. Gulls rarely loafed on the weedy water of the north bay. Later in the year, however, this section was the first frozen and the north bay became the preferred loafing area. Birds loafed both on the ice and in the water near the ice.

Swarm circling.—A flock of gulls often would rise in a compact swarm, circling presumably on a thermal upcurrent. The birds would go almost out of sight (around 3000 feet) and then return very quickly in a steep glide, approaching a dive. This is thought to be a defensive mechanism (Tinbergen, 1953) which might confuse or even intimidate an attacking predator. The passage of a low flying helicopter, the explosive launching of a cannon net and appearance of a Rough-legged Hawk all appeared, on occasion, to trigger the circling. At other times, however, the behavior was observed with no visible fright stimulus associated with it.

The roosting flight.—Roughly three hours before sunset, a large flock developed beside the dump, usually on water, and feeding activity decreased. After a period of "nervousness" involving chasing, preening, and quick circling, also noted by Schreiber (1967), the birds left singly or in small groups, retracing the morning route to the roosts.

Most birds roosted on the sheltered water northeast of Simcoe Island although some also roosted on Salmon Island. As the estimates of roosting gull numbers were consistently less than the total daily numbers, it is presumed that other roosts existed.

DAILY NUMBERS OF GULLS AND ENVIRONMENTAL CONDITIONS

Food supply.—The Kingston City Dump is operated as a sanitary landfill operation, with food refuse being covered with earth soon after it is dumped. Dumping is carried out daily from Monday to Saturday with no significant variations in amounts trucked in from day to day. On Sundays, however, there is no dumping and little edible material remains on the surface from the previous day, and considerably fewer birds visit the feeding area. The average of 19 Sunday counts was 678 and for 137 week-day counts was 1382. The Sunday average is 49 per cent of the week-day average. The

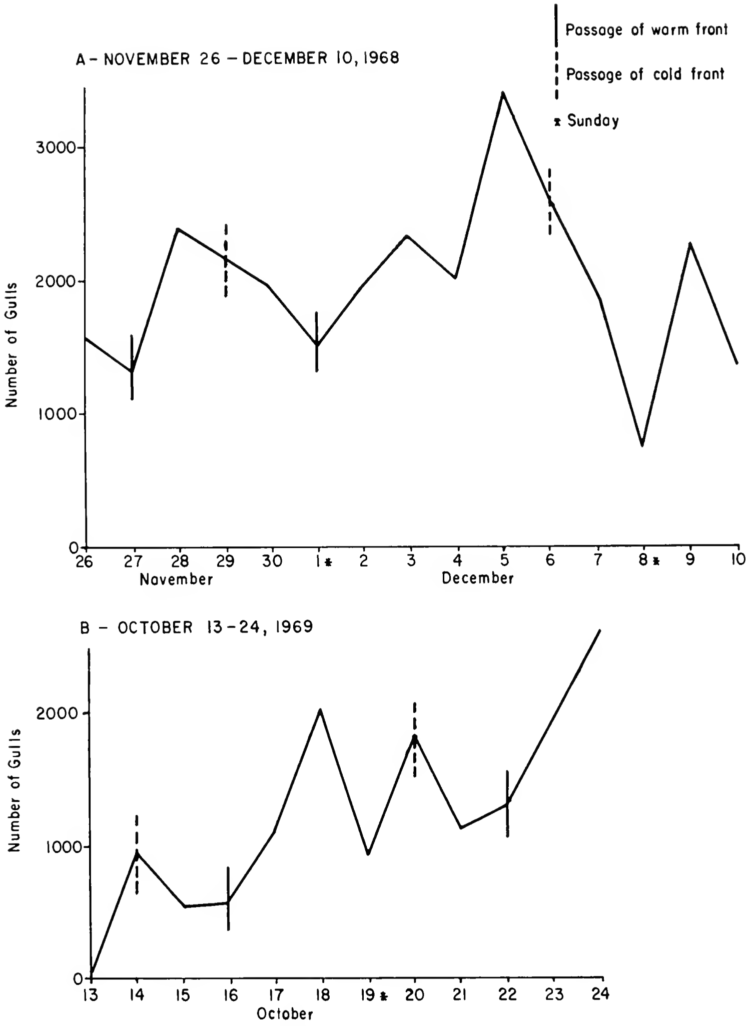


Fig. 2. Relationship between weather fronts and daily number of gulls.

counts were made around noon. On Sundays, the birds arrived as normal in the morning but left the feeding area, some to the loafing areas and others away from the vicinity of the dump altogether. We suspect that the whole flock initially came but dispersed on finding no food.

Weather conditions.—During the week, when there was adequate food on the dump, the numbers still fluctuated. A decrease in temperature and an increase in barometric pressure both tended to signal a decrease in gull numbers,

TABLE 2

RELATIONSHIP BETWEEN GULL NUMBERS AND WEATHER FRONTS

	Final Day of Warm Front Interval		Final Day of Cold Front Interval	
	Date	Count	Date	Count
1968	26 September	715	27 September	640
	8 October	1010	10 October	1352
	18 October	1643	21 October	1081
	23 October	2011	26 October	1439
	28 October	1266	1 November	1177
	2 November	1606	4 November	1640
	15 November	2325	16 November	2150
	22 November	3784	26 November	1658
	28 November	2395	30 November	1950
	5 December	3429	10 December	1321
	12 December	2710	16 December	324
	18 December	2296	20 December	35
1969	18 October	2030	21 October	1146
	24 October	2674	29 October	1183
	31 October	2338	4 November	2370
	6 November	1495	12 November	800
	18 November	1945	20 November	1222
	22 November	2320	26 November	1865
	28 November	1915	1 December	700
	3 December	1400	5 December	1350

and so an attempt was made to correlate the numbers and the passage of warm and cold fronts. Figure 2 provides examples of two sample periods. Generally the numbers increased during the period between the passage of a warm front and the arrival of the associated cold front (hereafter, warm front interval). Conversely, numbers decreased after the cold front and before the next warm front (hereafter, cold front interval). Table 2 presents the counts on the final day of both the warm and cold front intervals throughout the two seasons of observation. The final-day counts were chosen as they demonstrated the maximum effect of that weather interval. Using the Wilcoxon matched-pairs signed ranks test (Siegel, 1956), we found that the decrease of gull numbers at the end of the cold front interval as compared to the previous warm front interval count was significant at the 0.02 level. Sunday counts were omitted.

Although trends of changes in population size are evident, the absolute numbers of gulls cannot be accurately predicted from this knowledge of weather conditions. The actual effect of these conditions on the gulls is still

TABLE 3

MEAN WEEKLY COUNTS OF GULLS IN 1968 AND 1969

1968		1969	
Week Ending	Mean Count	Week Ending	Mean Count
28 September	496	27 September	542
5 October	1320	4 October	402
12 October	971	11 October	592
19 October	1210	18 October	1059
26 October	1377	25 October	1632
2 November	1354	1 November	1741
9 November	1457	8 November	1439
16 November	1919	15 November	1099
23 November	2844	22 November	1608
30 November	1809	29 November	1834
7 December	2399	6 December	1060
14 December	2154	13 December	210
21 December	823		
28 December	155		

unexplained. Associated with those periods after warm fronts are increased temperatures, decreased barometric pressure and a veering of the wind to the southwest. After a cold front comes decreased temperature, increased pressure and a wind change to the north. All these parameters not only correlate with the gull numbers but also correlate with one another and so it is impossible to analyze which, if any, of the individual factors affects the birds. It seems likely, however, that wind direction and speed play a major role. Southwest winds reach Kingston from Lake Ontario and might aid flight of birds to Kingston from other urban areas around the lake.

Fright stimulus.—A cannon net was discharged within a large loafing flock on 30 September 1969 catching 65 gulls. Although 1000 gulls were present on that day, only 190 were seen the next day and not until eight days later were numbers back to their previous level. Since the passage of weather systems was not involved, it is felt that the fright stimulus of the trapping activities was sufficiently strong to deter many birds from returning for some time.

WEEKLY AND SEASONAL VARIATION IN FLOCK SIZE

There was a progressive rise in numbers as the season proceeeded (Table 3). The initial rise was found highly significant in both years ($P = 0.00011$ in 1968 and $P = 0.0046$ in 1969, Kendall rank correlation test). In both years, the rise ended in late November or early December. Numbers then decreased and great fluctuations occurred. As Lake Ontario began to freeze around Kingston, gulls were no longer seen daily on the dump and only periodical appearances, correlated with the passage of warm fronts, were made. Freeze-up took place during the first week of January in the two years, and by the middle of the month, gulls were seen only sporadically in very small numbers. This relative absence of gulls may have been caused by the lack of drinking water in the vicinity of the garbage dump. The nearest open water area was 2½ miles from the feeding area.

The initial, gradual rise of numbers in the fall can be explained if the general Herring Gull population of Lake Ontario increased during that time. This could be due to Herring Gulls moving east from the western Great Lakes as reported by Smith (1959) and Hofslund (1959). In the fall of 1968, J. B. Steeves (pers. comm.) also found an increase in Herring Gull numbers in Montreal which peaked a week after the counts in Kingston. This may indicate that gulls, after initially increasing in numbers in eastern Lake Ontario, move down the St. Lawrence River to Montreal. Gross (1940) found little post breeding movement up the St. Lawrence River. Similarly, Poor (1943) showed that Herring Gulls breeding in the Gulf of St. Lawrence almost never moved towards Montreal, and instead dispersed to the Atlantic. This, therefore, leaves the Great Lakes and Upper St. Lawrence region with its large gull population as the most likely contributor of gulls to the Montreal flock.

SUMMARY

The activities of a flock of gulls, which congregated daily to feed on the Kingston City Dump were studied in order to investigate the factors leading to the daily and seasonal fluctuations in flock size.

The daily numbers of gulls on the dump were found to be influenced by food supply, severe fright stimulus, availability of water, and weather. The period after a warm front was associated with an increase in numbers while that after a cold front was usually associated with a decrease.

First and second year gulls were found to spend considerable more time feeding than the adult and third year birds.

The mean weekly numbers were found to increase gradually to a peak in late November or early December. This is thought to be due to the influx of Herring Gulls from the western Great Lakes. The final disappearance of gulls from the Kingston area came just after the local freezing of Lake Ontario and it is postulated that the lack of drinking water near the dump triggered the departure.

ACKNOWLEDGMENTS

This study was performed under contract for the Canadian Wildlife Service. We would like to thank members of the Kingston Field Naturalists for their assistance in field work, and Dr. B. N. Smallman, who piloted us for the aerial surveys. Finally, we would like to thank members of the Kingston City Works Department for their kind cooperation in allowing access to the city dump.

LITERATURE CITED

DRURY, W. H., JR., AND W. J. SMITH. 1968. Defense of feeding areas by adult Herring Gulls and intrusion by young. Evolution, 22:193–201.

DWIGHT, J. 1925. The gulls (Laridae) of the world; their plumages, moults, variations, relationships and distribution. Bull. Amer. Mus. Nat. Hist., 52:63–402.

GROSS, A. O. 1940. The migration of Kent Island Herring Gulls. Bird-Banding, 11: 129–155.

HOFSLUND, P. B. 1959. Fall migration of Herring Gulls from Knife Island, Minnesota. Bird-Banding, 30:104–113.

KADLEC, J. A. AND W. H. DRURY, JR. 1968. Structure of the New England Herring Gull population. Ecology 99:644–675.

POOR, H. H. 1943. Color-banded immature Herring Gulls in the New York region. Bird-Banding, 14:101–115.

SCHREIBER, R. W. 1967. Roosting behavior of the Herring Gulls in central Maine. Wilson Bull., 79:421–443.

SCHREIBER, R. W. 1968. Seasonal population fluctuations of Herring Gulls in central Maine. Bird-Banding, 39:81–106.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York.

SMITH, W. J. 1959. Movements of Michigan Herring Gulls. Bird-Banding, 30:69–104.

TINBERGEN, N. 1953. The Herring Gull's world. Collins, London.

DEPARTMENT OF BIOLOGY, QUEEN'S UNIVERSITY, KINGSTON, ONTARIO, 8 DECEMBER 1970.

PUBLICATION NOTES AND NOTICES

RARE OR ENDANGERED FISH AND WILDLIFE OF NEW JERSEY. Edited by Donald S. Heintzelman. Science Notes No. 4, New Jersey State Museum, Trenton, N.J., 1971: 8½ × 11 in., paper covered, mimeographed, 23 pp. Free. Request from the Science Bureau, New Jersey State Museum, 205 West State Street, Trenton, N.J. 08625.

The last natural history survey in New Jersey was conducted more than 60 years ago. Since then, enormous environmental changes have taken place, resulting in declines of many species of vertebrates. The present report lists animals which are considered rare or endangered, or whose status is unknown. It is sobering to find that there are 37 rare species (including 14 birds), 18 endangered species (6 birds), and 22 species (6 birds) of undetermined status. The modest format of this report belies its importance as a conservation document. The report calls attention to the urgent need for surveys of the current status of wildlife resources in New Jersey, and for measures to protect vanishing animals.—P.S.

VARIATIONS IN SONGS OF VESPER SPARROWS IN OREGON

Donald E. Kroodsma

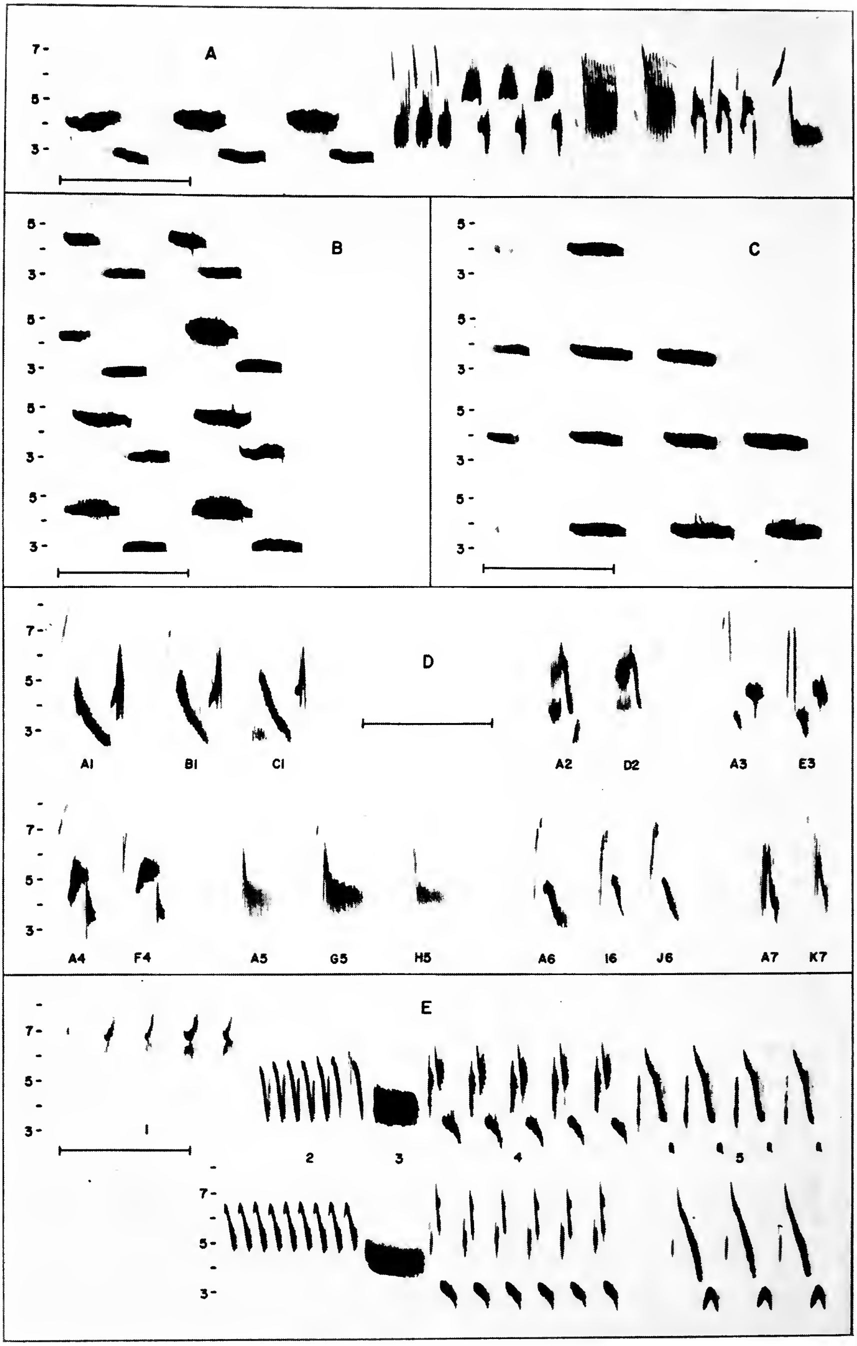
The Vesper Sparrow (*Pooecetes gramineus*) is an abundant breeding bird throughout much of its range, yet little is known about the behavior of this species. During the summers 1969–1971 I have listened to and recorded many Vesper Sparrow songs in the Willamette Valley of Oregon. Here I describe and discuss: 1) the song in the individual male, 2) noticeable dialect patterns in the songs, and 3) an apparent example of mimicry of a Bewick's Wren (*Thryomanes bewickii*).

I recorded songs at a tape speed of 7.5 ips on a Uher 4000 Report-L tape recorder using a MD405S Cardioid microphone in a 60 cm diameter parabolic reflector. The Kay Sonagraph with the wide (300 Hz) bandpass filter was used to prepare the sonagrams.

DESCRIPTION OF THE SONG

The songs of the Vesper Sparrow in Oregon are similar to those of the eastern subspecies described by Borror (1961). The song is a series of trills, and consists of two–four syllables of relatively long whistled notes followed by as many as seven trills (mean = 4.8, n = 507) of more rapidly repeated syllables (for terminology see Mulligan, 1966). A typical song from the William L. Finley National Wildlife Refuge (Fig. 1A) consists of three introductory syllables followed by five trills. The last trill is frequently abbreviated to a single syllable.

The introductory pattern in the songs of a given bird differ primarily in the number of syllables; when stimulated (e.g., by playback) fewer syllables are used with the more rapid singing rate. The remainder of the song is highly variable; in 400 songs from one individual I found 43 different trill types. Ten of the 43 different trills (often a single syllable) were used relatively infrequently (a total of 48 times) and only on the end of the song. No trill type was used exclusively following the introductory whistles, though two trill types were used here in 363 of the 400 songs (90.8 per cent). I found 218 different trill sequences in the 400 songs; the maximum number of consecutive songs with identical sequences was eight, but 175 of the 218 sequences were used only once. Some commonly used patterns involving two–three trills were apparent within the song, but the highly variable nature of the song is evident. Analyses of recordings from other males did reveal comparable variability.


A
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J6
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5

DIALECTS

For the eastern subspecies Borror (1961:170) describes the notes of the introductory pattern as being of "2 types, the first one or two being weaker and lower pitched than the rest." Peterson (1947, 1961, 1963) in his three field guides to the United States uses the same description. These are attempts to characterize the introductory phrases over large geographical areas, but a closer examination reveals apparent dialect patterns. At the Finley Refuge, Vesper Sparrows sing an introductory pattern as shown in Figure 1A and 1B; the syllables consist of two relatively pure frequency notes, the first higher pitched than the second. Only 5 km to the northwest, the introductory patterns are quite different, and consist of two–four notes of the same frequency (Fig. 1C). Approximately 8 km to the northeast from the Finley Refuge I heard still another introductory pattern from several males; it consisted of four notes, the first two of a higher frequency than the last two. This pattern of geographical variation in the introductory phrase is similar to the pattern found in the songs of some passerines where juvenile males learn their adult songs (e.g., Marler, 1967).

Of 60 trill types recorded from other Vesper Sparrows on the Finley Refuge, 10 (16.7 per cent) were identical to those in the repertoire of the single individual discussed above (Fig. 1D). Only one of 16 (6.2 per cent) trill types recorded from the location 5 km distant were identical. The sample size is insufficient as proof, but is suggestive that inter-locality differences may occur, probably as a result of song learning.

One prerequisite for maintenance of local dialects is that birds show a high degree of site tenacity to the locality where songs are learned. Adults do generally return to previous breeding sites (George, 1952), but no data are available for the young.

APPARENT INTERSPECIFIC MIMICRY

Further evidence suggesting that juvenile male Vesper Sparrows might learn their songs lies in the apparent mimicry of a Bewick's Wren song by a Vesper Sparrow (Fig. 1E). Vesper Sparrows are highly variable songsters.

←

Fig. 1. A, a typical Vesper Sparrow song from the Finley Wildlife Refuge. B, introductory patterns from songs of four different individuals at the Finley Refuge. C, introductory patterns from songs of four different individuals 5 km northwest of the Finley Refuge. D, seven syllable types of the well studied male (A) compared with syllable types of other males (B–K) on the Finley Refuge. Syllable types 1, 5, and 6 were found in 2 neighbors of Bird A. E, an atypical Vesper Sparrow song (top) and portions of two Bewick's Wren songs believed to be mimicked (below). The time markers indicate ½ sec, and the vertical scale is marked in kHz.

TABLE 1.
ANALYSIS OF 604 SONGS FROM ATYPICALLY SINGING VESPER SPARROW

Trill Sequence	Number of songs	Per cent
1–2–3–4–5	330	54.6
1–2–3–4–5–6	58	9.6
1–2–3–4–6	69	11.4
1–2–3–4–6–7	147	24.3
	$\Sigma = 604$	$\Sigma = 99.9$

and Armstrong (1963:73) rightly warns that "Very loquacious birds are apt to utter calls fortuitously resembling those of other species just as a silly person who talks incessantly will occasionally say something sensible." However, several facts do suggest the bird was indeed mimicking a Bewick's Wren. The introductory portion is very unlike that of any Vesper Sparrow; the average frequency is higher than that of any other trill encountered in this study, but is very similar to the high frequency notes which often precede the song of a highly stimulated Bewick's Wren. Syllable types 2–4 (Fig. 1E) are almost identical to those found in a single song type of most Bewick's Wrens at the Finley Refuge, and syllable type 5 is like that found in another song type shared by many of the wrens. I found no simple buzzes like syllable type 3 inserted into normal Vesper Sparrow songs. I studied 604 songs from this individual; all began with syllable types 1–4, but one or two other trills (numbers 6 and 7, not illustrated), both typically Vesper Sparrow, were also used (see Table 1). This relative lack of variability in number (only seven) and sequences (only four) of trill types is very atypical for Vesper Sparrows (see above), but the rigid sequence is like that found in the song types of the Bewick's Wren.

Spectrographic analysis revealed the apparent mimicry, but the reactions of three neighboring, territorial male wrens indicated that even the wrens mistook the identity of this bird. The Vesper Sparrow usually sang from several trees in a small clearing which was bordered on two sides by dense riparian vegetation. Early in the spring when the sparrow approached the riverbottom, the wrens responded with the *pit* or *chit* notes used nearly exclusively in territorial encounters (Miller, 1941, and pers. observ.). In addition, the wrens frequently countersang with the song type in their repertoire which resembled the song of the Vesper Sparrow. Later in the season it appeared as if the wrens had habituated to the song, for they responded less aggressively.

Thus, the evidence indicates that Vesper Sparrows may learn part or perhaps all of their songs. Normal song development in many species requires hearing conspecific males. Wild birds of these species may incorporate into their subsong the calls or songs of other species, but the adult song is usually free of such mimicry. If juvenile males are isolated in captivity and tutored with the songs of other species, they do occasionally learn that species' song. The Chaffinch (*Fringilla coelebs*) and the Western Meadowlark (*Sturnella neglecta*) are two examples (Thorpe, 1961 and Lanyon, 1960, respectively). Non-captive Indian Hill Mynahs (*Gracula religiosa*) learn their call notes from conspecifics, and do not normally mimic other species; captive Mynahs, on the contrary, are renowned for their imitative abilities (Bertram, 1970).

Varying degrees of isolation in the field could also prevent sufficient exposure to songs of conspecifics. A bird raised by an isolated pair and which subsequently wanders through marginal habitats could be insufficiently exposed. Since Vesper Sparrows normally migrate to southern California and if young males are normally receptive in the fall, a bird of a very late summer brood might be exposed to few songs prior to migration. Occasionally a few birds do over-winter in the Willamette Valley. A non-migratory bird would very likely be totally isolated from birds of its own species. In a migratory species it is unlikely that a critical period for song learning occurs during the winter season when most males are silent. However, if young males are usually receptive in the spring, the onset of territorial behavior and perhaps the critical period for song learning in an over-wintering juvenile male could occur prior to the return of conspecifics. As in the laboratory, a secondary preference for the songs of other species might then be expressed. Exposure to wren songs is no difficulty, for wrens are abundant and remain territorial and sing throughout the year.

The very reduced repertoire of this atypically singing Vesper Sparrow perhaps also suggests some isolation from singing conspecifics. One intuitively expects, within limits of course, that if songs are learned or developed through listening to adults, the greater the exposure the more will be learned. Thus, juvenile male Bewick's Wrens learn their songs from adult males during their first summer, and those hatched early in the breeding season develop more syllable types and song types than those hatched later when the singing intensity of adults is reduced (Kroodsma, in prep.).

SUMMARY

The song of the Vesper Sparrow in Oregon consists of a whistled introductory phrase followed by as many as seven different trills. One well-studied individual had a repertoire of 43 different trill types, and sang 218 different trill sequences in 400 songs. The similarities of the trills among neighboring males and the consistent inter-locality differences in the introductory whistled notes suggest that Vesper Sparrows learn at least portions of their songs from adult conspecifics. One male had a reduced song repertoire and sang like a Bewick's Wren; insufficient exposure to songs of adult conspecifics may cause interspecific learning.

ACKNOWLEDGMENTS

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LITERATURE CITED

ARMSTRONG, E. A. 1963. A study of bird song. Oxford Univ. Press, London.

BERTRAM, B. 1970. The vocal behavior of the Indian Hill Mynah, *Gracula religiosa.* Anim. Behav. Monogr., 3:79–192.

BORROR, D. J. 1951. Songs of finches (Fringillidae) of Eastern North America. Ohio J. Sci., 61:161–174.

GEORGE, J. L. 1952. The birds on a southern Michigan farm. Unpubl. Ph.D. Thesis, University of Michigan, Ann Arbor. (Cited in: Berger, A. J. 1968. Eastern Vesper Sparrow. *In*: O. L. Austin, Jr. (Ed.) Life histories of North American cardinals. grosbeaks, buntings, towhees, finches, sparrows, and allies. U. S. Natl. Mus.. Bull. 237:868–882.)

LANYON, W. E. 1960. The ontogeny of vocalizations in birds. p. 321–347. *In*: W. E. Lanyon and W. N. Tavolga (Eds.). Animal sounds and communications. A.I.B.S., Washington, D. C.

MARLER, P. 1967. Acoustical influences in birdsong development. Rockefeller Univ. Review, Sept.–Oct.:8–13.

MILLER, E. V. 1941. Behavior of the Bewick Wren. Condor. 43:81–99.

MULLIGAN, J. A. 1966. Singing behavior and its development in the Song Sparrow. *Melospiza melodia.* Univ. California Publ. Zool., 81:1–76.

PETERSON, R. T. 1947. A field guide to the birds. Houghton Mifflin Co., Boston.

PETERSON, R. T. 1961. A field guide to western birds. Houghton Mifflin Co., Boston.

PETERSON, R. T. 1963. A field guide to the birds of Texas and adjacent states. Houghton Mifflin Co., Boston.

THORPE, W. H. 1961. Bird song: The biology of vocal communication and expression in birds. Cambridge Univ. Press, Cambridge.

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PUBLICATION NOTES AND NOTICES

PESTICIDES AND WILDLIFE. [By J. A. Keith and R. W. Fyfe.] Canadian Wildlife Service, Ottawa, 1971: 6½ × 9 in., paper covered, 24 pp., photographs. No price given.

A collection of four articles about research, chiefly in Canada, on the side effects on various wildlife species of the use of agricultural and industrial chemicals. The authors are biologists in the Canadian Wildlife Service. The articles repeat each other to some extent and the story is no longer new; nevertheless the message is well set forth in non-technical language. To quote Fyfe: "If I have been attacking anything, it is all untested and unjustified use, together with the continued defense of widespread applications, of the broad spectrum persistent biocides which are affecting this environment: our environment and that of our children."—P.S.

FACTORS INFLUENCING PELLET EGESTION AND GASTRIC pH IN THE BARN OWL

Charles R. Smith and Milo E. Richmond

The volume of literature considering the food habits of owls approaches prodigious proportions (see Earhart and Johnson, 1970). Much of this information has been derived from analysis of the pellets of non-digestible matter which these raptors egest periodically. A number of authors have reviewed this technique and its applications (Craighead and Craighead, 1956; Errington, 1930, 1932; Fisher, 1893, 1896; Glading, Tillotson and Selleck, 1943; Moon, 1940). In spite of the widespread interest in raptor-pellet analysis and application of this procedure for estimating food intake of these birds in the wild, very little information is available on the factors relative to the processes of pellet formation and egestion in birds of prey (Farner, 1960).

The Great Horned Owl (*Bubo virginianus*) is the only owl for which pellet formation has been studied (Reed and Reed, 1928). Other papers considering pellet "formation" in owls have been concerned largely with the intervals between feeding and pellet egestion and have not dealt directly with the digestive processes involved in pellet formation or the factors which determine pellet egestion (Chitty, 1938; Howard, 1958; Sensenig, 1945). Two extensive life history studies of the Barn Owl (*Tyto alba*) by Guérin (1928) and Wallace (1948) offer some information relative to pellet formation and egestion in that species. It is the intent of this paper to present further information relative to the processes involved in pellet formation and egestion in the Barn Owl.

MATERIALS AND METHODS

The Barn Owl used in this investigation was obtained near Johnson City, Tennessee, at the age of approximately 20 days, as determined by plumage description (Bent, 1938; Roberts, 1955). The bird was kept in captivity and fed small mammals and birds (both alive and dead), beef liver, and a commercial liquid vitamin supplement ("ABDEC") until it was about 8 weeks old. At the age of 8 weeks, the bird was moved from its outdoor cage into a laboratory at East Tennessee State University and tests which required regular handling were begun. The owl adapted readily to laboratory conditions and required no special housing or handling technique. A laboratory colony of prairie voles (*Microtus ochrogaster*) provided the primary food source for the owl. At first, the voles were fed to the owl dead; later, the owl learned to take and kill live voles which were either released into the cage or placed on the floor of the lab.

To determine the pH of the gastric contents, a stomach sample was obtained by inserting a 10-mm pipette equipped with suction bulb into the esophagus of the bird until it reached the region of the gizzard. By this method samples of volume from 0.5 to 1 ml could be withdrawn from the region of the gizzard and from the proventriculus. The bird showed no adverse effects from this procedure which was sometimes conducted

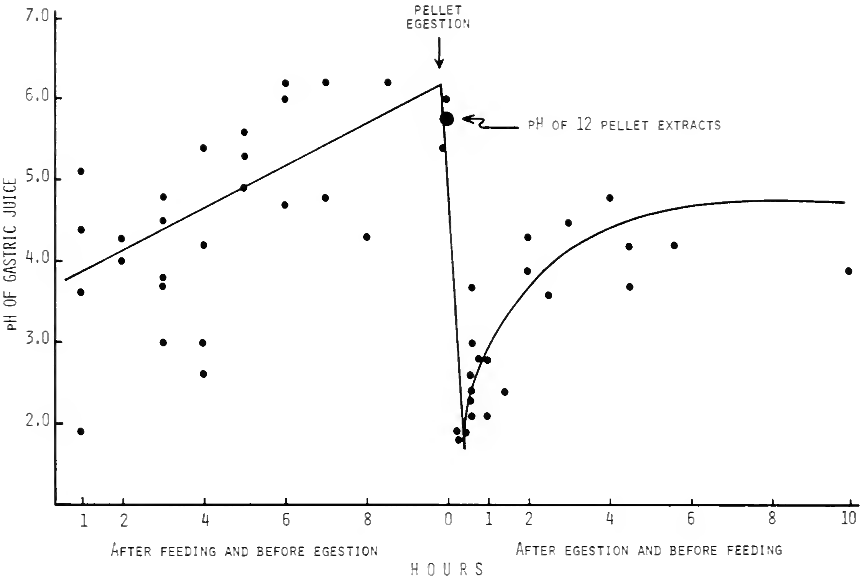

Fig. 1. Changes in gastric pH of the Barn Owl before and after feeding (curve fitted by inspection).

at hourly intervals for a 12-hour period. The pH of the samples was determined by using a Corning "Model Six" portable pH meter. The presence or absence of free HCl in stomach samples was detected with standard Topfer's solution, but the sample size was insufficient for accurate titration of the quantity of free HCl. The pH of extracts squeezed manually from newly egested pellets was also determined with the pH meter.

RESULTS AND DISCUSSION

Gastric acidity.—A total of 58 stomach samples, taken both before and after the bird had eaten, provided data for the cumulative graph of gastric acidity in Figure 1. The data show that the pH gradually rises after feeding and continues to increase until pellet egestion. Within an hour after pellet egestion, there is a precipitous drop, followed by another rise until the pH values stabilize in the vicinity of 4.0. Farner (1960), reported a gastric pH range of 3.53–4.90 for the Barn Owl. Our data (Fig. 1) show a much wider range of pH extending from 1.9 to 6.2. The low pH values immediately following egestion indicate a gastric state especially conducive to high peptic activity and proteolysis since the optimum state for these activities is in the vicinity of pH 2.0 (Farner, 1960).

Figure 2 shows the results of two separate days of pH recordings at hourly intervals under different conditions. Equal amounts of food were given at

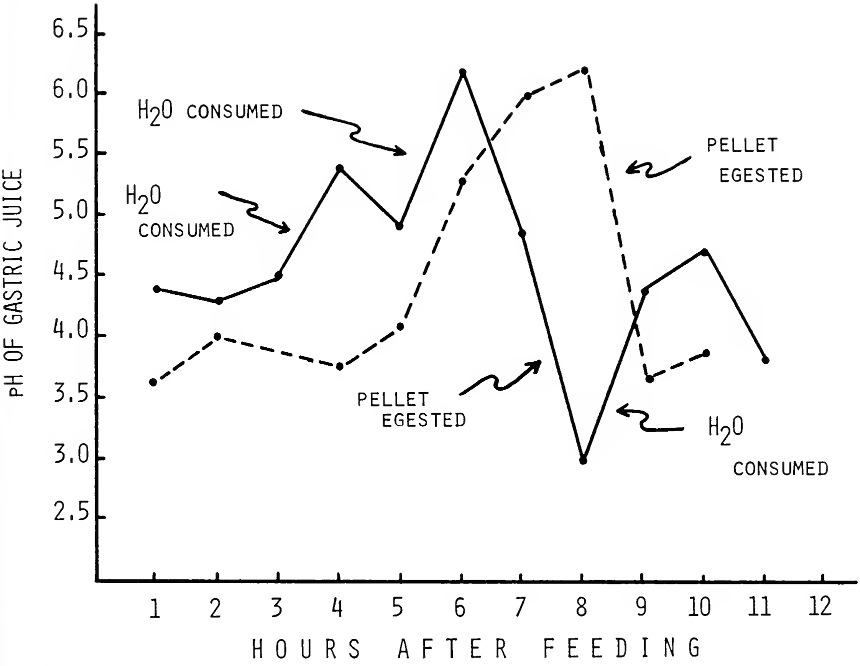

FIG. 2. Hourly changes in the pH of the gastric juice of the Barn Owl with (solid line) and without (dashed line) water available.

the same time on each day; however, in one case drinking water was available and in the other it was not. Excess food was not available in either case. With water available, the increase in pH during hours 4 and 6 and the generally higher pH values prior to pellet egestion followed known water consumption. Clearly, the water consumed reduced the acidity of gastric contents. The graph of gastric acidity obtained in the absence of water closely resembles the graph of Figure 1, which also was made in the absence of drinking water. The pH values of extracts from freshly egested pellets were very similar to the pH values of stomach samples taken within an hour before pellet egestion. Contrary to the observations of Reed and Reed (1928) on the Great Horned Owl, free HCl was found in stomach samples from the Barn Owl on six separate occasions when pH values ranged from 1.9 to 3.4. Free HCl was present most often immediately after pellet egestion or soon after the owl had been shown a live vole.

Classically, there are three phases to the secretion of gastric juice: the cephalic, the gastric, and the intestinal (Houssay, 1955). The cephalic phase involves the stimulus of gastric secretion as a result of external factors, such as the sight or smell of food, mediated through the cerebral cortex. The mechanisms involved form the basis for classical Pavlovian conditioning. According to Farner (1960), a true cephalic phase of gastric secretion is lacking in the domestic fowl. Walter (1939), however, reported gastric juice secretion in ducks in the response to auditory stimuli. Our results would indicate that a cephalic phase of gastric secretion is present in the Barn Owl. We learned, for example, that the pH of gastric contents decreased markedly within one-half hour after we entered the room in which the owl was kept. This decreased pH, indicative of increased HCl secretion in anticipation of food, was observed numerous times when live voles were placed in view of the owl but outside its cage. Free HCl was also present in stomach samples taken after the owl had been shown a live vole, and the same marked drop in gastric pH was observed in the bird after it had been fasted and then was allowed to observe live prey.

Pellet formation.—There is some disagreement in the literature as to where in the digestive tract pellet formation occurs. Welty (1963) suggests that the pellet is formed in the gizzard. Wallace (1955) states that pellet formation occurs in the proventriculus. Guérin (1928) felt that the gizzard played a significant role in pellet formation because of its highly muscular qualities. He also reported that dissection revealed pellet material in both the proventriculus and gizzard at different times, but he did not relate its place of occurrence to either times of feeding or pellet egestion.

Probing with the pipette while taking gastric samples indicated the presence of pellet material in both the proventriculus and the gizzard at different times. However, probing immediately before egestion indicated that the pellet was located in the proventriculus and not in the gizzard.

Reed and Reed (1928) reported that the "stomach" musculature in the Great Horned Owl is weak and not capable of exerting a great deal of force. These authors apparently were referring to the glandular stomach (proventriculus) since the gizzard is noted for its muscular structure. The muscular ability of the proventriculus of the Barn Owl closely resembles that of the Great Horned Owl. This seems to argue against the proventriculus playing any major role in the process of pellet formation. However, it is possible that the proventriculus could function as a repository for a freshly formed pellet prior to egestion. It is our contention, then, that the pellet is formed by the muscular action of the gizzard during digestion. At some stage after the completion of digestion, the freshly formed pellet passes out of the gizzard into the proventriculus where it remains until the proper stimulus for egestion is received.

Pellet egestion.—Initial observations suggested that the time of feeding had some influence on the time of subsequent egestion. To test this possibility, food was offered at various times of the day and night. All feedings between

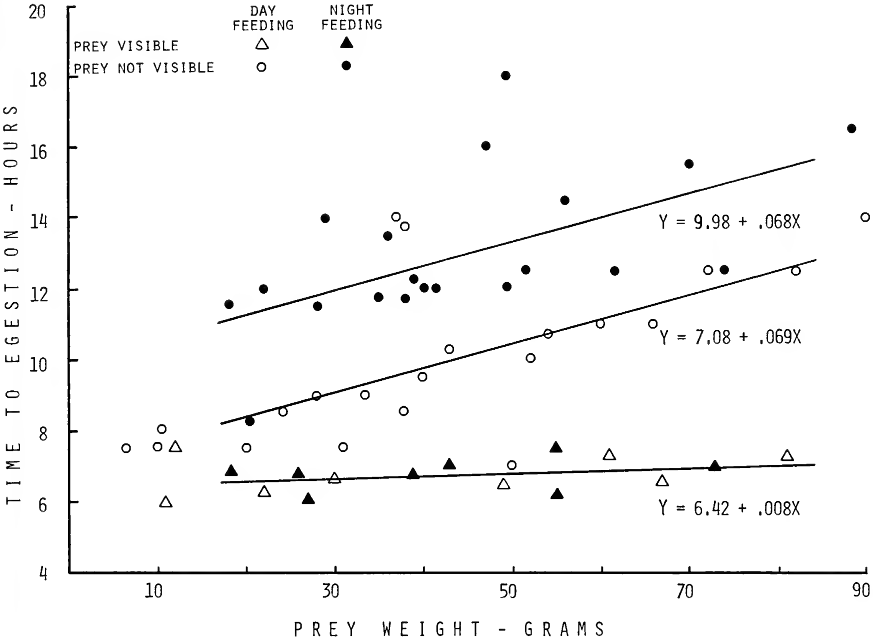

FIG. 3. The effects of feeding time, prey weight and visible prey on pellet egestion in the Barn Owl.

06:00 and 14:00 were arbitrarily grouped as "day feedings," while feedings from 16:00 until 24:00 were considered "night feedings." Figure 3 illustrates the effects of both time of feeding and food weight on the subsequent egestion of a pellet. The Y intercepts of the two lines (day = 7.08, night = 9.98) are different, showing that time between feeding and pellet egestion is longer at night than during the day. The calculated slopes from day and night feedings are significantly different from zero ($P \leqslant 0.05$) but not different from each other, pointing out that increasing prey weight delayed pellet egestion in the experimental owl regardless of time of feeding. Similar observations have been reported for the Short-eared Owl (*Asio flammeus*) (Chitty, 1938).

The Great Horned Owl (Reed, 1925) and the Tawny and Short-eared Owls (Chitty, 1938) have been observed to egest a pellet when presented with another food item. Guérin (1928) reported a similar phenomenon in the Barn Owl in Europe, and Reed (1897) observed a similar reaction in American Barn Owls. Our Barn Owl could be induced to egest a pellet simply by allowing it to see a live vole after a sufficient time had elapsed since the last feeding.

In order to examine the degree of influence of excess available prey on the normal pattern of pellet egestion, the bird was fed a prey item of known weight after which a wire cage containing additional live prey was placed in view of the bird. The owl could be observed from outside the room and as soon as the pellet was egested, the bird was given another weighed meal. This was continued with different size prey during both day and night periods until the owl killed and stored the prey instead of eating it. A total of 16 food-induced pellets, obtained in this manner, provided the data for the bottom line in Figure 3 which indicates that no difference in time until pellet egestion exists between day and night feedings when the owl is aware of the possibility of a subsequent meal. In addition, the slope from the pooled day-night feedings does not differ from zero even though prey weight varied from 10 to 81 grams. Since the stimulation provided by live prey was present during both day and night feedings, and since the prey consumed varied in weight from 10 to 81 grams, it is obvious that neither quantity consumed nor time of feeding delayed pellet egestion when a potential meal was in view.

The minimum time elapsing before the owl could be induced to egest a pellet by additional prey was about 6.5 hours ($Y = 6.42$ hours). A few pellets have been recovered under unusual circumstances in less time but the normal pattern for the bird is to continue eating prey when available prior to the 6.5-hour critical period and then form one large pellet which is egested long after the first meal was taken. Guérin (1928) also showed that subsequent feeding delayed pellet egestion in the Barn Owl. Few of our data relate to this, but the indication is that mice swallowed at intervals of less than 6 hours act to delay pellet egestion until the last prey item is digested. Obviously, this delaying effect has limits governed by the bird's capacity, but on several occasions two, three, and four mice have been consumed over an 8-hour period and all have been incorporated into a single pellet. Likewise, it is not unusual to find four, five, and even six *Microtus* skulls in a single Barn Owl pellet collected at a roost. Such instances are probably the result of continuous food intake with the intervals between successive meals never exceeding the critical 6.5-hour period after which a pellet would be formed and could be egested in response to the detection of a potential prey item.

Since pellet egestion can be prey-induced but is normally delayed when capture intervals are short, a bird completing a successful night of hunting would require the daylight hours to digest the mass of food it had collected. In the case of either a successful night of hunting or a poor night during which no mice were caught late enough to stimulate pellet egestion, the pellet formed and egested at the day roost would contain remains of everything the bird had consumed. The factors which determine the length of time that a pellet will be retained are (1) the length of time since the last food was consumed, which in this study was at least 6.5 hours, and (2) the detection or capture of a prey item by the bird. Chitty (1938) suggested that hunger determines the length of time that a pellet is retained in the digestive tract before egestion. Hunger, however, would be a direct consequence of the bird not having prey available. In the absence of prey the pellet would be retained, not as a result of hunger, but as a result of a lack of the proper stimulus (available prey) for pellet egestion. This does not mean that egestion cannot occur in the absence of a stimulus but clearly it is delayed in such instances.

It is reasonable to assume, then, that most of the pellets collected at the roost site of a wild Barn Owl represent one successful night of hunting for each pellet. The possible exception to this would be those pellets egested on the feeding ground on a night of hunting during which only two or three mice were caught, with a period of 7 to 8 hours between any two successive captures (e.g., during a long winter night). In such a situation, a pellet would probably be egested away from the roost site, as suggested by Craighead and Craighead (1956) and reported by Guérin (1928). The egestion of such a pellet would be triggered by the last mouse caught. The pellet egested the next day, however, would still represent as much as half of the previous night's catch. One could judge the possibility of such an occurrence by determining the owl's hunting success as indicated by the number of prey items in each of the pellets collected at the roost. Small pellets containing only one prey item would be indicative of egestion away from the roost site and detract from the reliability of making judgments about food consumption from roost pellet collections.

SUMMARY

The factors influencing rates of pellet formation and egestion were studied in a Barn Owl kept in captivity for 6 months. The pH of the gastric contents changes according to a regular pattern from feeding until pellet egestion, but it could not be implicated definitely as a mechanism that triggers actual egestion. Data on gastric pH demonstrate the presence of a cephalic phase of digestion. The pellet is formed in the gizzard within 6 hours after ingesting a meal, and is passed into the proventriculus where it is held until egestion. Pellets are not egested at a fixed interval after taking a meal; the interval is dependent in part upon quantity of food consumed, time of feeding and availability of a subsequent meal. Increased prey weight and night feedings prolong the time to egestion but have no effect when a subsequent meal is available.

LITERATURE CITED

Bent, A. C. 1938. Life histories of North American birds of prey. U. S. Natl. Mus. Bull., 170.

Chitty, D. 1938. A laboratory study of pellet formation in the Short-eared Owl (*Asio flammeus*). Proc. Zool. Soc. London, Ser. A, 108:267–287.

Craighead, J. J., and F. C. Craighead, Jr. 1956. Hawks, owls, and wildlife. Stackpole Co., Harrisburg, Pennsylvania.

Earhart, C. M., and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor, 72:251–264.

Errington, P. L. 1930. The pellet analysis method of raptor food habits study. Condor, 32:292–296.

Errington, P. L. 1932. Technique of raptor food habits study. Condor, 34:75–86.

Farner, D. S. 1960. Digestion and the digestive system. *In* A. J. Marshall (Ed.), Biology and comparative physiology of birds, Vol. 1, Academic Press, New York, pp. 411–467.

Fisher, A. K. 1893. The hawks and owls of the United States in their relation to agriculture. U. S. Dept. Agric., Div. of Ornithol. and Mammal., Bull. 3.

Fisher, A. K. 1896. Food of the Barn Owl. Science, 3:623–624.

Glading, B., D. F. Tillotson, and D. M. Selleck. 1943. Raptor pellets as indicators of food habits. California Fish and Game. 29:92–121.

Guérin, G. 1928. La vie des Chouettes. Regime et Croissance de l'Effraye commune *Tyto alba alba* (L) en vendée. P. Lechevalier. Paris.

Houssay, B. A. 1955. Human physiology. McGraw Hill. New York.

Howard, W. E. 1958. Food intake and pellet formation of a Horned Owl. Wilson Bull., 70:145–150.

Moon, E. L. 1940. Notes on hawk and owl pellet formation and identification. Trans. Kansas Acad. Sci., 43:457–466.

Reed, B. P. 1925. Growth, development, and reactions of young Great Horned Owls. Auk, 42:14–31.

Reed, C. I., and B. P. Reed. 1928. The mechanism of pellet formation in the Great Horned Owl (*Bubo virginianus*). Science, 68:359–360.

Reed, J. H. 1897. Notes on the American Barn Owl in eastern Pennsylvania. Auk, 14: 374–383.

Roberts, T. S. 1955. A manual for the identification of the birds of Minnesota and neighboring states. Univ. of Minnesota Press. Minneapolis.

Sensenig, E. C. 1945. The formation of pellets by the Barred Owl. Wilson Bull., 57: 132.

Wallace, G. J. 1948. The Barn Owl in Michigan. Tech. Bull. 208. Michigan State College Agric. Expt. Sta., East Lansing. Michigan.

Wallace, G. J. 1955. An introduction to ornithology. Macmillan Co., New York.

Walter, W. G. 1939. Bedingte Magensaftsekretion bie der Ente. Acta Brevia Neerl., 9:56.

Welty, J. C. 1963. The life of birds. Alfred A. Knopf. New York.

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ANALYSIS OF MEASUREMENTS, WEIGHTS, AND COMPOSITION OF COMMON AND ROSEATE TERN EGGS

Charles T. Collins and Mary LeCroy

An abundance of data has been presented on various aspects of the eggs of birds. Most studies have been concerned with intraclutch, intraspecific, and interspecific variations in egg color and dimensions (Coulson, 1963; Preston, 1953, 1957; Preston and Preston, 1953; and others) with little information being given on egg weights and almost none on the proportions of the various egg components. Data of all sorts are particularly incomplete for semiprecocial species as skuas, gulls, and terns. In this light it seemed worthwhile to gather information on this aspect of the annual cycle of the Common Tern (*Sterna hirundo*) and Roseate Tern (*Sterna dougallii*) as a part of a wider study of the reproductive biology of these species nesting on Great Gull Island, Suffolk County, New York. Further information on this colony and the growth and development of chicks of both tern species is presented elsewhere (Cooper, Hays, and Pessino, 1970; Hays, 1970; LeCroy and Collins, 1972).

METHODS

For this analysis 20 freshly laid eggs of each species were collected at random on Great Gull Island in early June 1967, at which time egg laying was just beginning. To insure freshness, eggs were only taken from areas which were checked daily for new nests and from nests containing but a single egg. In most cases this would be the first egg of a multi-egg clutch but some cases may have represented single egg clutches. It was expected that removal of eggs this early in the reproductive cycle would result in renesting by the pair and thus minimize any losses to the colony. A larger sample size was not considered necessary and might in fact have interfered with other studies being conducted in the colony. Weights were taken to the nearest tenth of a gram on a triple beam balance. Linear measurements were made to the nearest tenth of a millimeter by means of dial calipers. The data collected in this study are presented as a mean ($\bar{x}$) accompanied by the range and ± twice the standard error of the mean ($S_{\bar{x}}$) which for large samples closely approximates the 95 per cent confidence interval. When these intervals are nearly equal in length and nonoverlapping, the difference between the samples can be considered significant at the 5 per cent level (Simpson, Roe, and Lewontin, 1960:353).

EGG SIZE

The data on the size of Common and Roseate Tern eggs are presented in Table 1. Roseate eggs were significantly narrower than those of Common Terns, leading to an also significantly lower shape index. This difference in shape did not, however, appreciably affect the overall weight of the eggs, which was similar in both species (Table 1.). It should be remembered that

TABLE 1
SIZE OF COMMON AND ROSEATE TERN EGGS

	Mean ($\bar{x}$)	Twice Standard Error ($\pm 2 S_{\bar{x}}$)	(Range)
Common Tern (N = 20)			
Length (mm)	42.94	±0.642	(40.4–45.9)
Width (mm)	30.49	±0.316	(29.2–31.9)
Shape Index[a]	72.91	±1.378	(67.3–78.4)
Weight (g)	21.01	±0.540	(18.7–23.8)
Roseate Tern (N = 20)			
Length (mm)	43.90	±0.890	(40.5–48.5)
Width (mm)	29.90	±0.272	(28.8–31.0)
Shape Index[a]	69.82	±1.470	(64.5–76.8)
Weight (g)	20.56	±0.540	(19.2–23.7)

[a] 100 × width/length.

these samples represented only the first egg of multi-egg clutches or in some cases single egg clutches. As there is a great deal of intraclutch variation in linear measurements (Gemperle and Preston, 1955; LeCroy, unpubl.) these apparent specific differences may not hold true when the full scope of egg sizes in the colony are considered. Such interspecific differences were not found for the remaining data collected on the eggs of these terns. Thus it is unlikely that the conclusions based on these data would be altered by larger sample sizes or analysis of intraclutch variation.

EGG SIZE RELATIVE TO BODY WEIGHT

No body weights for adult Common and Roseate Terns are available for a period when eggs were being laid or when eggs used in this study were collected. Adult body weights for both species for the period 29 June–2 July 1968 are as follows: Common Tern (N = 56) 116.1 ± 1.646 g (range, 103–129 g); Roseate Tern (N = 46) 107.7 ± 1.898 g (range, 92–125 g). Using these values, the eggs of Common and Roseate Terns are respectively 18.1 per cent and 19.3 per cent of adult body weight. Such high values seem typical of many terns and other semiprecocial birds while those for most altricial species are appreciably lower, frequently less than 10 per cent (Lack, 1968). The larger bird species in nearly all taxa show a pronounced decrease in the egg weight/body weight ratio which is independent of developmental pattern (Lack, op. cit.).

TABLE 2
COMPOSITION OF COMMON AND ROSEATE TERN EGGS

	Shell	Albumen	Yolk
Common Tern	2.22 ± 0.094[a]	12.87 ± 0.422	5.94 ± 0.256
(N = 20)	(10.6%)	(61.2%)	(28.2%)
Roseate Tern	2.21 ± 0.086	12.26 ± 0.416	6.10 ± 0.248
(N = 20)	(10.7%)	(59.6%)	(29.7%)

[a] Mean weight in grams ± 2 standard errors of the mean.

COMPOSITION OF THE EGG

The composition by weight and on a per cent basis are highly similar in both species as shown in Table 2. The egg contents were poured from one half-shell to the other until the albumen had been separated from the yolk. The weight of the remaining shell and yolk was subtracted from the whole egg weight to determine the weight of albumen removed. The shell (including shell membrane) was then weighed separately and the yolk weight determined by subtraction. As the weighing was done in the field at the colony no attempt was made to determine dry weights for any of these components as has been done by some other workers (Reid, 1965).

DISCUSSION

Newly hatched young birds have long been assigned to one or the other of two categories by their degree of maturity at hatching, e.g., precocial or altricial. Analysis of egg sizes associated with these categories has shown that species producing precocial young tend to lay large eggs relative to their body weight, and ones in which the yolk makes up 30 to 40 per cent of the total egg weight. On the other hand, those species producing altricial young tend to produce smaller eggs relative to their body weight and ones containing only 15 to 25 per cent yolk. As noted earlier, the eggs of larger birds in most taxa are smaller, relative to body weight, and they also tend to contain relatively less yolk than those of closely related but smaller species.

The wide variation in developmental regimes makes the separation into but two categories extremely difficult and misleading. The expanded classification of Nice (1962:18) recognizes eight categories of maturity at hatching based on the manner of getting food, amount of down, activity, and development of sight at hatching. In addition to making it possible to categorize newly hatched young in a more realistic manner, this classification sequence serves to point out the existence of a gradual transition in developmental patterns from that of the highly precocial species which are nearly indepen-

TABLE 3

COMPARISON OF EGG CHARACTERISTICS IN PRECOCIAL, SEMIPRECOCIAL, AND ALTRICIAL SPECIES

	Egg Components (percentage by weight)			Yolk/Albumen Index
	Shell	Albumen	Yolk	
Precocial Birds				
Average of 10 species[a]	11.9	52.9	35.2	.665
Average of 5 species[b]	10.5	56.4	33.1	.586
Semiprecocial Birds				
Common Tern	10.6	61.2	28.2	.470
Roseate Tern	10.7	59.6	29.7	.506
South Polar Skua[c]	8.6	65.2	26.2	.409
Altricial Species				
Average of 10 species[a]	7.0	73.2	19.8	.276
Average of 4 species[b]	7.7	70.9	21.4	.305

[a] From: Romanoff and Romanoff, 1949.
[b] From: Asmundson, Baker, and Emlen, 1943.
[c] From: Reid, unpublished, in Reid, 1965.

dent at hatching to that of the extremely helpless altricials requiring great amounts of parental care at the other. Semiprecocial birds, as skuas, gulls, and terns, fall near the middle of this sequence in that at hatching they are down covered, their eyes are open, yet they stay in or near the nest and are fed by the adults for several weeks.

The available information suggests that there has also been a gradual shift in the relative amount of the components of bird eggs which goes along with this transition in developmental pattern. The species with the more precocial young tend to produce larger eggs with relatively more yolk. The extremely precocial species of megapodes have eggs containing in excess of 60 per cent yolk, while the eggs of most precocial species have 30–40 per cent and most altricials 15–25 per cent yolk (Nice, 1962:25). Our data for Common and Roseate Terns and that of Reid (1965) for the South Polar Skua (*Catharacta maccormicki*) along with that previously available for other species (Nice, 1962:25) indicate that the intermediacy of semiprecocial species extends to the component characteristics of their eggs as well (Table 3). Eggs of semiprecocial species usually contain between 25–30 per cent yolk which is more than is found for the altricial and semialtricial groups but less than for the eggs of precocial species. Table 3 also shows that the relative amount of albumen increases during the transition from the precocial to altricial mode of development. Shell weight is believed to be more a product of the size of the bird and the incubation regime to which it is subjected (Welty, 1962). The yolk/albumen index (Table 3) incorporates the relative changes of both of these components with the different levels of maturity at hatching and thus may be more helpful in indicating the changes in the components of eggs associated with the several developmental patterns utilized by birds. Further study is needed before the relative role of these components can be determined for the different developmental patterns. Laboratory analysis of the chemical composition of these components in species with different developmental patterns would also seem a fruitful area for further work.

SUMMARY

Eggs of Common (*Sterna hirundo*) and Roseate (*Sterna dougallii*) Terns, were collected on Great Gull Island in June 1967. Roseate Tern eggs were significantly narrower than those of Common Terns and had a significantly lower shape index. Such specific differences were only found for the linear measurements and even these differences may not be consistent when the full range of interclutch and intraclutch variation is considered. Egg weight of Common and Roseate Terns was 18.1 per cent and 19.3 per cent respectively of adult weight, which is typical of values recorded for other species of terns. The weights of egg shell, yolk and albumen were highly similar for both species with yolk making up 28–30 per cent. This is appreciably higher than in the eggs of altricial species and less than for precocials. These data point out the correlation between the changes in egg component proportions and the several developmental patterns of birds.

ACKNOWLEDGMENTS

We would like to thank all of the investigators who have been working in the tern colony on Great Gull Island, whose work has helped and complemented ours. Gary and Mary Sue Schnell very kindly allowed us to use their unpublished weights of adult terns. Great Gull Island research was supported by the Mae P. Smith Gull Fund, the Anne S. Richardson Fund, and by the Linnaean Society of New York. Preparation of the manuscript for publication was supported by a grant from the United States Atomic Energy Commission at (38-)-310 to the University of Georgia.

LITERATURE CITED

Asmundson, V. S., E. A. Baker, and J. T. Emlen. 1943. Certain relations between the parts of birds' eggs. Auk, 60:34–44.

Cooper, D., H. Hays, and C. Pessino. 1970. Breeding of the Common and Roseate Terns on Great Gull Island. Proc. Linnaean Soc. New York, 71:83–104.

Coulson, J. C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. Proc. Zool. Soc., London, 140: 211–227.

Gemperle, M. E., and F. W. Preston. 1955. Variation in shape in eggs of the Common Tern in the clutch sequence. Auk, 72:184–197.

Hays, H. 1970. Great Gull Island report on nesting species 1967–1968. Proc. Linnaean Soc. New York, 71:105–119.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. Ltd., London.

LeCroy, M., and C. T. Collins. 1972. Growth and survival of Roseate and Common Tern chicks. Auk, 89:In Press.

NICE, M. M. 1962. Development of behavior in precocial birds. Trans. Linnaean Soc. New York, 8:1–211.

PRESTON, F. W. 1953. The shapes of birds' eggs. Auk, 70:160–182.

PRESTON, F. W. 1957. Pigmentation of eggs: Variation in the clutch sequence. Auk, 74:28–41.

PRESTON, F. W., AND E. J. PRESTON. 1953. Variation of the shapes of birds eggs within the clutch. Ann. Carnegie Mus., Pittsburgh, 33:129–139.

REID, B. 1965. The Adelie Penguin (*Pygoscelis adeliae*) egg. New Zealand J. Sci., 8:503–514.

ROMANOFF, A. L., AND A. J. ROMANOFF. 1949. The avian egg. John Wiley and Sons, New York.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative zoology. Harcourt, Brace & World, Inc., New York.

WELTY, J. C. 1962. The life of birds. A. A. Knopf, New York.

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NEW LIFE MEMBER

A new Life Member of the Wilson Society is Dr. Ronald A. Ryder, Professor of Wildlife Biology at Colorado State University, Ft. Collins, Colorado. Dr. Ryder holds two degrees from Colorado State and has his doctorate from Utah State University. He is the author or co-author of more than 60 scientific papers on a wide variety of subjects. His professional interests have centered on waterfowl, raptors, and grassland birds. He is an Elective Member of the AOU, and a member of the Cooper Society, Western Bird-Banding Association (Past President), The Wildlife Society, Sigma Xi, Society of American Mammalogists, and several other conservation societies. Dr. Ryder is married and has two children, and as is typical of most of the professional members of the Society, his hobbies also center around wildlife and other outdoor activities. Many members of the Society will remember Dr. Ryder as the efficient Chairman of the Local Committee for the 1970 joint meeting with the Cooper Society at Ft. Collins.

THE ROLE OF AVIAN RICTAL BRISTLES

Roger J. Lederer

It has long been assumed by many workers that rictal bristles are characteristic of insectivorous birds and are employed as accessory food-capturing structures (Welty, 1962; Van Tyne and Berger, 1965). Others have said that the bristles serve a tactile function (Küster, 1905; Chandler, 1914; Stresemann, 1934; Wallace, 1955; Pettingill, 1970). No convincing evidence has been gathered to date to demonstrate the actual function of these bristles but it appears that their use as an insect scoop is negligible or nonexistent.

Facial bristles are modified hairlike feathers which may run along the rictal region as rictal bristles in many diverse groups of birds such as the Apterygidae, Caprimulgidae, Aegothelidae, Mimidae, Accipitridae, and Tyrannidae. They may also encircle the eyes as eyelashes and lie over the top of the bill as loral bristles in numerous species. Facial bristles are fairly stiff, tapering to a point at the end and there may be barbs present on the rachis (Fig. 1). Filoplumes are hairlike also, but the shaft is weak and naked except for the tip which has a few barbs. The distribution, length, and number of bristles vary widely among species.

One function proposed for these structures is sensory, analogous to vibrissae in mammals. Küster (1905) reported finding avian lamellar corpuscles at the base of the rictal bristles in some owls. Küster suggested that the bristles may react to sound waves and that they are similar to mammalian tactile hairs. Schildmacher (1931) reported finding pressure-sensitive corpuscles at the base of many feather-types.

Chandler (1914) proposed that rictal, as well as other facial bristles, cover the face where ordinary feathers would be subject to excessive wear and tear.

Seemingly the most obvious application of rictal bristles is as an aid to in-flight feeding by facilitating prey capture. Theoretically, a bird which captures insects in flight would be benefited by stiff hairlike structures positioned about the bill in such a way as to form a funnel and thus giving the bird a larger effective gape, providing a more efficient capturing mechanism. It seems that the bird would only have to make some minor head movements to implement the device. However, this appears not to be the case.

A cursory examination of a number of bird families indicates that there is little or no relation between the presence, dimensions, or number of facial bristles and a tendency towards aerial feeding or insectivorous habits. The Tyrannidae, Parulidae, and Caprimulgidae, for example, capture flying insects and possess well developed rictal bristles. But the Mimidae, Turdidae,

FIG. 1. Cluster of rictal bristles of the Alder Flycatcher (*Empidonax traillii*). Seven millimeters in length.

Icteridae, Corvidae, and Apterygidae (Kiwi), which are somewhat insectivorous, yet rarely, if ever (the Kiwi, never), feeding in flight, also possess well developed bristles.

Figures 2 and 3 are examples of bristle arrangement in two species with

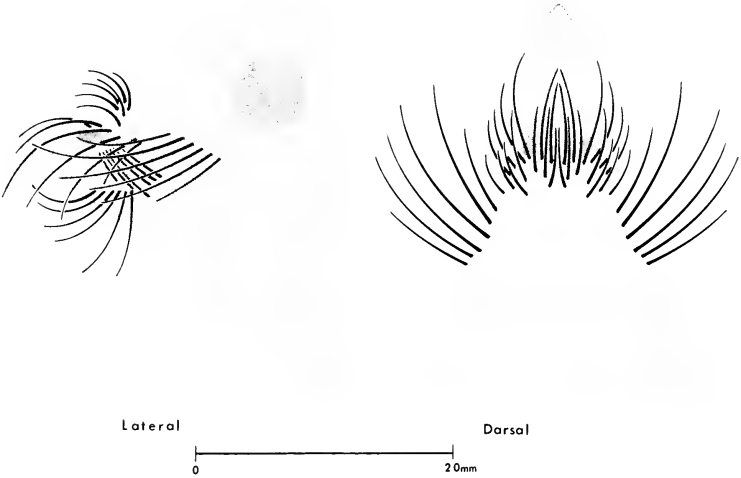

FIG. 2. Dorsal and lateral views of the head of *E. traillii*, showing the number and arrangements of facial bristles. Length of skull is 31 mm, width at widest point is 22 mm.

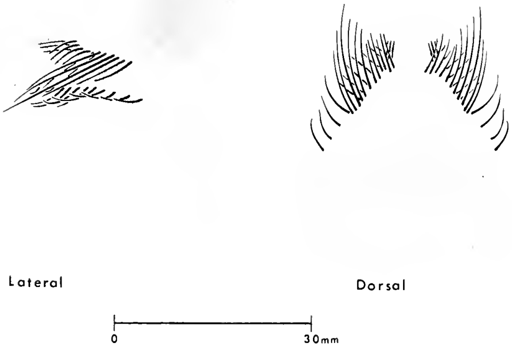

FIG. 3. Dorsal and lateral views of the head of the Brown Thrasher (*Toxostoma rufum*), showing the number and arrangement of facial bristles. Length of skull is 61 mm, width at widest point is 36 mm.

different feeding habits. The Alder Flycatcher (*Empidonax traillii*) forages by sitting erect on a low perch, watching for an insect to fly by, occasionally flying out to capture one, and returning to the same perch or one nearby (Bent, 1942; personal observation). The Brown Thrasher (*Toxostoma rufum*) forages in the ground litter by poking with its bill for insects, seeds, and berries; frequently the bill is thrust into the ground in search of prey (Engels, 1940). If there is any relation between the arrangement and/or number of rictal bristles and feeding behavior in these two species, it is not apparent.

I have direct evidence that, at least in several tyrant flycatchers, rictal bristles perform no function associated with prey capture. With the use of a high-speed motion picture camera, I photographed mid-air captures of flesh flies (*Sarcophaga bullata*) by the Crested Flycatcher (*Myiarchus crinitus*), Eastern Phoebe (*Sayornis phoebe*), Eastern Wood Pewee (*Contopus virens*), and some *Empidonax* species which could not be identified in the film. The films were taken while the birds were confined in a large glass-fronted cage into which the flies were introduced. Photographs were taken at the rate of 375 frames per second and analyzed on a stop-action projector. Over 30 sequences of prey capture were recorded and in every instance in which a capture or near-capture was made, the insect was caught between the tips of the mandibles.

The prey are captured in the bill tips, rather than farther back in the mouth as would be the case if rictal bristles were utilized. Observation indicates that flycatchers normally seize their prey with a rapid closure of the bill, frequently resulting in an audible "snap." The upper mandible of these birds also forms a distinct downward hook at its anterior end (Fig. 2). It appears that this hook is an aid to seizing and holding prey. My observations in the field and laboratory both indicate that mid-air captures of insects by flycatchers occur as follows: a) The bird approaches the insect with jaws agape; b) when the tips of the mandibles are in close proximity to the prey, the jaws begin to close; c) the jaws close rapidly, trapping the prey in the bill tips.

I suggest that flycatchers and probably other birds with similarly shaped bills that catch insects in flight, do not use their rictal bristles in the process. Non-aerial feeders probably do not use their bristles in feeding, at least not for prey capture. Some birds which are aerial feeders but have very different bills, such as goatsuckers, swallows, and swifts, have a large gape. They probably do not use bristles in prey capture, although I would not exclude this possibility.

It appears as if the use of rictal bristles as an aid to aerial prey capture by arthropod-eating birds has been casually accepted without definitive evidence.

The most logical explanation for the presence of rictal bristles is that they perform some sort of sensory function. Further investigation is obviously warranted.

SUMMARY

Proposed explanations for rictal bristles are that they perform tactile functions, serve as an insect scoop, or protect other facial feathers. In the Tyrannidae, at least, motion pictures indicate that they do not play a part in prey capture.

ACKNOWLEDGMENTS

I would like to thank Drs. T. H. Frazzetta, S. C. Kendeigh, M. F. Willson, and Mr. D. Schemske for their helpful comments on the manuscript. The Zoology Department at the University of Illinois provided funds for photographic equipment and supplies. Miss A. Boatwright kindly rendered the drawings.

LITERATURE CITED

Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U. S. Natl. Mus. Bull., 179.

Chandler, A. 1914. Modifications and adaptations to function in feathers of *Circus hudsonius.* Univ. California Publ. Zool., 11:329–396.

Engels, W. L. 1940. Structural adaptations in the thrashers with comments on interspecific relationships. Univ. California Publ. Zool., 42:341–400.

Küster, E. 1905. Die Innervation und Entwicklung der Tastfeder. Morphol. Jahrb., 34:126–148.

PETTINGILL, O. S., JR. 1970. Ornithology in laboratory and field. Fourth ed. Burgess Publishing Co., Minneapolis.

SCHILDMACHER, H. 1931. Untersuchungen über die Funktion der Herbstschen Körperchen. J. Ornithol., 79:374–415.

STRESEMANN, E. 1927–1934. Aves. *In* Kükenthal u. Krumbach, Handbuch der Zoologie. Volume 7, Part 2. Walter de Gruyter, Berlin.

VAN TYNE, J., AND A. J. BERGER. 1959. Fundamentals of ornithology. John Wiley and Sons, Inc. New York.

WALLACE, G. J. 1955. An introduction to ornithology. Macmillan Co., New York.

WELTY, J. C. 1962. The life of birds. W. B. Saunders Co., Philadelphia.

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PUBLICATION NOTES AND NOTICES

FAMILIES OF BIRDS. By Oliver L. Austin, Jr. Illustrated by Arthur Singer. Golden Press, New York City, 1971: 4 × 6 in., 200 pp. Many illustrations in color. Paper cover $1.95, hard cover $5.95.

An attractive reference book that provides thumbnail sketches of all known orders and families of birds, both living and fossil. A surprising amount of information is contained in a small space. The illustrations, generous in supply, depict species that are typical of their families; they are nicely executed and well printed, and are real aids in characterizing the families. This guide "is designed for those who have familiarity with birds and who would like to known more about their relationships to one another." Distribution, characteristics, and habits are adequately summarized within the limits of the book, but very little is said about relationships. Nevertheless this guide can serve well as a handy reference tool for ornithologists.—P.S.

NATIVE BIRDS OF MT. DESERT ISLAND AND ACADIA NATIONAL PARK. By James Bond. The Academy of Natural Sciences of Philadelphia, 1971: 5 × 7 in., paper covered, v + 28 pp. $1.50.

This is the second revised edition of an annotated list of the 138 species of birds that are known to breed or to have bred on Mt. Desert Island and adjacent islands, Maine, during the past 40 years. It is primarily a guide to bird finding in this ornithologically well known area but also gives remarks on the historical status of species.—P.S.

NATIVE AND WINTER RESIDENT BIRDS OF TOBAGO. By James Bond. The Academy of Natural Sciences of Philadelphia, 1970: 4 × 7 in., paper covered, v + 30 pp. $1.50.

An annotated list of the nearly 200 species of birds reported from Tobago. This island on the continental shelf of South America has a much richer avifauna than any of the other Antilles of comparable size. Six excursions for finding birds are suggested. The booklet gives aid for identification of indigenous and South American species but it is intended to be used with a field guide.—P.S.

GENERAL NOTES

Probable Bulwer's Petrel off Key West, Florida.—I observed a small, all dark petrel with a long wedge-shaped tail that I identified as a Bulwer's Petrel (*Bulweria bulwerii*) off the Florida Keys, about 15 miles east-southeast of Rebecca Light on 14 May 1969. Rebecca Light is west of Key West, approximately two-thirds of the distance to the Dry Tortugas, from which islands we were returning at the time.

One of a group of three petrels flew in to within 50 feet of our boat and stayed alongside for almost a minute. It was a uniform brownish-black with a somewhat lighter brownish band across the upper surface if its wings. Its flight was more like a shearwater than a storm petrel. It did not have the latter's fluttering flight, but rather had a gliding flight and used its wings only sparingly and then only in short bursts. In size, this bird was much smaller than Audubon's Shearwater (*Puffinus lherminieri*), several of which we had seen only a few minutes before, and larger than the storm petrels, even than the Black Petrel (*Loomelania melania*). While I realize that size comparisons based on non-contemporaneous sight records are open to some question, I had seen Black Petrels less than three weeks earlier when three of them followed our ship from the Gulf of Panama toward the Galapagos for two days.

Dr. George E. Watson of the Smithsonian Institution, who concurs with my identification, adds "In the Atlantic Ocean the Bulwer's Petrel breeds only on Madeira and the Cape Verde Islands but regularly, it seems, migrates south and west toward the Americas. It has been recorded in the Caribbean and may even be a regular migrant in the southeast Caribbean and near Trinidad. Many more observations are needed from that part of the Caribbean to establish any regular pattern of occurrence (if indeed a pattern exists). Your observations near the Tortugas, however, may only be regarded as extraordinary vagrants."

The 1957 edition of the A.O.U. Check-list in its Hypothetical List contains an old and uncertain record of the Bulwer's Petrel from Greenland. Until such time as a specimen or photograph of this bird can be obtained for North America, it must remain as a hypothetical.—Joseph W. Taylor, *20 Parish Road, Honeoye Falls, New York 14472, 19 November 1971.*

Spring migration of the Gannet in Florida waters.—The Gannet (*Morus bassanus*) is a regular winter visitor to Florida waters (Sprunt, Florida bird life, Coward-McCann, New York, 1954, p. 17), but little is known of its spring migration. Palmer (Handbook of North American Birds, 1:308, 1962) reports that spring migration begins in March with the majority of birds gone from Florida waters by about mid-April. The earliest dates of migration for Florida are 3 March off the east coast at Cocoa (Stevenson, Audubon Field Notes, 12:273, 1958) and 15 March off the Gulf coast at Alligator Point, near Panacea (Stevenson, Audubon Field Notes, 9:252, 1955) but these birds may not have been migrants. The latest dates are 2 June at Alligator Point (Cunningham, Audubon Field Notes, 20:497, 1966) and 27 June about 12 miles northwest of Key West (Sprunt, Auk, 65:315, 1948).

Palmer (op. cit.:308) states that for the first three years Gannets stay at sea all year. Thomson (Brit. Birds, 32:286, 1943) reports that some young, non-breeding British Gannets remain in African waters, the winter range of the population, throughout the breeding season. I know of no records of Gannets of any age in Florida waters for July and August. Several observers have described a correlation between the age of Gannets and the time of migration. Cruickshank (Birds around New York City, Amer.

Mus. Nat. Hist., 1942) notes that in the New York area the majority of the early migrants are in adult plumage, and the majority of the later migrants are younger. Wodzicki and Stein (Emu, 58:296, 1958) note the same correlation for New Zealand Gannets. Stevenson (Audubon Field Notes, 12:273, 1958; 13:286, 1959) reports that adult-plumaged birds outnumbered younger birds in migration on two occasions in March off the east coast of Florida.

During the spring of 1971 I recorded Gannet movements and plumages in the Straits of Florida about 5 miles southeast of Marathon, Key Vaca, where on three occasions small, compact flocks were seen flying steadily northeast low over the water. No fishing or other activities were noted. The 70 Gannets I observed flew over water 75 to 100 feet deep near a reef parallel to the Florida Keys. Water depth increases rapidly seaward of the reef into the Straits of Florida. On 28 February 44 adult-plumaged Gannets were seen moving northeast in flocks of two to seven at the rate of nine birds per hour. On 4 April 23 Gannets, 18 adult-plumaged and five subadult and immature-plumaged, were seen moving northeast at the same rate. The largest flock was five. On 10 May three Gannets, one subadult and two immature-plumaged, were seen flying northeast at the rate of two birds per hour. No Gannets were seen during three subsequent trips on 17 and 31 May and 7 June.

These observations indicate that Gannet migration off Florida has begun by late February, which is earlier than previously supposed, and terminates in May. Furthermore, my observations indicate that adult-plumaged birds begin migration at an earlier date than subadults and immatures, with a mixing of age classes in April. That the Gannets followed the reef edge and avoided deep water suggests they are offshore and not pelagic birds. This may explain the lack of records of the species in the West Indies (Bond, Check-list of birds of the West Indies, 1940 and supplements) even though they occur annually in the southern Straits of Florida. This offshore habit is characteristic of other Gannet populations (Thomson, op. cit.:283–284), although New Zealand Gannets are known to migrate over sea from New Zealand to Australia by crossing the Tasman Sea and to Indian Ocean pelagic waters (Wodzicki and Stein, op. cit.:289). I wish to thank Dr. William B. Robertson, Jr. of the U. S. National Park Service and Dr. Glen E. Woolfenden of the University of South Florida for helpful suggestions on improving this manuscript.—Terry C. Maxwell, *CMR Box 7248, Homestead AFB, Florida 33030 (Present Address: 1025 Cactus Lane, San Angelo, Texas 76901), 10 July 1971.*

Aerial feeding in the Snowy Egret.—The Snowy Egret (*Leucophoyx thula*) is well known for its diversified feeding behavior. Catching aquatic prey while in flight has been noted by several authors. Bond (Auk, 51:500–502, 1934), Sprunt (Auk, 53:203, 1936), Grimes (Auk, 53:439, 1936) and Meyerriecks (Wilson Bull., 71:153–158, 1959) described a feeding behavior which Meyerriecks (op. cit.:154) called "hovering-stirring." An egret so engaged hovers near the water and with one or both feet agitates the water or stirs vegetation or debris beneath it. I have observed Snowy Egrets using hovering-stirring on several occasions in southern Florida. I have also witnessed a different method of aerial feeding which may be called "foot-dragging." Employing this technique, an egret flies just above the water with legs dangling beneath. It drags the toes of both feet through the water and takes prey from the water while in direct flight without hovering. I have only seen small organisms taken during such behavior and these were swallowed while the bird was in flight. A third type of aerial feeding has been noted by Dickinson (Auk, 64:306–307, 1947) and Jenni (Ecol. Monogr., 39:258, 1969) who reported Snowy Egrets feeding in direct flight but without dragging their feet.

I first observed foot-dragging on 22 March 1969 at a pond in the Big Cypress Swamp of southern Florida. Additional observations were made at Mrazek Pond in Everglades National Park on 10 December 1970. Certain conditions prevalent during the first series of observations are pertinent in accounting for the use of such active feeding techniques.

The pond, 0.25 hectares in area, is composed of two vegetation zones—a peripheral area of emergent grass (*Paspalium* spp.) and a central area which during periods of high water is filled with submerged naiad (*Najas flexilis*). During intervals of low rainfall, the water level in the Big Cypress Swamp drops. Fish and other aquatic organisms become concentrated within the pond from the surrounding swamp and marshlands. If low water levels occur at the proper time, these organisms provide a highly concentrated food source for numerous herons, storks and ibises which then frequent the pond. The feeding aggregation of wading birds and other aspects of the ecology of this pond were described by Kushlan (An ecological study of an alligator pond in the Big Cypress Swamp of southern Florida. M.S. Thesis, University of Miami, Coral Gables, Florida. 1972, 197 pp.). On 22 March 1969 herons began to arrive at the pond at 06:10 just after first light. Snowy Egrets first flew into the pond at 06:17 and began to feed immediately; by 06:45, 450 Snowy Egrets were feeding there. These birds were dispersed throughout the shallow emergent zone where they stood upon the trampled grass and used stand and wait feeding behavior exclusively. By 07:00 many herons including several hundred Snowy Egrets had left the pond. At 07:15 one Snowy Egret began feeding using foot-dragging behavior while flying from one side of the pond to the other. On each pass it flew low over the grass and upon reaching the open water of the central area it began to drag its feet in the water continuing this for the length of the pond—a distance of approximately 30 meters. Four other Snowy Egrets joined the first and these birds fed in this manner for 10 minutes. Meanwhile other Snowy Egrets continued to stand in the grass and although some successfully captured prey most did not attempt to feed.

In this instance stand and wait behavior was used early in the morning when the oxygen concentration of the water is lowest and fish are concentrated near the surface of the pond (Kushlan, op. cit.). Snowy Egrets began to use the more active technique when fish were less available and, from qualitative observation, success using stand and wait behavior was limited. These observations support the contention of Meyerriecks (Nat. Hist., 71:57, 1962) that such active feeding methods are resorted to when other methods fail or when other areas of habitat are not productive. Further evidence is derived from observations of Louisiana Herons (*Hydranassa tricolor*) at the pond. Few were present in 1969 during the period when the wading bird aggregation actively utilized the pond. However several fed in the pond on 30 March 1969 after the activities of wading birds had reduced fish density (Kushlan, op cit.). At that time Louisiana Herons along with Snowy Egrets fed by hovering-stirring almost exclusively.—JAMES A. KUSHLAN, *Department of Biology, University of Miami, Coral Gables, Florida 33214, 4 October 1971.*

Observations on the status, ecology, and behavior of Soras wintering in Trinidad, West Indies.—The Sora (*Porzana carolina*) winters from the southern United States to northern South America, but it has been considered rare on Trinidad, West Indies (Leotaud, Oiseaux de l'Isle de la Trinidad, 1866, p. 495; Herklots, The birds of Trinidad and Tobago, Collins, London, 1961, p. 74). Belcher and Smooker (Ibis, 1935: 279–297, 1935), who found most of the other species of rails known from the Island, never collected the Sora, although they did attribute to this species a nest, on which basis they hypothesized the existence of a local breeding race. Although the egg measurements they list do fall within the size range reported for the Sora by Bent (U.S. Natl. Mus. Bull., 135:305, 1926) no such race has been discovered, and the measurements also match those given by the same authors (op. cit.) for *Laterallus exilis.*

From February to May 1965, I studied the ecology of a freshwater impoundment on the northeastern edge of the Caroni Swamp in Trinidad, and during this time I saw and heard many Soras. My observations were made only during the dry season. I first observed Soras foraging on exposed mudflats among the extensive beds of rushes (*Cypressus articulatus* and *Eleocharis mutata*), and later flushed them from these rushes wherever there was standing water. I occasionally flushed Soras from the dense stands of the emergent arum (*Montrachardia arborescens*) on the banks of the Caroni River itself, but I did not find them among the lower emergent vegetation such as water hyacinth (*Eichornia crassipes*) and a "morning glory" (*Ipomea aquatica*) which were frequented by the smaller Yellow-breasted Crake (*Porzana flaviventer*). This latter species, only recently reported from Trinidad, (ffrench and ffrench, Wilson Bull., 78:5–11, 1966), was also common in the marsh.

As the dry season progressed, more and more of the marsh was left without standing water, and the Soras moved into the remaining wet areas with taller vegetation (up to 1.2 meters) which they had previously shunned. The same shift in habitat was noted for the Common Gallinule (*Gallinula chloropus*), Wattled Jacana (*Jacana jacana*), and Stripe-backed Bittern (*Ixobrychus involucris*), but not for the Spotted Rail (*Rallus maculatus*) nor Yellow-breasted Crake which are perhaps more tolerant of drier conditions.

Several authors (Bond, Birds of the West Indies, Houghton Mifflin Co., Boston, 1961; Slud, Bull. Amer. Mus. Nat. Hist., 128:84, 1964; and Wetmore, Smithsonian Misc. Coll., 150:350, 1965) have indicated that the Sora is not very vocal on its wintering grounds, and Soras which I observed elsewhere in the West Indies were, indeed, silent. On Trinidad, however, I often heard spontaneous calls which I attributed to Soras. Two notes, a brief nasal *ka* and a more plaintive *peeyanh* ending with a rising inflection were similar to call notes I have heard from Soras on their breeding grounds. Once in April I heard the typical "whinny" call. The size of the wintering Sora population was estimated from the number of birds flushed while walking transects through the marsh, from the number of spontaneous calls, and from calls elicited by exploding firecrackers. I estimated that no fewer than 40 and perhaps 50 to 80 Soras were present in 26 hectares of marsh. Of the birds seen well two-thirds were in immature plumage. Soras were encountered on all 15 visits from 25 February to 24 April, but despite careful coverage none were found on 4 visits from 30 April to 6 May. The maximum daily count was 30 birds on 20 March, but this probably reflects unusually extensive coverage rather than an influx of northbound migrants from South America. No birds were collected so information on stomach contents is not available, but on one occasion a Sora was observed apparently feeding on small gastropods adhering to the emergent vegetation.—Michael Gochfeld, *Department of Ornithology, American Museum of Natural History, New York, New York 10024, 16 March 1971.*

Young Common and Roseate Terns learning to fish.—There is very little information in the literature on young terns learning to fish for themselves. Palmer (Proc. Boston Soc. Nat. Hist., 41:93, 1941) observed the young birds following the adults in flight and returning to shore to be fed, but he was unable to observe the changeover to self-feeding. Tomkins (Wilson Bull., 71:320, 1959) noted that in the Least Tern flying young accompany the adult, who catches a fish and alights on the water to give it to the young. In view of the scarcity of information on this critical period, observations I made on Great Gull Island, Suffolk County, New York, may be of interest.

On 29 September 1969, in the mouth of the Thames River at New London, Connecticut, about 7 miles north of Great Gull Island, many terns were resting on the exposed rocks and old pilings near shore. One juvenile Common Tern (*Sterna hirundo*) was begging with head directed upward, apparently toward an adult overhead. The young bird flew suddenly upward, circled once and landed on the water. The adult landed in front of the chick and put its bill into the water. The young bird, very close in front of the adult, put its bill into the water, then raised it and swallowed a fish. The adult had apparently passed a fish to the young under water.

On 26 September 1970, after most of the terns had left Great Gull Island, I noticed four Common Terns fishing near the western end of the island. There were two adult-juvenile pairs, as Tomkins (loc. cit.) reported for the Least Tern. For approximately 10 minutes I observed the adults skimming, diving, flying just above the surface and circling the area; they were closely followed in these maneuvers by the young. Fish must have been abundant and near the surface as both adults caught fish easily. After about 10 minutes the original four birds were joined by another adult—young pair of Common Terns and by an adult—young pair of Roseate Terns (*S. dougallii*). These eight birds continued the follow-the-leader actions described above for another 20 minutes before leaving the vicinity of the island.

During the 30 minutes of observations the young terns were never seen to actually enter the water, always halting their dives abruptly just short of the surface, nor were they seen to catch a fish. Once an adult caught a fish and flew up with it until it was in front of the young, dropped it and caught it again before it had fallen more than a few feet. While adult terns do occasionally drop fish and catch them in this manner, it seemed significant that the adult flew to the young before dropping the fish.

A Common and a Roseate Tern caught as downy chicks and offered live killifish regularly for several weeks in captivity, watched the live fish from a distance but never ate one, although both learned to eat cut up fish from a bowl. This behavior and the observations reported above lead me to believe that the young tern must learn to respond to living fish as an item of food and must then learn and perfect the technique for catching them. Presumably the learning period is lengthy. Hays and Donaldson in a study of post-breeding dispersal (in prep.) report a young Common Tern nine weeks of age being fed by an adult. Partial dependence on the parents may extend even to the wintering quarters (Ashmole and Tovar S., Auk, 85:90–100, 1968) especially for chicks hatching late in the season.

I would like to thank Dean Amadon and Helen Hays for comments on the manuscript. —MARY LECROY, *Department of Ornithology, The American Museum of Natural History, New York, N. Y. 10024, 26 July 1971.*

Lek behavior in the Broad-tailed Hummingbird.—I recently observed behavior in the Broad-tailed Hummingbird (*Selasphorus platycercus*) which I interpret as communal male displays, or lek behavior. These observations were made daily from 11–14 June 1971 at Moraine Park in Rocky Mountain National Park, Colorado, at an elevation of about 8,000 feet. I observed three male Broad-tailed Hummingbirds performing their characteristic U-shaped climbing and diving display flights along a steep, semi-wooded hillside of ponderosa pine. The three birds were separated from each other by about 7 meters and while I was unable to recognize individuals, identical locations were occupied on each of the four consecutive days. During these four days, I observed the display performance for a total of seven hours, during which time a single female approached to within about 2 meters of one of the end males on the second day (12 June). She remained quietly on a branch for 55 seconds and remained within sight of the display area, with occasional brief departures, for 39 minutes. At no time did she associate directly with any of the males, beyond her initial, brief approach.

The appearance of the female resulted in an increase in the frequency of courtship flights by each of the three males: I obtained a group mean of 4.8 seconds per complete display circuit per individual ($n = 18$, S.D. $= 0.8$) from arbitrarily-chosen samples during a ten-minute period beginning 15 minutes after the female's departure and a group mean of 3.5 seconds per display ($n = 11$, S.D. $= 0.6$) while the female was in the immediate area. The differences were significant ($p < 0.01$, t-test). An equivalent increase in display "intensity" upon arrival of females has been reported for the gallinaceous lek species.

I observed seven aggressive incidents among the three displaying males. Six of these were obviously initiated by the arrival of one male in the immediate vicinity of another. In all these cases, the intruding male retreated to his own display area following a brief confrontation in which the victorious proprietary male flew quickly at the intruder and then hovered immediately in front of him. In two cases, this was followed by a brief, mid-air scuffle lasting less than 3 seconds, while in the remaining four incidents, the intruder retreated immediately following this mid-air encounter. The seventh aggressive incident occurred in apparently "neutral" territory, following which both participants returned to their display areas with no obvious victor.

Isolated male-female courtships may still be the rule in the Broad-tailed Hummingbird. Thus, I observed four other examples of male courtship displays in which there was a female nearby and no other males were apparent. The frequency of display at this time appeared to be greater than in the lek with the female absent but lower than in the lek with the female present. It may also be significant that I never observed isolated males displaying in the absence of a female, while the three lek males described above displayed steadily with no female present.

I believe this to be the first report of lek behavior in a North American hummingbird. Possible selective advantages of lek behavior include providing greater stimulation to the female and hence increasing the probability of a successful mating by one of the participating males, possible stimulatory effects on the males themselves—hence resulting in a greater probability of a successful mating than if each were courting independently, greater range of selection for the female with a minimum of energy expenditure and/or facilitating location and recognition of males. Balanced against this would be the possible disadvantages of attracting greater numbers of predators to a commonly-used display area and the evolutionary disadvantage to individual males which may be consistently discriminated against in favor of a possible "master" within each lek.

These observations were made while conducting research supported by the Research Foundation of the State University of New York, the Theodore Roosevelt Memorial Fund of the American Museum of Natural History and The Society of the Sigma Xi.—David P. Barash, *Biology Department, State University College, Oneonta, New York 13820, 8 October 1971.*

Evidence of two Tree Swallow females sharing the same nest box.—On 13 June 1971, I observed eight eggs in a Tree Swallow (*Iridoprocne bicolor*) box, located in John F. Kennedy Memorial Wildlife Refuge, 6 miles south of Massapequa, Nassau County, New York. As I opened the box, I was able to capture and band a bird believed to be a female as it had a well developed brood-patch. A few hours later, I checked the box again and captured a different bird with an equally well developed brood-patch, incubating the eight eggs. I also banded this bird.

On 14 June there were five eggs and three young in the box; on 16 June, as well as on the following day, there were four eggs and four young; on 18 June, two eggs and six young; and on 19 June there were eight young. On all these days three birds staunchly defended the box. On numerous occasions, I waited until one of the three birds entered the nesting box and then I walked over and trapped the bird inside. Each time it was one of the two banded females. Once or twice the other two birds would alight on the nesting box when the third bird was inside.

The third bird was mist-netted and banded on 19 June, and had no evidence of an incubation patch. Because the bird had had no incubation patch, and because it never entered the box I believed it to be a male. According to (Kuerzi, Proc. Linnaean Soc., 52–53:27, 1941) and (Low, Bird-Banding 3:2, 1932) under normal conditions the female Tree Swallow incubates the eggs, and the male usually perches outside.

On 26 June all the young were found to be partially feathered, but on 5 July no young were found in the box although the nest was intact.

The young did not seem to be hindered by the extremely crowded conditions in the box and the three adults (two females and one male) were always observed near the box. Although adjacent boxes were also occupied and were as close as 50 feet only at this box were there three birds defending the nest. In four years of Tree Swallow study in this area, this was the first occurrence of more than six eggs (Schaeffer, EBBA News, 34:216–222, 1971). There is mention of four seven egg clutches (Paynter, Bird-Banding, 25:35–58; 102–110; 136–148, 1954). Yunick (Kingbird, 21:47–56, 1971) mentions two cases of eight egg clutches and in one of the cases there were two different egg shapes, pointing to a suspicion of two separate layings. Bent (Life histories of North American flycatchers, larks, swallows, and their allies, 1942), mentions two males and one female using the same box but makes no mention of two females and one male. It is possible that this is a case of two females sharing a nest because all the other boxes in this general area were taken; however, it is also possible that this is an isolated case of polygny, but other than the above I cannot offer solid evidence. I did not observe copulation between the male and any other bird because no visits were made to the Refuge during the appropriate time period.—HARVEY FARBER, *112-50 78th Avenue, Forest Hills, New York 11375, 22 September 1971.*

Steller's Jays prey on Gray-headed Juncos and a Pygmy Nuthatch during periods of heavy snow.—Members of the family Corvidae are typically omnivorous in their feeding habits, their diet consisting primarily if fruits, grains, berries, insects and occasionally eggs and nestlings of various small birds. There are also several reports in the literature of the unexpectedly high frequency of Blue Jay (*Cyanocitta cristata*) predation on red bats (*Lasiurus borealis*) (see D. F. Hoffmeister and W. L. Downes, Southwestern Naturalist, 9:102, 1964). Roth (Condor, 73:113, 1971) has recently reported an account of the Mexican Jay (*Aphelocoma ultramarina*) attacking and killing a small sparrow under conditions of heavy snow in southeastern Arizona.

Observations at feeding stations in Flagstaff, Coconino Co., Arizona, inhabited throughout the winter by juncos and Steller's Jays (*Cyanocitta stelleri*) have been made for several years. During periods of mild weather, jays and juncos show no antagonistic behavior toward each other, but during periods of extended cold weather and/or snow the presence of jays at the feeders is sufficient to keep juncos out of the immediate area.

In late December of 1970 Dr. and Mrs. Edwin H. Colbert observed a Steller's Jay capture and partially consume an adult Pygmy Nuthatch (*Sitta pygmaea*). A large flock of nuthatches had been attracted to a suet feeder near the Colbert house. An individual nuthatch flew into an open area in a large stand of pine (*Pinus ponderosa*) and was about 10 ft off the ground when a jay that had been perched on a branch in a nearby tree, swooped down on the nuthatch catching it in mid-air with its feet. The jay then flew back to its perch and as Dr. Colbert observed through binoculars, the jay used its beak to pluck and kill the nuthatch, holding it down with one foot while grasping the perch with the other. When the jay was approached it flew off into a deeper portion of the woods still clutching the dead nuthatch in its feet.

Another incident of Steller's Jay predation occurred on 20 February 1971, when during a heavy snowfall a jay was observed (Balda) attacking an adult Gray-headed Junco (*Junco caniceps*). The jay dove down to a platform feeder and caught the junco with its feet; it then flew about 40 ft to a perch in a pine where it proceeded to pluck and eat portions of the smaller bird. When the jay was approached it dropped the partially eaten carcass under the tree. Two days later when the snow began to melt, two other dismembered and partially eaten carcasses of Gray-headed Juncos were discovered. We believe these birds met their demise in the same manner as described above.

The weather preceding both of these incidents had been cold; the mean daily temperature for December 1970 was 4°C, with −11°C being the mean low for this month. Snow had fallen intermittently from 14 to 22 December, reaching a maximum depth of 53.3 cm by 22 December. The mean daily temperature for February 1971 was 7.3°C and the mean low was −8.3°C. Snow had begun falling on 17 February reaching a maximum depth of 30.5 cm by 21 February (U. S. Weather Bureau Records, 1970 and 1971, Flagstaff, Arizona).

Although jays are known to hold food objects with their feet while tearing them apart with their beak, we know of no other observation wherein a jay has been reported to capture prey with its feet during flight. Whether or not Steller's Jays make a habit of consuming other bird species as a food source during times of limited food availability is unknown. It is probable that during particularly harsh portions of the winter, lack of suitable vegetable material and insects force the jays to exploit alternate food sources. The facility with which the jays reported herein captured their unusual prey indicates that this food source may be exploited by jays to a greater extent than was previously thought.—Steven W. Carothers, N. Joseph Sharber, *Museum of Northern Arizona, Flagstaff, Arizona 86001* and Russell P. Balda, *Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86001, 1 October 1971.*

Adult Carolina Chickadee carries young.—On rare occasions when nests are disturbed certain species of birds have been known to pick up and move their eggs to different locations (Truslow, Natl. Geogr. Mag., 130:882–884, 1966; Pettingill, Ornithology in laboratory and field, Burgess Publ. Co., Minneapolis, 1970, p. 357). In addition, Welty (The life of birds, Alfred A. Knopf, New York, 1962, p. 336) and Pettingill (op. cit.:392) consider at least 10 known instances of non-passerine young being picked up and carried by their parents. This type of behavior is considered to be exceptional.

During the morning of 11 April 1971 we were examining a nest of a Carolina Chickadee (*Parus carolinensis*) which was located 10 m from shore in a small excavated cavity of a one meter-high post over the water of Cross Lake, near the western boundary of Shreveport, Louisiana. Due to a brisk wind the lake water was choppy so that some difficulty was had in maintaining the boat against or near the post in order to see into the nest. Because of the action of the waves, the post was jarred several times over a period of several minutes. There were four newly-hatched chickadees in the nest. After leaving the nest site, we saw an adult chickadee enter the nest and leave with something that was pink in color. It carried the object over the shoreline and disappeared into a grove of trees 50 m from the post. Shortly thereafter, the adult returned with what appeared to be food and entered the nest. With the aid of binoculars we now saw the adult leave the nest carrying a young bird. The bird flew in the same direction as the first time, holding the young bird in the beak, which was positioned around the body of the young bird. The additional two young were removed in the same manner. The entire removal took place in about 30 minutes. When observed again, the nest was empty of young and over a period of time the adult or adults did not reappear. Not more than one adult was seen at any one time. The shore area, where the adult disappeared with the young was searched but the new nest, if any, was not located.

In our observations of over 5,000 different nests that contained eggs or young, including the nests of 125 Carolina Chickadees, in northern Louisiana since 1963, we have never seen a parent bird carrying either its eggs or young, up to this time.—JOHN W. GOERTZ AND KIM RUTHERFORD, *Department of Zoology, Louisiana Tech University, Ruston, Louisiana 71270, 27 September 1971.*

Habitat differences of Swainson's and Hermit Thrushes.—Most Swainson's Thrushes (*Hylocichla ustulata*) along the coast of Maine nest in spruce forests; as a result, they seldom if ever overlap with Wood Thrushes (*H. mustelina*) or Veeries (*H. fuscescens*) in their breeding habits (see Morse, Wilson Bull., 83:57–65, 1971). However, potential overlap does occur with Hermit Thrushes (*H. guttata*), and here I report spatial relationships of these two species.

I censused populations of thrushes in spruce forests and mixed coniferous-deciduous forests on islands in Muscongus Bay (Lincoln and Knox Counties), and the adjacent mainland (Table 1). Techniques followed those prescribed in Audubon Field Notes for breeding bird censuses.

In the absence of congeners the Swainson's Thrush occupies a wider range of habitats than it does in their presence, as demonstrated by its presence on small islands (particularly on Wreck and Haddock Islands) (Table 1). Further, while Swainson's Thrushes were absent from certain islands some years, no Hermit Thrushes used them at these times (Table 1). Wreck and Haddock Islands support mixed forests of mountain and striped maples (*Acer spicatum* and *A. pennsylvanicum*), yellow birch (*Betula lutea*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). They have been damaged heavily by storms in some areas (described fully in Morse, Ecology, in press). Similar areas on the adjacent mainland are occupied by other species of *Hylocichla* (Morse, Wilson Bull., 83:57–65, 1971). In spruce forests on large islands and the mainland, Swainson's Thrushes usually appear in denser growth than does the Hermit Thrush. The spruce forests on Loud's, Harbor, and Marsh Islands (Table 1) have smaller trees (mean heights = 13–17 m) and denser growth than the mainland forests censused here, in Morse (op. cit.), and the forest on Hog Island (Morse, Ecology, 49:779–784,

TABLE 1
DISTRIBUTION AND NUMBERS OF BREEDING THRUSHES, 1967–1971.
Dash(–) indicates that area was not censused during a given year.

			Pairs of Hermit Thrushes					Pairs of Swainson's Thrushes				
Study area	Size of forest (ha) censused	% Coniferous Foliage	1967	1968	1969	1970	1971	1967	1968	1969	1970	1971
Sample study areas in large forests (25 ha+)												
Mainland	4.20	99	–	–	2	2	1	–	–	1	0	0
Hog Is.	4.50	99	–	–	1	1	1	–	–	1	0	0
Loud's Is.	4.50	99	–	–	–	1	0	–	–	–	4	3
Harbor Is.	4.50	99	–	–	–	–	0	–	–	–	–	5
Marsh Is.	2.40	99	–	–	–	0	0	–	–	–	2	1
Small forests (entire island censused)												
Wreck Is.	3.86	55	0	0	0	0	0	2	2	1	2	1
Haddock Is.	1.86	61	0	0	0	0	0	1	0	0	1	0
Thief Is.	1.50	99	0	0	0	0	0	1	2	2	2	1
Indian Is.	0.69	85	0	0	0	0	0	1	0	0	0	0
Crane Is.	0.53	99	0	0	0	0	0	0	0	0	0	0
Jim's Is.	0.49	90	0	0	0	0	0	0	1	0	0	1
Ram Is.	0.39	90	–	0	0	0	0	–	0	0	0	0
Crow Is.	0.35	60	0	0	0	0	0	0	0	0	0	0
Crotch Is.	0.16	98	0	0	0	0	0	0	0	0	0	0
Byer's Ship Ledge	0.11	96	0	0	0	0	0	0	0	0	0	0

1968) (mean heights = 19–21 m). Palmer (Bull. Mus. Comp. Zool., 102:1–656, 1949) also reported that Swainson's Thrushes frequented dense forests.

The expansion of Swainson's Thrushes on small islands into habitats similar to those occupied elsewhere by other Hylocichlas, combined with their absence in a wide variety of habitats adjacent to the spruce forests in this area (see Morse, Wilson Bull., 83: 57–65, 1971), suggest strongly that they usually are excluded from these areas by congeners. The absence of Hermit Thrushes on the small islands, even during years when several islands had no Swainson's Thrushes, is consistent with the argument that Swainson's Thrushes were not limiting the presence of Hermit Thrushes or other species on these islands.

While Swainson's and Hermit Thrushes use habitats somewhat differently, with the former being a more arboreal forager than the latter (Dilger, Wilson Bull., 68: 171–199, 1956), considerable spatial relief appears necessary (either vertically as in a tall forest, or horizontally as in the nature of blowdowns) for their coexistence. Dilger considers the Hermit Thrush to be a bird of forest-edge situations, and the Swainson's Thrush to be a bird of forest interiors. In spruce forests of this area, wind damage often produces a marked edge effect. Perhaps the largely undisturbed old-growth spruce forests are open enough to provide these characteristics as well.

The basis for the absence of Hermit Thrushes from the outer islands is not clear, but it parallels the absence of certain warblers characteristic of spruce forests (Morse, Ecology, 52:216–228, 1971). In that case, however, forest-edge species occur on the smallest islands supporting warblers (Myrtle, *Dendroica coronata*, and Parula, *Parula americana*, Warblers); in the case of thrushes the species typical of forest interiors (Swainson's) is the one present. The warblers found on the smallest islands are socially subordinate species. Inadequate data exist upon social interactions of Hermit and Swainson's Thrushes to establish clearly the existence of a hierarchy. I have seen only two encounters between these two species; in both cases Hermit Thrushes supplanted Swainson's Thrushes. Dilger (Auk, 73:313–353, 1956) does not report any interactions between them. However, the habitat relationships of the two species are similar to those of Wood Thrushes and Hermit Thrushes and Wood Thrushes and Veeries, where clear social hierarchies exist (Morse, Wilson Bull., 83:57–65, 1971). These observations suggest that Swainson's Thrush is socially subordinate to the Hermit Thrush. The information thus supports the argument that interspecific social relationships may be a major determinant in deciding what species will occur in any given habitat. This interpretation is consistent with predictions made elsewhere (Morse, Annu. Rev. Ecol. Syst., 2: 177–200, 1971) that socially subordinate species will generally exhibit greater plasticity than social dominants.

These observations were made while conducting research sponsored by the National Science Foundation (GB-6071).—Douglass H. Morse, *Department of Zoology, University of Maryland, College Park, Maryland 20742, 18 November 1971.*

Breeding Status of the Purple Gallinule, Brown Creeper, and Swainson's Warbler in Illinois.—In view of the program to revise the American Ornithologists' Union's 1957 Check-list of North American Birds, the following comments on several species in Illinois seem pertinent.

Purple Gallinule (*Porphyrula martinica*).—In 1963 this species nested and raised young at Lake Mermet, Massac County (Waldbauer and Hayes, Auk, 81:227, 1964)—the first known instance of breeding Purple Gallinules in Illinois. However, in compliance with the demands of boaters and fishermen, the water plants that made Lake Mermet a suitable nesting locality for gallinules were removed during early spring of 1964. Gallinules reappeared at the lake soon after this occurred (John Schwegman, pers. comm.) but departed without attempting to nest. Purple Gallinules are not known to have nested in Illinois since.

Brown Creeper (*Certhia familiaris*).—The 1957 A.O.U. Check-list does not mention this species as a breeding bird in Illinois, which in the central and southern portions of the state it undoubtedly is. Kendeigh (Audubon Bull., 153:19, 1970) cites various bird watchers who report recent summering creepers from Piatt County southward to the Ohio River-Mississippi River confluence near Cairo; one such report refers to a nest with young.

I collected (W.G.G. No. 2254) a heavily molting juvenile female in a hemlock grove near Cobden, Union County, on 20 August 1968. The bird exhibited a nearly wholly unossified skull and no conspicuous fat deposits. Since the molt of young creepers is completed prior to the fall migration and the migrants do not arrive in Union County before the first week of October. the August juvenile strongly indicated the presence of a local breeding population. Not surprisingly, then, a bird-banding project at Crab Orchard Lake Wildlife Refuge, Williamson County, which is close to Union County, yielded a creeper with a brood patch in 1970 and another in 1971 (Kleen and Bush, Amer. Birds, 25:750–753, 1971), while on 28 May 1971, I observed paired creepers near Pine Hills Field Station, Union County.

Creepers probably colonized southern Illinois long ago, as indicated by Otto Widman's discovery (fide Pickering, Migrant, 8:49–50, 1937) of several nesting specimens in the cypress swamps of southeastern Missouri in 1894 and 1898 (records not heeded in the 1957 AOU Check-list). Our Illinois birds seem adherents of the Missouri pattern, being a handful of birds scattered widely about in the floodplain forest and cypress-tupelo swamps.

However, it should be noted that in the eastern United States, the Brown Creeper appears at present to be expanding its nesting range southward and downslope in mountainous regions (Hall, Redstart, 36:98–103, 1969); hence all or a proportion of our Illinois birds may be participants in this phenomenon.

Swainson's Warbler (*Limnothylpis swainsonii*).—Of the various accounts of summer occurrences of Swainson's Warbler in Illinois (Ridgway, Bull. Nuttall Ornithol. Club, 4:163, 1878; Howell, Auk, 27:216, 1910; Gross, Auk, 25:225, 1908; Hardy, Wilson Bull., 67:60, 1955; Brewer, Audubon Bull., 106:9–11, 1958), none provides unequivocal evidence of breeding. An adult female that I obtained accidently in a tree-shaded canebrake along Cave Creek in the Shawnee National Forest near Pomona, Jackson County, on 8 August 1966, is such evidence, the bird exhibiting a brood patch; and more recently even nests have been found and young observed (see below).

The Cave Creek birds exist at the northern limits of the range of their own species and of the cane (*Arundinaria*) with which the distribution and nesting of Swainson's Warbler appear closely correlated, except in the Appalachian Mountains (see Meanley, Natural History of Swainson's Warbler. N. Amer. Fauna 69, 1971, for a fine discussion of this and related data).

John William Hardy (op. cit.) who with Richard Brewer first detected singing males at Cave Creek in 1951 and revisited the site often during the early fifties, described the canebrake as "extensive," a statement no longer accurate because of reduction of some cane stands and elimination of others. When Hardy introduced me to the area in 1966, the canebrake was more or less as he remembered it, though a logging operation threatened the forest canopy along the creek. The logging largely has ceased; but during the past five years almost all large canes have been cut down by men collecting cheap fishing poles and beanstalk supports. Today the two largest stands of cane include fewer than 300 sq meters of ground each and contain almost no canes greater than 1.5 cm in diameter at the base or 2.5 meters in height. One dense cane thicket through which Hardy and I forced our way with some difficulty consists now of only scattered thin-stemmed plants. Fortunately, an agreement to rescue this canebrake from further dismemberment has been worked out between the property owner (U. S. Forest Service) and the Department of Zoology at Southern Illinois University.

The Swainson's Warbler population at Cave Creek varies in size from a single pair in some years (see Hardy, op. cit.; Brewer, op. cit.) to two or at most three pairs. They arrive in early May and I have seen bob-tailed fledglings in late June and large fledglings still being fed by adults in early August. In 1971 I found two nests; each was located in cane; one, abandoned prior to egg deposition, has been added (along with the skin of the female warbler mentioned earlier) to the collections of the Museum of Zoology at Southern Illinois University. This nest agrees in its measurements and construction with several of those described by Meanley, and is very similar in appearance to the photographed example shown in Meanley's figure 25.

The closest avian associates of Swainson's Warbler at Cave Creek include not only all the species listed as associates by Meanley but also the Indigo Bunting (*Passerina cyanea*), a few of which nest in cane at Cave Creek and hence perhaps compete with Swainson's Warbler for nesting sites.

As Meanley does not mention the response of Swainson's Warbler to its taped voice, I think it may be useful to know that, at times at least, both males and females are strongly attracted by the recorded notes of the characteristic male song. For example, during May, 1971, Charles T. Clark, playing the Pennsylvania-taped [= Maryland.—Ed.] song from the Peterson Field Guide Record Series, repeatedly succeeded in drawing a pair of these warblers into clear view at Cave Creek.

I thank the Pine Hills Field Station and the Department of Zoology of Southern Illinois University for financial support in 1971.—William G. George, *Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901, 15 November 1971.*

LIFE MEMBER

Lovett B. Williams, Jr. of Gainesville, Florida has recently become a Life Member of the Wilson Society. Mr. Williams, who is a wildlife biologist for the Florida Game and Freshwater Fish Commission, is a graduate of Florida State University and holds a Master's degree from Auburn University. His work with the Commission has involved mostly the study of the biology and management of the wild Turkey, but he has also been concerned with studies on the Sandhill Crane and the Brown Pelican. He has published a number of technical papers on the Turkey as well as several general ornithological papers, and some popular conservation articles. Mr. Williams is currently President of the Southeastern Section of the Wildlife Society, as well as being a member of the AOU, the AAAS, the Ecological Society of America, and several other conservation organizations. He is married and has one child.

ORNITHOLOGICAL NEWS

Alfred S. Romer, Alexander Agassiz Professor Emeritus of Harvard University delivered the first annual George Miksch Sutton Lecture at the University of Oklahoma on 29 March 1972. These lectures, which will bring distinguished lecturers on ornithology and related fields to the University campus each year were endowed by a gift by Dr. Sutton to the University, who then named the series for the donor.

The name of Clarence S. Jung was inadvertently omitted from the list of members who had completed 50 years of activity in the Society which was printed in the December 1971 issue.

The formal dedication of the Delaware Museum of Natural History building at Greenville, Delaware took place on 13 May 1972.

Request for information.—Information about breeding records and other records of birds on Barro Colorado Island is needed for a revision of the list published in 1952 by E. Eisenmann. Contact Edwin O. Willis, Department of Biology, Princeton University, Princeton, New Jersey 08540.

The Smithsonian Institution has received word from the Bombay Natural History Society of Bombay, India, that the Society would be pleased to provide facilitative services to advanced pre- or post-doctoral students in ornithology who wish to pursue field research projects in India and who would be willing to demonstrate to Indian graduate students up-to-date ornithological research techniques, particularly in quantitative studies in ecology, population dynamics, food and feeding habits, migration and similar areas.

The Bombay Natural History Society can offer its own study facilities, reference collections and library and can provide the Indian institutional base necessary for foreign research projects in India, but cannot offer financial support.

Interested ornithologists are invited to seek support, for their travel, maintenance and research expenses in India from the Smithsonian Special Foreign Currency Program. Under this program, the Smithsonian makes grants in PL-480 foreign currencies, including Indian rupees, to support the basic research activities of American institutions in a number of disciplines including the natural sciences. These grants are awarded on a competitive basis after review by leading senior scientists in the discipline concerned. Other countries where these excess currencies are available include Poland, Yugoslavia, Egypt, Tunisia and Pakistan.

Inquiries about the Smithsonian Foreign Currency Program should be addressed to the Director, Smithsonian Foreign Currency Program, Smithsonian Institution, Washington, D. C. 20560.

HAWAIIAN BIRDS 1972*

Andrew J. Berger

More kinds (species and subspecies) of birds have become extinct in Hawaii than on all continents of the world combined. These endemic Hawaiian birds have become extinct since 1840, and most of them have succumbed since the 1890s. Table 1 lists the endemic Hawaiian birds which are presumed to be extinct.

Moreover, Hawaiian birds account for nearly one-half of the birds in the U. S. Bureau of Sport Fisheries and Wildlife's Red Book of rare and endangered species. The following list contains 16 of the rare and endangered Hawaiian birds: Newell's Manx Shearwater (*Puffinus puffinus newelli*), Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*), Harcourt's Storm Petrel (*Oceanodroma castro cryptoleucura*), Nene or Hawaiian Goose (*Branta sandvicensis*), Koloa or Hawaiian Duck (*Anas wyvilliana*), Laysan Duck (*Anas laysanensis*), Hawaiian Hawk (*Buteo solitarius*), Hawaiian Gallinule (*Gallinula chloropus sandvicensis*), Hawaiian Coot (*Fulica americana alai*), Hawaiian Black-necked Stilt (*Himantopus himantopus knudseni*), Hawaiian Crow (*Corvus tropicus*), Large Kauai Thrush (*Phaeornis obscurus myadestina*), Molokai Thrush (*Phaeornis o. rutha*), Small Kauai Thrush (*Phaeornis palmeri*), Nihoa Millerbird (*Acrocephalus familiaris kingi*), and the Kauai Oo (*Moho braccatus*). To this list may be added the non-migratory Hawaiian population of the Black-crowned Night Heron (*Nycticorax n. hoactli*).

But, there are even more endangered Hawaiian birds! Because of their special interest to ornithologists, I include a second table (Table 2) to cover Hawaii's only endemic bird family, the Hawaiian honeycreepers or Drepanididae. What this table means in terms of the 22 species and 24 subspecies of honeycreepers that were delineated by Amadon (1950) is that there is not a single species, whose range once included more than one of the Main islands, that does not have populations that either are already extinct or have endangered populations on one or more islands!

The honeycreepers that currently are considered non-endangered are found primarily on the islands of Kauai, Maui, or Hawaii, although the Amakihi and Apapane on Oahu are not classified as endangered. The Anianiau (*Loxops parva*) is endemic to Kauai only. Only the Kauai race of the Akepa (*Loxops coccinea caeruleirostris*), and only the Kauai (*Loxops maculata bairdi*) and Maui (*L. m. newtoni*) races of the Creeper are thought not to be endangered. The Apapane, Amakihi, and Iiwi are still common in suitable habitat on Kauai, Maui, and Hawaii. This is a pitiful remnant of a family of birds that demonstrated the results of adaptive radiation to a far more striking degree than even the Galápagos Finches.

In view of this depauperization of Hawaii's unique avifauna, what can one say about the prospects for preserving the dwindling populations that exist in 1972? Unfortunately, one must say that the prospects are poor, indeed. Unfortunately, too, this essay probably will serve only two functions: to document what has been, and still is, happening, and to give me a writing exercise. I am but one in a long series of people who have decried the rape of the Hawaiian biota.

Scott Wilson, an English ornithologist, called attention to some of the problems as

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* The Conservation Committee of the Wilson Ornithological Society, recognizing that bird conservation problems in the Pacific islands have unusual urgency, decided to concentrate its efforts for 1971–72 upon them. This report by Dr. Berger is the first portion of the Committee's report for the year. *Gustav A. Swanson, Chairman.*

TABLE 1
EXTINCT HAWAIIAN BIRDS

Full Species

Laysan Rail, *Porzanula palmeri*
Hawaiian Rail, *Pennula sandwichensis*
Oahu Oo, *Moho apicalis*
Molokai Oo, *Moho bishopi*
Black Mamo, *Drepanis funerea* (Molokai)
Kioea, *Chaetoptila angustipluma* (Hawaii)
Hawaii Oo, *Moho nobilis*
Greater Amakihi, *Loxops sagittirostris* (Hawaii)
Greater Koa Finch, *Psittirostra palmeri* (Hawaii)
Lesser Koa Finch, *Psittirostra flaviceps* (Hawaii)
Grosbeak Finch, *Psittirostra kona* (Hawaii)
Ula-Ai-Hawane, *Ciridops anna* (Hawaii)
Mamo, *Drepanis pacifica* (Hawaii)
Akialoa, *Hemignathus obscurus* (all three subspecies are extinct: Oahu, Lanai, and Hawaii)

Subspecies

Laysan Millerbird, *Acrocephalus f. familiaris*
Laysan Honeycreeper, *Himatione sanguinea freethii*
Oahu Thrush, *Phaeornis obscurus oahensis*
Oahu Akepa, *Loxops coccinea rufa*
Oahu Nukupuu, *Hemignathus l. lucidus*
Lanai Thrush, *Phaeornis obscurus lanaiensis*
Lanai Creeper, *Loxops maculata montana*

Extinct Populations of Surviving Species

Iiwi, *Vestiaria coccinea*, on Lanai
Ou, *Psittirostra psittacea*, on Oahu, Molokai, and Lanai
Crested Honeycreeper, *Palmeria dolei*, on Molokai

TABLE 2
RARE AND ENDANGERED HONEYCREEPERS

Kauai Nukupuu, *Hemignathus lucidus hanepepe*
Kauai Akialoa, *Hemignathus procerus*
[1]Kauai Ou, *Psittirostra psittacea*
Oahu Creeper, *Loxops m. maculata*
Oahu Iiwi, *Vestiaria coccinea*
[2]Molokai Creeper, *Loxops maculata flammea*
Molokai Iiwi, *Vestiaria coccinea*
Lanai Apapane, *Himatione s. sanguinea*
Lanai Amakihi, *Loxops virens wilsoni*
Maui Akepa, *Loxops coccinea ochracea*
Maui Nukupuu, *Hemignathus lucidus affinis*

Maui Crested Honeycreeper, *Palmeria dolei*
Maui Parrotbill, *Pseudonestor xanthophrys*
[2]Maui Ou, *Psittirostra psittacea*
Hawaii Ou, *Psittirostra psittacea*
Hawaii Creeper, *Loxops maculata mana*
Hawaii Akepa, *Loxops c. coccinea*
Akiapolaau, *Hemignathus wilsoni*
Palila, *Psittirostra bailleui*
Laysan Finch, *Psittirostra c. cantans*
Nihoa Finch, *Psittirostra c. ultima*

[1] A single species once inhabited Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii; all populations are either extinct or endangered.

[2] May be extinct.

long ago as 1890; H. W. Henshaw and R. C. L. Perkins wrote of others in 1902 and 1903; William A. Bryan, J. F. Rock, George C. Munro, Harvey I. Fisher, Frank Richardson, Richard E. Warner, and others made pleas for protection of the birds and their habitat during the long period between 1912 and 1964. All wrote in vain.

One has a choice, of course: to remain silent and be liked, or to speak out and be disliked. Obviously, I agree with Hawaiian environmentalist Tony Hodges, who remarked that "the people in the ecology movement are in it to survive, not to make friends."

Unless there is, in the immediate future, a drastic change in the attitudes of State and Federal officials toward the native Hawaiian ecosystems, Scott Wilson's prediction of 1890 surely will come true—"it would not be rash to say that ere another century has elapsed but few native species will remain."

In Hawaii, as elsewhere, the greed and bureaucratic policies of men lie at the root of the problem. Following are the major subjects that need immediate attention.

I. INTRODUCED HERBIVORES

Cattle, horses, goats, sheep, and English pigs were first given their freedom on the Hawaiian Islands between 1778 and 1803. Game mammals were introduced later: axis deer, 1868; mouflon sheep, 1954; pronghorn, 1959; mule or blacktail deer, 1961. Feral horses apparently were exterminated in the 1930s, but all of the other grazing and rooting mammals continue to devastate the vegetation today. What is being done to correct the problem?

A. In an attempt to pave the way for increasing substantially the size of Volcanoes National Park, the National Park Service published in 1970 a glossy, multicolor brochure entitled "The Island of Hawaii." Among the totally misleading statements that belie the Service's past performance, we find that enlargement of the Park will make it possible to "preserve the resources," that is, to "reestablish native ecosystems where practical; control, and where possible, eliminate nonnative species to protect the native biota."

In 1971 Park rangers estimated the goat population in Volcanoes National Park to number 14,000 animals! The Park Service announced that an effort finally would be made to exterminate the goats. However, the very small, but vociferous, group of local goat hunters appealed to their Congressional representatives, after which instructions to "lay off the goats" reached Hawaii from Mr. George B. Hartzog, Jr., Director of the National Park Service. Details of this story were discussed by Mr. Anthony Wayne Smith in the June, August, and November 1971 issues of *The National Parks and Conservation Magazine.*

The Hawaii Chapter of The Wildlife Society, the Hawaii Audubon Society, and other conservation groups have published "position papers" calling for the eradication of feral goats from Volcanoes National Park and Haleakala National Park on Maui. The Park Service, however, has taken only token measures to reduce the number of goats.

No meaningful action has been taken by the National Park Service to reduce the feral pigs in either of the parks, although the superintendents have given wide publicity to their plans to declare the newly acquired Kipahulu Valley segment of Haleakala National Park a "wilderness area." They propose to maintain Kipahulu Valley in a wilderness state, not by reducing or eliminating the pigs, goats, and exotic plants, but by making it virtually impossible for scientists and hikers to enter the area—because they might carry some weed seeds in their pant cuffs!

I propose that NATAPROBU (the National Association of Professional Bureaucrats) award the 1972 "Order of the Bird" to Mr. Hartzog and the National Park Service.

B. The only remaining, extensive mamani (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) ecosystem is found on Mauna Kea on the island of Hawaii. This endemic ecosystem provides the only known habitat for the endangered Palila, and it is the only habitat in which the even rarer Akiapolaau has been seen fairly regularly in recent years.

The mamani-naio forest is part of some 82,000 acres on Mauna Kea that are owned by the State of Hawaii. Of the total acreage, only about 30,000 acres are now forested, however; scattered tropical subalpine and alpine plants are found above the tree line, but the highest part of the mountain consists primarily of barren lava and cinder. Classified as a forest reserve for about 50 years, this land was turned over to the Division of Fish and Game in the early 1950s and was redesignated the Mauna Kea Forest Reserve and Game Management Area. Late in 1971, the Division of Forestry erected a large sign, announcing anew that this was the Mauna Kea Forest Reserve; it still is a game management area, as well. What actual value has been placed on this unique ecosystem by the Divisions of Forestry and Fish and Game?

1. The Division of Forestry has never conducted any significant research on either mamani or naio. Mamani seeds form a large part of the diet of the Palila.

2. Tree line of this dying forest once extended to about 10,000 feet. It now is found much lower, and continues to recede because of the overpopulation of both sheep and pigs. Except within exclosures, regeneration of mamani is virtually nonexistent because the seedlings are eaten by the sheep and rooted out by the pigs. Hunters in Hawaii have so much political power, however, that on several occasions they have forced the Division of Fish and Game to close or shorten the sheep-hunting season in order to allow the population to increase even more (Kramer, 1968). Consequently, no effort is being made to eradicate the feral sheep or even to reduce the herd to a reasonable size—carrying capacity of the range is a concept not considered in Hawaii. At the same time, great pressures are constantly being exerted to introduce the axis deer to this habitat. The influence of hunters upon these decisions seems remarkable in view of their small number, only 10,134 licensed hunters in Hawaii in 1970, according to a recent report by the Wildlife Management Institute.

3. The Kaohe Game Management Area (contiguous with the Mauna Kea Game Management Area) is open for archery hunting only, even though it contains a great overpopulation of both pigs and sheep. State personnel estimate that a fluctuating population between 500 and 1,000 sheep occupy this fenced area of approximately 6,500 acres. One would have to search far, indeed, to find more stark examples of "browse lines" than on trees in this dying forest. Moreover, more than 150,000 acres are open only to archery hunters on the island of Hawaii.

Richard E. Warner (1960) called attention to some of these problems more than a decade ago.

II. IF YOU HAVE SEEN ONE ENDEMIC TREE, YOU'VE SEEN THEM ALL!

The ohia (*Metrosideros collina* ssp. *polymorpha*) is the dominant tree in most of the Hawaiian rain forests, and tree ferns (*Cibotium* spp.) are the most conspicuous element in the understory. The ohia-tree fern ecosystem is the most important habitat for the majority of the surviving endemic forest birds. Koa (*Acacia koa*), a valuable endemic tree, was important for certain species of honeycreepers in the past, but there are few, if any, virgin koa ecosystems remaining. Sandalwood (*Santalum* spp.) was once a valuable native tree, but the commercial supply became exhausted in the 1830s.

The importance to certain endemic birds of the unique mamani-naio ecosystem was mentioned earlier.

How do State and Federal employees view these endemic ecosystems?

A. C. S. Judd, then the Superintendent of Forestry for the Territory of Hawaii, wrote in 1918 that "the destruction of the Hawaiian forest in the past was deplorable, but that it should continue in the present ... seems inexcusable." He added that the prime value of Hawaiian forests was "in their ability to serve as a protection to watersheds," and, therefore, that foresters should be "chiefly concerned with forest protection." In 1927 he wrote that it was time to conduct research on "some of the ecological problems" in Hawaii. Unfortunately, Mr. Judd's successors did not follow his recommendations.

In 1957 the State Division of Forestry initiated a cooperative agreement with the U. S. Forestry Service to conduct a forest survey and the necessary research aimed at developing a timber industry in Hawaii. Since that time, the Institute of Pacific Islands Forestry, Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S.D.A., in Honolulu has given guidance to the State foresters. The board-feet-oriented Federal foresters repeatedly refer to the endemic Hawaiian ecosystems as "decadent forests" and as consisting of "unproductive forest land," and they have developed an "effective and efficient technique for eliminating cull" ohia trees—by "injecting undiluted herbicides into tree trunks."

More than 46,000 acres have been cleared and planted with exotic trees, most of which do not have even a potential commercial value. More importantly, much of the planting effort has been concentrated on already-forested land. This has caused the utter destruction of near-virgin native forests: for example, along the Kulani Prison road on Hawaii. More than 1,500 acres were "reforested" within so-called forest reserves during fiscal year 1969–1970.

U. S. Forestry personnel in Hawaii finally decided in late 1970 that some research on koa should be considered, and in 1971, they voiced concern about ohia. There can be little doubt but that this belated interest in some of the endemic trees resulted partly because of the constant prodding of conservationists in Hawaii, although another event undoubtedly was important. On 13 May 1970, Norman Carlson, the highly respected manager of the Bernice P. Bishop Estate agricultural and forest lands, addressed a forestry conference on Maui. Carlson recommended that the foresters de-emphasize exotic tree species and concentrate on the endemic koa and ohia. He said: "I know now that I should have studied koa when I first got involved in forest management. It is a native tree, adapted to our soils, and valuable as wood. So is ohia. ... We had basic data on exotics—growth rates, survival, soil types and tests [on wood properties] by Madison [Wisconsin]. From these we thought we knew the answer to our forest renewal [in Hawaii]. ... Koa is a beautiful wood, distinctive and native to Hawaii. ... It has evolved over the years and should be better adapted to Hawaii than any of the exotics. Ohia is another native we have casually dismissed, and someday we will rue this. ... Now that we are beginning to value koa, we must work toward the problems of koa forest management." He then gave a list of questions about koa for which the State and Federal foresters did not have answers.

Nevertheless, the 1972–1976, 5-year Forest Planting Plan of the State Division of Forestry does not mention koa, ohia, mamani, naio, sandalwood, or tree fern, but calls for the planting of 6,092 acres of public lands with 17 species of exotic trees at a cost of 1.3 millions of dollars. This despite Carlson's recommendations and despite the fact that there is not a viable timber industry in Hawaii, and some scientists believe that there never will be, nor should be.

George B. Harpole stated in his "Opportunities for Marketing Hawaii Timber Products" that "the introduction of plywood production, and the expansion of lumber production in Hawaii are presently technically and logistically feasible. Fiberboard or particleboard production could also be started. Mill residues may not provide a sufficient supply of wood chips, but additional volumes of raw materials could be developed from non-commercial stands of Hawaii's present timber supply, and from the State's other agricultural resources."

Harpole included maps of eight of the Hawaiian Islands to show the "major forest types in Hawaii." *The areas classified as suitable for commercial forestry include virtually all of the remaining ohia-koa-tree fern forests on the windward slopes of both Mauna Kea and Mauna Loa and on the Kona slope of Mauna Loa.* This view of the native ecosystems presumably is justified because "native forests in Hawaii are essentially static in terms of annual increases. In the unmanaged native forests, trees must fall from the damage of termites or rot, be blown over, or be harvested before new growth can appear."

Harpole's study was published in 1970 as U.S.D.A. Forest Service Research Paper PSW-61. This is an excellent example of the kind of "leadership" given by Federal foresters in Hawaii, and it demonstrates why conservationists have such a difficult time in their efforts to preserve what little remains of the endemic ecosystems.

Despite Harpole's statement about plywood production, "a plywood plant with a 5 million square foot capacity sits idle on the Big Island. Locally-produced craftwood is less and less able to compete with imports. More Christmas trees may soon be produced in Hawaii than can be sold. [In fact, this happened in December 1971, when high-priced locally grown trees did not sell well.] We must determine the standards which Hawaii's products must meet to compete in the marketplace, locally or as exports to Pacific Basin outlets. And the market potential of several timber species now being planted should be evaluated before they reach merchantable size" ("Forest Conservation Research Plan for the Seventies," Department of Land and Natural Resources, Honolulu, 1971).

According to the "Honolulu Advertiser" of 2 April 1971, Senator Hiram L. Fong reported that he and R. Keith Arnold, deputy chief of research of the U. S. Forest Service, would request the U. S. Congress to allocate $250,000 to Hawaii in order to start a southern pine timber industry. Congress was sympathetic, and actually allocated $414,000 to State and Federal foresters in Hawaii. To be sure, not all of these monies will be used for planting pine trees, nor, we have been assured locally, for destroying native ecosystems.

One of the "nice" things about Federal funds is that they are "free" to the states! It seems a little late in history, however, for one branch of the Federal Government to provide monies to destroy native ecosystems while at the same time another branch is providing funds for the acquisition of lands to preserve flora and fauna and to conduct research on rare and endangered species. Two Federal biologists of the rare and endangered species program are assigned to full-time study in Hawaii.

B. The Division of Forestry is not making any concerted effort to eradicate any of several introduced plant weed-species, some of which present a real threat to near-virgin forest areas, including the Alakai Swamp region of Kauai, which is the habitat for more endemic forest birds than can be found on any other island.

To be sure, the Division finally has become concerned about the serious infestation of banana poka (*Passiflora mixta*) on the Hamakua Coast of Hawaii. The Division's present solutions, however, appear to be either to cut down the forest or to open it to cattle grazing!

C. Conservationists in Hawaii were elated when the Governor finally appointed the Commissioners for a newly created Natural Areas Reserve System. During its first year, however, the State Division of Forestry effectively blocked all significant action by the Commission.

D. During 1969 and 1970, the Division of Fish and Game bulldozed (or, as they say, "selectively treated") some 400 acres of prime mamani-naio forest in order to "open it up" in the hopes that it would serve as better habitat for exotic pheasants. Further "habitat improvement" is planned for the future.

E. The State Department of Land and Natural Resources has established a very high standard for coining euphemisms. The Department announced in 1971 that it had "approved the experimental harvesting of ohia and koa trees on 500 acres zoned for conservation at Laupahoehoe on the Big Island." When translated, this means that the Department agreed to let a private individual destroy 500 acres of the Laupahoehoe Forest Reserve in order to get more wood to make bowls and other souvenirs for tourists! Actually, it was time by 1971 to approve this "experimental harvest": the wood-carving company began bulldozing the road through the forest reserve to the harvest area in 1969!

The Laupahoehoe Forest Reserve consists of some of the finest near-virgin ohia-koa-tree fern forests on the island of Hawaii, and there are very few such forests remaining in Hawaii. Such continuing rape and destruction of the little that remains of Hawaii's unique ecosystems demonstrate clearly the true value placed on those ecosystems by State and Federal personnel who manage the Hawaiian biota.

F. During 1971, the Bernice P. Bishop Estate applied for permission to harvest tree ferns from 3,000 acres of the Kilauea Forest Reserve, which is not only a conservation district but also is equal to the Laupahoehoe Forest Reserve as a remnant of this rain forest ecosystem. The tree fern logs, or hapuu, are harvested by bulldozers, which completely destroy the understory and, eventually, the forest. Nursery owners need hapuu logs as the substrate for growing orchids and other flowers! Perhaps some day, the Division of Forestry will investigate the feasibility of growing tree ferns in nurseries, rather than destroying endemic ecosystems to obtain the ferns.

III. STATE QUARANTINE LAWS

Rabies does not exist in Hawaii, and justified strict regulations are designed to prevent that fatal disease from reaching the islands. Similarly, every conceivable effort is made to prevent the introduction of any insect or bird species that might harm sugar or pineapple. Beyond these precautions, however, Hawaii's quarantine laws are a farce.

Except for psittacine and gallinaceous birds from foreign countries, pet store birds are not subjected to any quarantine regulations at all. More than 20 species of cage birds (primarily weaverfinches) have been released accidentally or intentionally in the Honolulu area since 1965. What new parasites or diseases these birds may have carried is unknown.

In 1970, a doctoral student at the University of Hawaii reported the first diagnosis for the Hawaiian Islands of a *Leucocytozoon* infestation of pigeons and two species of introduced doves, as well as four previously unreported species of *Plasmodium*, the protozoan parasite that produces bird malaria.

Excluding the Jungle Fowl, at least 78 kinds (species and subspecies) of potential game birds had been released in Hawaii as of 1967 (Walker, 1967). No thorough follow-up study by State personnel has been conducted on any of these. Lewin and Holmes (1971), however, reported that 13 of 33 game bird species that had been introduced on the Puuwaawaa Ranch on Hawaii had become established as breeding birds. Among 115 birds examined, the authors found 11 different species of worm parasites; they reported 13 new host records for these parasites and four species of parasites were recorded for the first time in Hawaii.

It must be admitted that we do not know what effect these parasites have on the birds, even though the early introduction of bird diseases to the Hawaiian Islands provided a "most logical" explanation for the extinction of so many endemic species and for the great reduction in numbers of others. However, as of 1972, there are no *reliable*, published data to substantiate this oft-repeated assertion. No careful, intensive studies have ever been conducted! Nevertheless, the accidental introduction of new ectoparasites and blood and other internal parasites would seem to be ample reason for initiating thorough studies of bird diseases, as well as for improving the quarantine laws. The State has taken no action in either direction. In fact, before passing "A Bill for an Act Relating to the Protection of Indigenous Fish, Bird, Animal, and Vegetable Life" in Hawaii, a legislative conference committee wrote on 28 April 1970 that the "conference committee would like to also allay the fears of pet shop owners by making it perfectly clear that this bill only applies to animals, birds, etc., introduced by the State and does not intend to affect pet shop owners who bring pets in for sale to the public." Moreover, the final bill was completely emasculated.

IV. A QUESTION OF PRIORITIES

During the past decade, the State Department of Land and Natural Resources spent millions of dollars (State and Federal monies) to destroy native forests and to import exotic plants and animals, but only a negligible amount was expended on endemic plants and animals.

A. The Coot, Gallinule, Stilt, and Black-crowned Night Heron are considered to be endangered species in Hawaii. The drastic reduction in population size of these birds is presumed to be due to the destruction of essential wetland habitat during the past 30 years. Despite this, no research has been conducted by personnel of the State Division of Fish and Game or of the U. S. Bureau of Sport Fisheries and Wildlife into the breeding biology, parasites, predator relationships, or food habits of any of these species. Nor has any study been made of potential chemical poisoning of the few wetland areas still extant, even though the Chairman of the State Department of Agriculture stated in a public lecture in 1969 (Forty-fifth annual meeting of the Hawaiian Academy of Science, 11 December 1969) that Hawaiian agriculturists apply 10 times the amount per square mile of chemical pesticides and herbicides than is used on the Mainland U.S.A., and that "local exterminators use 500 to 1000 times the amount of poison used in Mainland applications."

B. No intensive field study of introduced game birds has been conducted since Charles and Elizabeth Schwartz worked in Hawaii during 1946 and 1947 (a project that was financed by the Federal Aid to Wildlife program). Nevertheless, the State Division of Fish and Game requested $20,000 for the period 1971–1973 for "brush thinning" (that is, bulldozing the mamani-naio forest) on Mauna Kea in order to increase the "productivity of this area for providing game birds," and they requested an additional $5,000 to construct water tanks for game birds.

C. The Nene was considered close to extinction in 1949 (Schwartz and Schwartz, 1949).

The State Division of Fish and Game has carried on a very successful artificial rearing program at Pohakuloa on the island of Hawaii in recent years, and the Nene has been named the State bird. This work, however, has been supported almost exclusively by Federal funds ($15,000 per year from 1958 through 1967, and $25,000 per year since that time).

The role of Mr. H. C. Shipman of Hilo, Hawaii, and of the Wildfowl Trust in Slimbridge, England in the rearing of Nene in captivity deserves recognition, because their efforts contributed much toward saving the species from extinction, even though it is true that a large proportion of the several hundred Nene alive today are in captivity, or semi-captivity. As a private hobby Mr. Shipman had for years reared Nene in semi-captivity on his ranch on Hawaii so he was able to contribute two pairs of the birds to the State of Hawaii in 1949 for its artificial propagation efforts.

Then in the spring of 1950 Peter Scott, Director of the Wildfowl Trust, arranged for Mr. John Yealland, curator of the Trust and an acknowledged expert among experts in the rearing of waterfowl, to spend several weeks in Hawaii assisting the State in its propagation efforts. When Mr. Yealland returned to England, Mr. Shipman sent with him two female Nene, thought to be a pair, and later in the year shipped to the Trust a gander; from this breeding start of 3 birds the Wildfowl Trust has, through 1970, successfully reared more than 300 birds, of which 198 have been returned to Hawaii to be released in the wild by the State in its efforts to reestablish the species; the remainder have been placed in several collections of living waterfowl in England and on the Continent, to encourage the species' prospects of survival. These efforts at artificial propagation of the Nene are described by Smith (1952), and in the Annual Reports of the Wildfowl Trust from 1951–1952 (the Fifth) through 1971 (the 22nd). Beginning with the report numbered 19, appearing in 1968, the publication carries the title simply "Wildfowl." Nene also have been raised by S. Dillon Ripley II in Connecticut.

Almost 500 pen-reared Nene were released in the native habitat on Hawaii between 1960 and 1969. Unfortunately, very little has been learned about the annual cycle of the Nene in the wild. *The State Division of Fish and Game has admitted that it does not have any competently trained people assigned to the job!* Consequently, little more is known about the biology and status of wild populations than was known in 1958, and that was virtually nothing (Elder and Woodside, 1958).

Although it is uncertain that the Nene was ever a breeding species on the island of Maui (Baldwin 1945), 242 pen-reared birds were released in Haleakala Crater between 1962 and 1969. More than half of these birds were raised in England and Connecticut. Nesting is known to have occurred, but not a single young bird was known to have been raised to independence as of 1970; three "near-mature goslings" were observed in 1971, but their ultimate fate was not determined. No thorough study of the Maui population has ever been conducted.

Extramural funds are not limited to the $25,000 received annually for the Nene propagation program by the Division of Fish and Game. For example, there is an annual appropriation (on a 3:1 matching basis) of Pittman-Robertson Aid in Wildlife Restoration funds from the Federal Government. This varies from about $130,000 to $170,000 per annum. The Division uses this money to support "all wildlife development projects," and these include bulldozing the mamani-naio forest on Mauna Kea in the hopes that more pheasants will inhabit the area. Some of these funds are used for Koloa propagation, but the State also has received additional monies from the World Wildlife Fund for this program. (In addition to the funds received for wildlife, the Division of Fish and Game also is a beneficiary of the Federal Aid in Sport Fish Restoration Act, the Dingell-Johnson Act.)

The picture is clear, therefore: Nene and Koloa will be reared in captivity as long as non-State funds are available, but no meaningful effort will be made to study the biology of any endemic species in the native habitat, particularly with State funds. In fact, a grand total of $16,508 of State general funds was expended for "Wildlife Research and Management" for fiscal 1968–1969. Apparently none of this money was actually used for wildlife research or management (it was used for a non-game bird biologist position), but the phrase "wildlife research and management" looks better in official reports.

State money is available for other purposes, however. In 1971, the Division of Fish and Game awarded a contract for $45,000 to a California consultant to prepare "a comprehensive long-range fish and wildlife plan to serve as a guide for the orderly and rational development of its fish and wildlife resources to meet the future recreational, economic, scientific, aesthetic and educational demands that will be made on these resources." Nowhere in the resolution of the House of Representatives (dated 20 May 1969), which requested this study, nor in the contract for the consultant services is there mention of any endemic species of animal. The entire emphasis is on "recreational fishing and game hunting."

My critics may assert that the function of a State Division of Fish and Game is to provide fish and game for the citizens of that state, and, in general, I would agree. I do not agree, however, that that should be the sole function in the island State of Hawaii, in part because only about one per cent of the citizens purchase hunting licenses (1969–1970 Report to the Governor, Department of Land and Natural Resources, Honolulu, January 1971). I assert that the unique Hawaiian forests and their animal life belong to all of the people, not only of Hawaii but also of the entire United States, and, indeed, of the world.

D. A revealing document is the "Forest Conservation Research Plan for the Seventies," which was published by the Department of Land and Natural Resources in 1971. This potpourri contains overt and veiled reference to nearly all of the criticisms leveled at the Department during the past 10 or 15 years. It even uses such words and phrases as "ecology," "unique ecosystem," and "plant interactions and distribution dynamics." It is obvious to anyone knowledgeable about the Hawaii Department of Land and Natural Resources, however, that the Department has little or no intention of changing past policies of destroying native ecosystems, planting exotic tree species, and introducing more game animals.

Although all state positions are "frozen," the glossy publication recommends a "research program for the 70's equivalent to nearly 74 scientist-man-years of annual effort," even though "after 10 years [the 1960s] research devoted to forest conservation problems [which, in fact, meant, bulldozing endemic forests and planting exotics] totals about 40 scientists per year." Moreover, the elaborate table that compares the ostensible scientist-man-years per year expended during the 1960s and the recommended figure for the 1970s does not actually contain a single reference to any endemic ecosystem.

At the same time, I was interested to read the items listed in the recommended research projects on "Wildlife and Fish Habitat," partly because it includes the title of my research program ("Life history and functional anatomy of the Hawaiian honeycreepers"), which was funded originally by the National Science Foundation in 1966! At least 16 other research projects in the brochure were taken directly from Technical Report No. 1 (December 1970) of the Hawaii Island Ecosystems Stability and Evolution Subprogram of the United States International Biological Program.

The Division of Fish and Game also intends, during the 1970s, "to determine the effect of forest clearing on endemic birds." In other words, the Division of Forestry will destroy native ecosystems, after which the Division of Fish and Game can report that the endemic birds no longer inhabit those areas!

E. At the 1968 convention of the International Association of Game, Fish, and Conservation Commissioners, a committee presented a fine report on rare and endangered species, which included an appendix: "Suggested model state legislation for rare and endangered species." The committee stressed that "public awareness and support is a prerequisite to the success of the preservation program." The Chairman of the committee was the Director of the Hawaii Division of Fish and Game.

The Director of the Hawaii Division of Fish and Game has never presented the model law to the legislature; Hawaii is perhaps the only state in which the Division of Fish and Game has no budgeted funds for information and education of the public; and, except for propagation programs for the Nene and Koloa (conducted with non-State funds), there has been no effort to implement any of the philosophy expressed in the report of 1968.

The future of Hawaii's unique birds is bleak, indeed.

LITERATURE CITED

AMADON, DEAN. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Amer. Mus. Nat. Hist., 95:151–262.

BALDWIN, P. H. 1945. The Hawaiian Goose, its distribution and reduction in numbers. Condor, 47:27–37.

ELDER, W. H., AND D. H. WOODSIDE. 1958. Biology and management of the Hawaiian Goose. Trans. 23rd North Amer. Wildlife Conference 1958:198–215.

KRAMER, RAY. 1968. We're botching conservation! Honolulu, July 1968:20–21, 43–47.

LEWIN, V., AND J. C. HOLMES. 1971. Helminths from the exotic game birds of the Puuwaawaa Ranch, Hawaii. Pacific Sci., 25:372–381.

SCHWARTZ, C. W., AND E. R. SCHWARTZ. 1949. A reconnaissance of the game birds in Hawaii. Board of Commissioners of Agriculture and Forestry, Honolulu.

SMITH, J. DONALD. 1952. The Hawaiian Goose (Nene) Restoration Program. J. Wildl. Mgmt., 16: 1–9.

WALKER, R. L. 1967. A brief history of exotic game bird and mammal introductions into Hawaii—with a look to the future. Conference Western Assoc. State Game and Fish Commissioners, Honolulu, July 19, 1967:1–13.

WARNER, R. E. 1960. A forest dies on Mauna Kea. Pacific Discovery, 13:6–14.

WILSON, SCOTT. 1890. On some of the birds of the Sandwich Islands. Ibis, 1890: 170–196.

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ORNITHOLOGICAL LITERATURE

Studies of Bird Hazards to Aircraft. Canadian Wildlife Service Report Series—No. 14. Dept. of Indian Affairs and Northern Development, Ottawa, 1971: 8¼ × 11 in., 105 pp. paperback. $1.25.

Aviation was still in its infancy in 1910, when a bird-airplane collision claimed a human life for the first time. Thereafter the problem probably increased with the number of aircraft, especially as faster planes were developed, but there was relatively little public concern until 1960 when more than 60 airline passengers were killed as a result of a bird strike. Suddenly, governments showed increased interest in supporting studies of bird migration, and well they should have. As Gunn and Solman predict in this report (p. 22), bird strikes are likely to be even more disastrous in the immediate future, as bigger, faster planes with bigger engines (to scoop up more and/or larger birds) carry ever more passengers.

In 1963 the National Research Council of Canada undertook, or encouraged intensive as well as broad investigations of the problem of birds and aircraft, and this book presents some of the results of those studies. The book consists of seven technical papers, which deal with one aspect or another of the subject of bird migration. Most of the observations were made in Canada, but the papers are fairly strong on literature review, which in effect, gives them wider geographic coverage. Specific direct information on bird strikes or birds as hazards to aircraft is presented in the first two papers only.

There are few illustrations, but they make forceful comment on the problem of aircraft collisions with birds (and vice versa). A photograph (p. 18) showing part of the inner workings of an airplane engine heavily matted with gull feathers is a sight to give any pilot (or airline passenger) a twinge of fear, and a picture of a cloud of gulls is at once esthetically appealing and insidiously fearsome in company with text that tells us of nine F-104 Starfighters and two other possibles (at 1.5 million dollars each) being downed by birds, plus a statement that even a small bird can cause serious engine damage and loss of power. For civil flights, about three-fourths of the bird strikes occur near airports. Plane damage from such strikes at Canadian airports has already been reduced by applying knowledge gained from bird studies. The bird-aircraft collisions that occur while a plane is enroute between airports represent a more difficult set of problems.

It is suggested in this book (p. 22) that all major airports need bird-warning systems, i.e., staff and equipment to forecast bird flights, and that ports lacking such systems are guilty of negligence. The cost of a warning system is not actually estimated, but Solman (p. 11) hints that it would more than pay for itself in reduced aircraft damage and reduced insurance claims, not to mention the less calculable value of human life.

Through radar and field studies one such bird-warning system (at Cold Lake, Alberta) was tested for accuracy in forecasting the peaks of bird flights by 1–2 hours, and up to 24 hours. The forecasts were considered 50 per cent accurate in spring, but only 35 per cent accurate in fall. (By comparison, meteorologists claim about 85 per cent accuracy on 6-hour weather forecasts.) Even an accurate prediction of relative numbers of birds flying is no guarantee of aircraft safety. Snow Geese felled one Starfighter at Cold Lake at the very hour when forecasters had *accurately* predicted low flight densities. The forecasts are based to a large extent on radar observations, but low flight densities on any scale may still mean hundreds of birds near the airport, and it only takes one to drop a plane. Bird warning systems still have a very long way to go to become effective safeguards. Ultimately such systems are dependent upon detailed knowledge of the movements of hundreds, even thousands, of populations of birds, and toward this goal we are only well started. An excellent example of the kind of information needed comes from the nicely dove-tailed field and radar studies by Myres and Cannings (p. 23) on the flight of a Canada Goose population through British Columbia. The birds flew a narrow corridor at altitudes of 8,000 to 15,000 feet. This is important information for any pilot who flies in the area, and more so if the goose flights are predictable. That's fine as far as it goes, but when you realize that we do not even know the number of *other* populations that utilize that airspace, you get some measure of the complexity of forecasting bird flights.

The book deals at some length with the benefits and deficiencies of using radar in migration studies, and provides a good comparison between radar and lunar observations. We are repeatedly reminded that ornithological studies using radar are hampered because radar stations are operated primarily for meteorological work, and only incidently for bird surveillance.

The best feature of the work is the wealth of information on migration in Canada, especially near the Alberta-Saskatchewan line, a strategic location for comparison with the two other areas (Illinois and New England) where major radar studies of migration have been made. Thus, for example, the dominant spring flight direction of night migrants is northeast in New England and Illinois, but northwest in Alberta. The Canada studies also provide the best year-around coverage of flight densities and directions available for the continent, plus good discussions of migration and weather. Migration was most consistently correlated with following winds, not with temperature, and not consistently with pressure change. There were also instances of reverse migration and an example of Canada Geese apparently compensating for wind drift. Clearly this is an important reference for all students of migration.

The make-up of the book is extravagant of paper. There was an apparent effort to stretch the work into a book-sized publication. Several pages are actually or virtually blank, and many more are only one-half to two-thirds filled. This is a minor fault, however, beside the fact that one-third or more of the material presented has already been published elsewhere in essentially the same form by the same authors. One of the papers is an acknowledged duplication of a chapter in a 1968 symposium on the problems of birds as pests. In the history of science such wasteful duplication has never been acceptable, but at a time when many libraries are crowded with publications almost to the bursting point, and bibliographers are hard pressed to see even original works, such duplication is an extravagance that none of us should afford.—RICHARD R. GRABER.

THE MORPHOLOGY OF THE SYRINX IN PASSERINE BIRDS. By Peter L. Ames. Bulletin 37, Peabody Museum of Natural History, Yale University, New Haven, Conn., 1971: 7 × 10 in., paper covered, 194 pp., 21 pls. of pen and ink drawings. Price not given.

The literature of anatomy contains many descriptions of the syrinx in various species of birds, but almost nothing that goes beyond the descriptive stage of investigation. "The Morphology of the Syrinx in Passerine Birds" goes far beyond previous studies of this organ. In this study Dr. Ames describes details of muscle and cartilage structure in suboscine families and genera for which no previous descriptions are on record, and gives extensive references to earlier descriptions of these and other groups. He then uses these descriptions as bases for taxonomic and evolutionary interpretations.

In the first section of the book the author compares and relates the passerine taxa, a task involving a great amount of labor. Those who have worked with the syringeal morphology of this group of birds will appreciate the meticulous work and keen insight Dr. Ames used in bringing a large degree of order to passerine classification, based on his own findings in comparison with those of Garrod, Müller, Gadow, Ridgway, Peters, Wetmore, and others. He supports these authors in their use of the syrinx as a basis for passerine classification, and suggests certain shifts in taxonomic positions. He concludes (p. 153) that "Taken in conjunction with other anatomical characters, syringeal morphology suggests that the Passeriformes be divided into five suborders: Eurylaimi, Furnarii, Tyranni, Menurae, and Passeres (Oscines)."

While Dr. Ames provides logical reasons for assigning positions to various families and genera, he points out possible errors due to the complete lack of fossil evidence, and the very meager understanding of the actual functioning of the syringeal muscles, cartilages, nerves, and other tissues. Almost nothing is known of interactions among morphology, behavior, and evolution of the syrinx. His discussion points to several areas in which research is lacking.

The book includes excellent line drawings illustrating muscles and cartilages of the syringes of 76 suboscine species in nine families, and one drawing of *Corvus*, illustrating the oscine suborder. Drawings of cartilage details illustrate 23 other suboscine species. There is a comprehensive list of references and a record of specimen sources.

This book is an extensive, but not an exhaustive, study of passerine classification. It will be a valuable asset to students of passerine morphology and taxonomy, and the sections on evolution and development will also be of interest to persons interested in these topics. Dr. Ames is to be congratulated on his presentation.—Mildred Miskimen.

Natural Resources and Public Relations. By Douglas L. Gilbert. The Wildlife Society, Washington, D.C., 1971: 6¼ × 9¼ in., xxiv + 320 pp., numerous text figures. $6.50.

There presently exist two schools of thought among scientists as to the duty of the scientist in reporting his (her) findings to the public. If you believe, as I do, that a researcher is morally obligated to report any findings which bear upon the general welfare of the public to that public, then this volume will be most welcome. For in reporting to a non-scientific public there is a definite need for a background in public relations. Dr. Gilbert is attempting to provide just this type of background for workers in the field of natural resources.

The philosophy for the public relations approach is well stated by Dr. Gilbert (p. 162):

> "Most research done in natural resources management is reported only for scientific consumption, if at all. Publication should be the last step of every research project. Publication in a popular or semi-popular magazine is as equally important to the professional and to the research worker as is publication in a scientific journal. Many scientific findings are made known to non-professional publics only when the resultant management methods are used or an attempt is made to use them."

Further, Gilbert writes (p. 163):

> "... For example, most wildlife stories available today are the "how I got a full bag limit" type, or the "vicious killer meets death" kind. These should be minimized

> and replaced by the good sportsman, the good management or the good research project kind. This problem is not the fault of the magazine publishers. The blame is the natural resource managers for not writing the stories."

As stated in the Forward, this book is specifically designed for the workers in natural resources. It has been my experience that students in this general area definitely have a need for such background material. Dr. Gilbert touches on all aspects of communication in public relations, and presents in logical fashion the manner in which these various media should be handled; he also very candidly demonstrates how *not* to proceed. The 18 appendices provide a number of "tools" for use in public relations, although several are rather specialized and limited in value.

Although I welcome this needed volume, it is, unfortunately, full of printers' errors, and in my opinion somewhat excessive in certain respects. Citations are given for some rather commonplace statements (e.g. p. 84, line 13), resulting in a long section of literature cited. Also, it seems to me that too many illustrations have been included; many appear to detract from the text rather than clarify it. This despite Gilbert's statement (p. 115) that "Too many visual aids can complicate and confuse rather than clarify, and may be worse than none at all. Only those which are necessary and which will help the presentation should be used." I would like to see a revised edition published which would set higher standards of quality, and which would then be adopted by a wider segment of all scientists, including those involved in the natural resource area.—KEITH A. ARNOLD.

SOFTBILLED BIRDS. By Clive Roots. Arco Publishing Co., Inc., New York, 1970: 8½ × 5½ in., 158 pp., 36 col. pls. by Robin Brown, 30 text figs. $5.95.

The preface of "Softbilled Birds" tells us that its object is "... to provide information upon the practical aspects of maintaining softbills" in captivity. Many ornithologists and all zoo curators would be grateful for a serious contribution to the literature of aviculture but Softbilled Birds is disappointing.

The book opens with a discussion of the term "softbilled," nevertheless we are left confused about which species it is intended to include. In fact, the author divides "softbills" into five dietary aggregations; nectivorous, frugivorous, omnivorous, insectivorous, and carnivorous. Most medium to large sized birds are excluded, whatever their tastes in foods, and so are parrots and finches. Although the book is largely concerned with tropical species, English common names alone are used throughout. Where an attempt has been made to utilize the scientific nomenclature of families or genera, it has often ended badly.

Softbilled Birds is organized into two parts, the first dealing with the acquisition and care of softbills, and the second with the five dietary groups noted above. Two extremely brief appendices offer interesting analyses of rations for softbills in captivity, and recipes for mixtures which Mr. Roots has found adequate. The book is illustrated with numerous line drawings of varying quality, and 36 birds are shown in color photographs. The photographs and their color reproduction are poor and do not add to the reader's understanding of the captive maintenance of wild birds.

Unfortunately, the text makes little attempt to bring together the now considerable body of avicultural observation or to relate it to ornithology generally. Although subject coverage is superficial, sensible counsel is presented on several aspects of birdkeeping suitable for hobbyists.—WILLIAM G. CONWAY.

Breeding Biology of California and Ring-billed Gulls: A Study of Ecological Adaptation to the Inland Habitat. By Kees Vermeer. Canadian Wildlife Service Report No. 12, Dept. of Indian Affairs and Northern Development, Ottawa, 1970: 8½ × 11 in., paper covered, 52 pp., maps, charts, and photos. $1.25. Catalog Number R65-8/12.

American sociologists and Canadians are aware of a rising tide of Canadian nationalism, identity, and independence; often the effects of these changing attitudes are directed at and felt by Americans. Canadians take pride in their work and products; often Americans are criticized for lack of common sense and a sense of aesthetics. The Canadian Wildlife Service can be proud of this report. Compared with American publications and monographs, it is tastefully packaged, skillfully edited, and lavishly illustrated. Where American studies tend to dull one's mind just because of the format, design, and details of presentation, this study is so well presented as to be exciting just because of the methods of design which were used. American editors could learn a good deal from examining the careful use of varying type styles, line drawings, and column placement of this publication. I have long wondered why so many of our American journals and monographs are so dully presented; this publication makes it clear that such pedantry is false and unnecessary. It is also remarkably free of detracting typographical and editorial errors. The graphic presentations are pertinent and easy to understand.

Voluminous data are presented. This research, which was performed pursuant to a doctorate at the University of Alberta, was apparently designed to fill the many gaps in our knowledge about breeding of these gull species in prairie colonies. As with many of us who research areas where we do not know enough to generate firm hypotheses before the field work, Vermeer used the "shot gun" approach—he collected data on all aspects that might be important. The result is information on many aspects of the biology of these gull species. Some data bear on the central question of adaptation to the prairie-lake habitat; some data do not.

From a technical viewpoint, I wonder about the appropriateness of several of Vermeer's implicit assumptions and choices of ways to deal with data. For example, to my knowledge, few if any investigators have used insecticide analyses of uropygial glands to indicate potential involvement of birds with pesticide poisoning. It is questionable whether uropygial fat (lipid) is ever used by birds as an energy source. Probably, most investigators interested in levels of pesticides will not be able to relate Vermeer's data to existing information on levels of body fat. For example, the data (Table 18) comparing levels of residues in brains and uropygial glands of eight Ring-billed Gulls suggest that the glands are a poor choice of tissues to estimate loads of residues in lipids. Usually there is a 10 to 20-fold higher level of residues in body fat than in brain tissues; these data suggest a 2:3 ratio of tissue residues in brain: uropygial gland. The significance is obscure.

There are some surprising oversights in literature citations on Ring-billed Gulls. Valuable comparative data were available to Vermeer on Ringbills in writings of Belknap, Bent, Kutz, F. E. Ludwig, J. P. Ludwig, Ryder, Southern, and probably others. Vermeer's comparison of the California and Ring-billed Gull populations he studied with *other species* of Laridae is excellent and insight-filled, but his comparison with other Ringbill populations and colonies is almost non-existent. As an example, Vermeer omits comparison of dates of first egg-laying from his study with the dates available in Bent's monograph (U. S. Natl. Mus. Bull., 113, 1921). My own data on food samples for

Ringbills were not referred to (Ludwig, Great Lakes Research Div., Univ. of Michigan, Pub. 15, 1966). Other comparative data are omitted as well.

My fundamental criticism of Vermeer's interpretation is that I do not accept his implicit assumption that "gulls" in general do not have adaptations to the inland habitat where California and Ring-billed Gulls nest. To be sure, most "gulls" nest on marine coasts and coastal islands. One *can* assume thereby that "gulls" in general are not adapted to the inland habitat, but *this is an assumption.* Vermeer moves from this assumption to comparison of largely marine gull species with the gulls he studied in Alberta, concluding that Ring-billed Gulls and California Gulls do not show many adaptations to the inland habitat. This is apparently true when these species are compared to other gulls. Because I dispute the assumption, I cannot fully accept Vermeer's conclusion. I am also disturbed by the apparent assumption that adaptation to the habitat of Alberta will be reflected in morphological or behavioral attributes of the species. I think a better argument can be made that almost *all* gull species are adapted to survival in the face of regular castastrophe. Except for a very few species, gulls have very high potential reproductive rates (three eggs per year) and very low adult death rates (8–13 per cent annual mortalities). Thus the catastrophic loss of an age class or two is insignificant to almost all gulls. Gulls are adjusted to catastrophe. In this light, both California and Ring-billed Gulls are *pre-adapted* to conditions of a capricious, often hostile prairie habitat. Thus, Vermeer's conclusion that California and Ring-billed Gulls show few *specific* adaptations to the prairie habitat may be correct. His implication that these species are not well adapted to the prairie habitat is most surely incorrect.

For the serious student of gulls, this is an important report. It provides abundant data. It is valuable for other workers who will wish to compare their larid studies with other studies. Vermeer's treatment of the adaptation problem is particularly valuable when he compares other species to those he studied. In summary—a tastefully presented valuable piece of work, subject only to criticism of detail and interpretation.—JAMES P. LUDWIG.

SIGNALS FOR SURVIVAL. By Niko Tinbergen and Hugh Falkus; drawings by Eric Ennion. Clarendon Press, Oxford, 1971: 8¾ × 11¼ in., 80 pp. $8.00.

This fascinating and informative book, liberally illustrated by photographs and drawings, deals with communications among Lesser Black-backed Gulls. The authors explain the intricate language of these birds, "a system of signalling, comprising posture, movement, sound and color," as they describe it. A gull colony on Walney Island off the coast of Lancashire is the location for the book. The life of this seemingly chaotic colony is shown to be very ordered, with the island divided into territories maintained by the male birds' unmistakable (to others of their species) calls and actions: loud trumpeting calls, much aggressive strutting, and fighting. The story of the gulls' behavior starts with these territorial border disputes and proceeds to the male's attraction of a female, their adjustment to each other, choice of a nest site, egg-laying, and hatching (illustrated by wonderful photographs of a chick breaking its way out of an egg). The account continues with the raising and protection of the young, the chick's recognition of its parents voice, food preferences of individual gulls, and finally the young birds' learning to fly and departure for Africa. All this is described and explained by a well written text and excellent illustrations. The book makes its information accessible to young readers and non-biologically oriented adults as well as to those who are already interested in animal communications.—SALLY LAUGHLIN.

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1st	1914	Chicago, Illinois
2nd	1914	Chicago, Illinois
3rd	1915	Columbus, Ohio
4th	1916	Chicago, Illinois
5th	1917	Pittsburgh, Pennsylvania
6th	1919	St. Louis, Missouri
7th	1920	Chicago, Illinois
8th	1921	Chicago, Illinois
9th	1922	Chicago, Illinois
10th	1923	Cincinnati, Ohio
11th	1924	Nashville, Tennessee
12th	1925	Kansas City, Missouri
13th	1926	Chicago, Illinois
14th	1927	Nashville, Tennessee
15th	1928	Ann Arbor, Michigan
16th	1929	Des Moines, Iowa
17th	1930	Cleveland, Ohio
18th	1931	New Orleans, Louisiana
19th	1932	Columbus, Ohio
20th	1934	Pittsburgh, Pennsylvania
21st	1935	St. Louis, Missouri
22nd	1936	Chicago, Illinois
23rd	1937	Indianapolis, Indiana
24th	1938	Ann Arbor, Michigan
25th	1939	Louisville, Kentucky
26th	1940	Minneapolis, Minnesota
27th	1941	Urbana, Illinois
28th	1946	Omaha, Nebraska
29th	1947	Columbus, Ohio
30th	1949	Madison, Wisconsin
31st	1950	Jackson's Mill, West Virginia
32nd	1951	Davenport, Iowa
33rd	1952	Gatlinburg, Tennessee
34th	1953	Cheboygan, Michigan
35th	1954	Cape May, New Jersey
36th	1955	Stillwater, Oklahoma
37th	1956	Buffalo, New York
38th	1957	Duluth, Minnesota
39th	1958	Wheeling, West Virginia
40th	1959	Rockland, Maine
41st	1960	Gatlinburg, Tennessee
42nd	1961	Huntsville, Ontario, Canada
43rd	1962	Lafayette, Indiana
44th	1963	Charleston, South Carolina
45th	1964	Kalamazoo, Michigan
46th	1965	Sylvan Lake, South Dakota
47th	1966	University Park, Pennsylvania
48th	1967	Crawford Notch, N. Hampshire
49th	1968	Carbondale, Illinois
50th	1969	Williamsburg, Virginia
51st	1970	Fort Collins, Colorado
52nd	1971	Dauphin Island, Alabama
53rd	1972	Cape May, New Jersey

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FALL MIGRATION IN COASTAL LOUISIANA AND THE EVOLUTION OF MIGRATION PATTERNS IN THE GULF REGION

Kenneth P. Able

Many passerine birds make long overwater flights during the course of their seasonal migrations; it is obvious that natural selection has favored these flights in spite of the risks and energetic demands involved. The Gulf of Mexico is one region where the arrival and departure of overwater migrations can be observed to advantage.

Even at the height of the exchange between Lowery (1945) and Williams (1945) concerning the occurrence of spring trans-Gulf migration, it was generally assumed that autumn migrants regularly cross the Gulf in large numbers (e.g., Williams, 1947). In the years following the controversy, spring migration in the Gulf region has been extensively studied, but there have been few concentrated investigations of fall migration. More or less anecdotal observations of birds crossing the Gulf in fall were made by Griscom (1945), Paynter (1951, 1953) and Siebenaler (1954). Buskirk (1968) studied the arrival of migrants on the north coast of Yucatán.

The extensive investigations of vernal trans-Gulf migration have shown that the pattern of air flow around the Bermuda high-pressure system characteristic of that season is conducive to overwater flights (Lowery, 1951; Gauthreaux, 1971). Indeed, Gauthreaux has shown that trans-Gulf migrations early in spring, when the Bermuda high is not a consistent feature, occur in spurts which are dependent upon the establishment of southerly air flow over the Gulf. After the beginning of April, moist tropical air moves northward across the Gulf, interrupted only by the infrequent penetration of powerful cold fronts. The consistency of this favorable flow pattern has probably been a strong selective force in the evolution of vernal trans-Gulf migration. If this is true, one would predict the development of a different pattern in fall because wind patterns are not favorable for regular, large-scale Gulf crossings.

During the fall of 1969 I obtained data on the direction and magnitude of bird flow in southwestern Louisiana while I was conducting field studies on the orientation of nocturnal migrants. These observations shed light on three questions: What is the general flow pattern of autumn migration on the northwestern Gulf coast?; How is this pattern related to major weather systems?; and What evolutionary strategy has led to the broad-front migration patterns we see today?

METHODS

I conducted this study on 34 nights in August, September, and October at Lake Charles, Louisiana, about 23 nautical miles north of the Gulf coast. The nights were not selected in any way, except that no data were used from nights with several hours of rain. I used the WSR-57 radar at the U. S. Weather Bureau station to determine the traffic rates (in birds per mile of front per hour) of nocturnal passerine migration as described by Gauthreaux (1970). I determined the direction of passerine movement (tracks) on the same nights using two portable ceilometers and a 20 × 60 telescope (see Gauthreaux, 1969).

For comparative purposes in the following discussion, I have used the maximum hourly traffic rate recorded on each night as the magnitude of migration on that night. The flight direction parameters of the birds observed with the portable ceilometer (half-hour samples taken 19:00–20:00 or 20:00–21:00 CST) were determined according to Batschelet (1965).

GULF WEATHER PATTERNS IN AUTUMN

The typical low-altitude air flow across the Gulf of Mexico in fall is similar to that in late spring and summer. The southeasterly flow characteristic of these seasons is produced by the clockwise circulation of air around the strong Atlantic subtropical high-pressure system (Bermuda high) and the cyclonic circulation around a low-pressure area over the Mexican Plateau. As autumn progresses, the Gulf area comes under the increasing influence of a continental high-pressure system over central North America. This cold air mass is separated from the Atlantic high by a cold front. Wind conditions over the Gulf in autumn depend upon the juxtaposition of these two pressure systems and the polar front (Petterssen, 1958). When the front passes into the Gulf, as it does infrequently in fall, northerly winds conducive to trans-Gulf flights occur. These conditions occur most regularly later in fall, after the bulk of passerine migrants has passed. During the longer periods between invasions by the continental high, the predominantly southeasterly winds are generally opposed to direct flights from the northern Gulf coast to Yucatán.

The prevailing weather situations during autumn, 1969, were typical for the region and fall rather neatly into five categories as follows:

I. This condition is dominated by the continental high pressure system when it is situated in the central or eastern United States. Figure 1 shows this pattern, which occurs after the passage of a cold front into the southeastern states. The degree of penetration of the front and the exact position of the high-pressure area will determine the orientation of isobars and winds, but the air flow is generally from the northeast or east. This was the most frequent of the five weather conditions, occurring on 11 (35.5 per cent) days during the study (9–10, 10–11, 11–12, 12–13, 18–19, 19–20, 20–21, 21–22 September, 8–9, 22–23, 23–24 October).

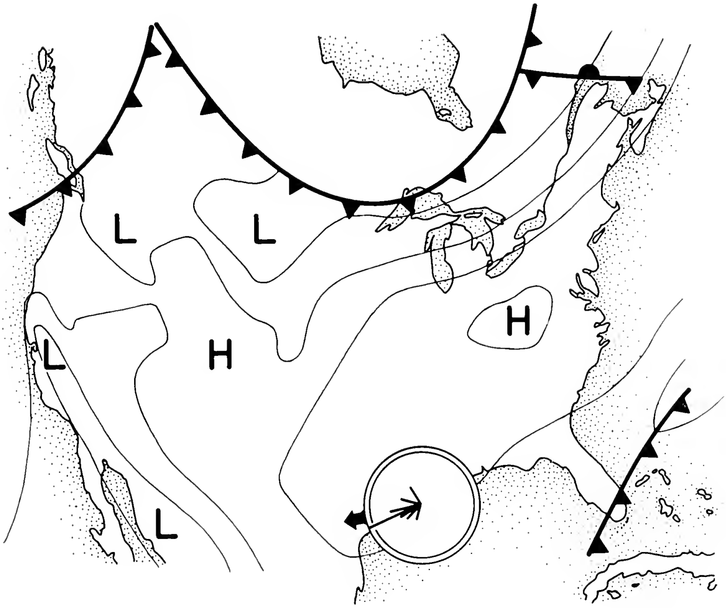

FIG. 1. The flight directions of birds in Weather Pattern I. The vector diagram is plotted so that the radius equals the greatest number of birds in any 7.5° sector. The arrowhead denotes the mean flight direction. See text for a discussion of the weather patterns. The weather map shown is that for 12 September 1969.

II. High pressure over the southeastern United States generates southeasterly winds over most of the Gulf. This condition occurred on 8 (25.8 per cent) days during my study and was particularly characteristic in August. A typical example is shown in Figure 2. (5–6, 6–7, 7–8, 25–26, 26–27, 27–28, 28–29 August, 3–4 October).

III. This pattern is characterized by a well-developed southerly air flow on the back side of a high-pressure system just ahead of a cold front. Winds tend to be strong and thundershowers are frequent. This weather pattern occurred on 5 (16.1 per cent) days during my observations and is shown in Figure 3 (17–18, 22–23 September, 10–11, 11–12, 12–13 October).

IV. Pattern IV is more or less intermediate between II and III. It is dominated by southerly winds in the central and western Gulf produced by the northward flow of moist tropical air in the warm sector of a high-pressure ridge over the eastern United States. This condition usually occurs as a cold front approaches from the west, but the air is more stable than that closer to the front. This pattern occurred on 4 (12.9 per cent) days and is illustrated in Figure 4 (1–2, 2–3, 4–5, 9–10 October).

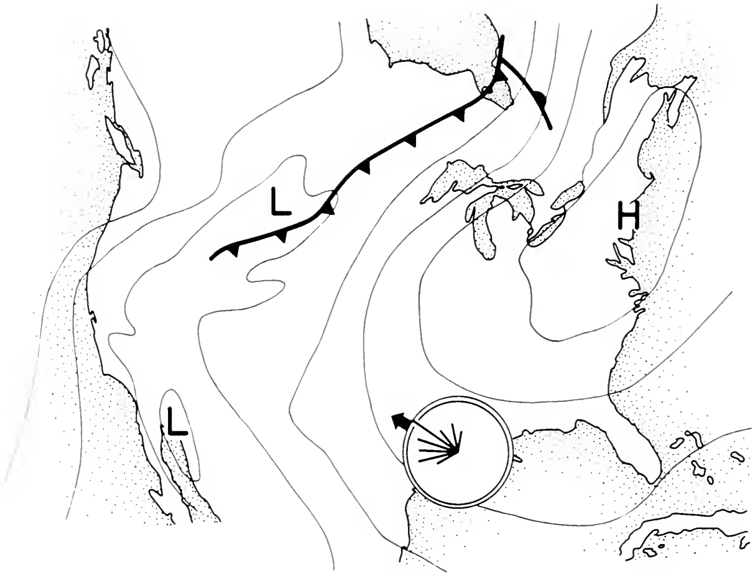

FIG. 2. The flight directions of birds in Weather Pattern II, plotted as in Figure 1. The weather map shown is that for 28 August 1969.

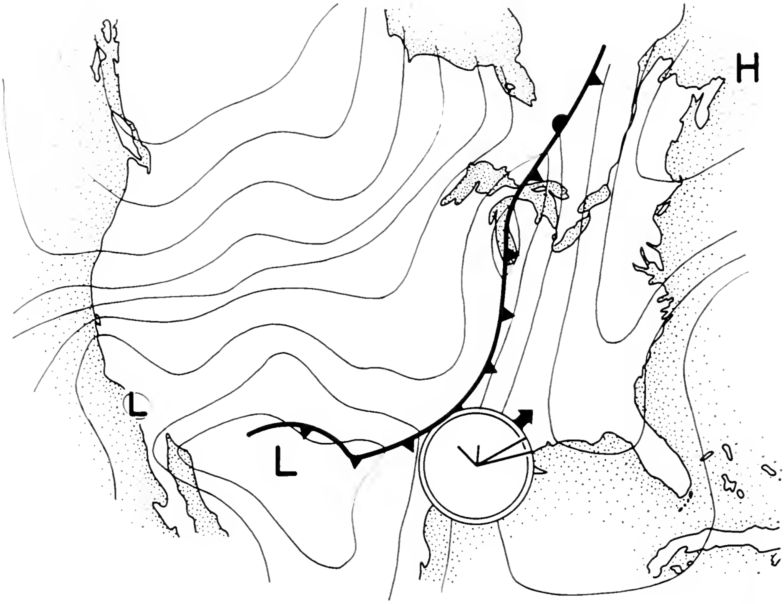

FIG. 3. The flight directions of birds in Weather Pattern III, plotted as in Figure 1. The weather map shown is that for 11 October 1969.

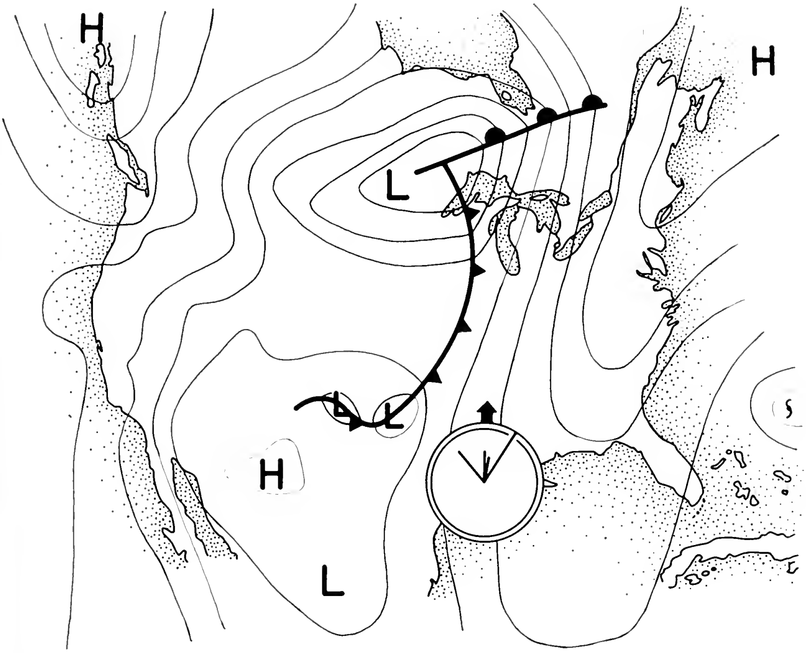

FIG. 4. The flight directions of birds in Weather Pattern IV, plotted as in Figure 1. The weather map shown is that for 10 October 1969.

V. Conditions most conducive to autumnal trans-Gulf flights occur shortly after the passage of a massive cold front which penetrates far into the Gulf. The anticyclonic circulation around the continental high generates northerly winds, the persistence of which depends largely upon the strength of the frontal system. Only three cold fronts passed Lake Charles during fall, 1969, and Pattern V characterized 3 (9.7 per cent) days during this study. It was thus the most infrequent weather condition. A typical example of this pattern is shown in Figure 5. (7–8, 13–14, 14–15 October).

The five weather patterns encompass all but three days during the study. (30 September—1 October, 20–21, 21–22 October). These three days were each dominated by inconsistent, complex weather situations with low-pressure centers in the Gulf of Mexico. Migrations on each of the three nights were of low magnitude.

RESULTS

Flight directions of birds and weather patterns.—To obtain an overall view of the flow of autumn migration on the northern Gulf coast, I constructed a vector diagram of the direction and magnitude of nocturnal passerine mi-

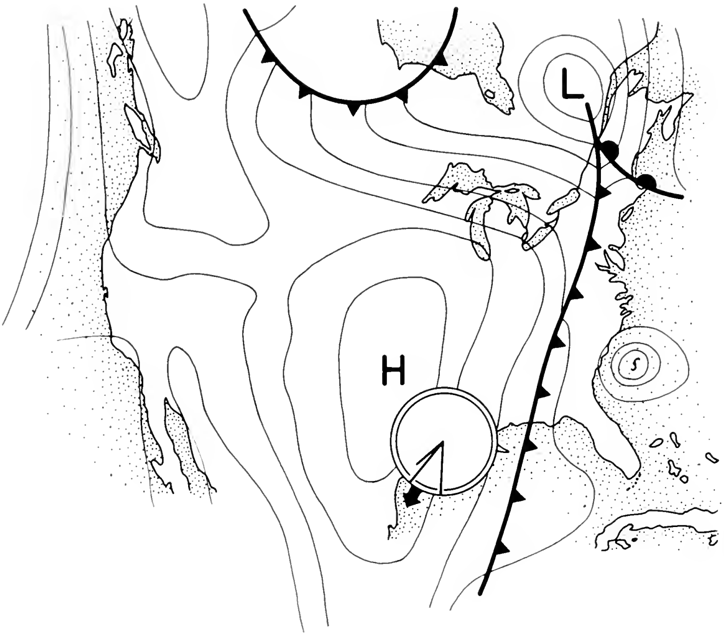

FIG. 5. The flight directions of birds in Weather Pattern V, plotted as in Figure 1. The weather map shown is that for 14 October 1969.

gration on all 34 nights of the study. For each night, the mean flight direction of landbirds was weighted by the $\log_{10}$ maximum traffic rate recorded during that night. The resulting distribution is shown in Figure 6*a*. The mean flight direction, and thus the net flow of birds, was toward the west (274°), but considerable dispersion in flight directions is indicated by the large angular deviation (s) of 55.7° and the resultant vector length (r) of 0.53. In Figure 6*b* are plotted the directions of surface winds on the 34 nights of the study. There is a remarkable similarity between the distribution of wind vectors and bird vectors and the mean wind direction (269°) and dispersion ($s = 54.9°$) do not differ significantly from the same parameters of the bird distribution (parametric two-sample F-test; Batschelet, 1965). If this relationship has sufficient generality, seasonal migration patterns in other geographic regions could be predicted from long-term wind direction data.

It is more instructive to examine the flight directions of the birds under each of the five weather patterns. These data are plotted in Figures 1–5.

Pattern I is one of two (with Pattern V) weather situations which is generally favorable to fall migration, i.e., winds usually have a southward com-

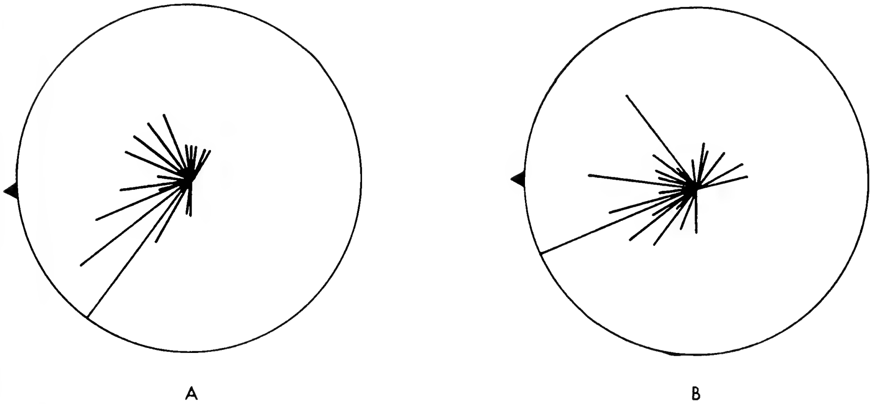

FIG. 6. A. Vector diagram of the mean flight directions of the birds (half-hour samples taken 19:00–20:00 or 20:00–21:00 CST) weighted by the $\log_{10}$ maximum traffic rate during the same night. B. Vector plot of the directions of surface winds, taken at the times of ceilometer samples, on the 34 nights of the study. The vectors are plotted as in Figure 1.

ponent. In general, air flow in this system parallels the Louisiana-Texas coast and large movements of birds were observed flying in this west-southwesterly direction. Under this general weather condition the mean flight direction was 255° and the relatively small amount of dispersion about the mean (s = 28.8°) shows that the flight directions of the birds are fairly consistent from night to night, reflecting the relative constancy of winds in this pattern.

Patterns II, III, and IV are characterized by winds blowing from the south, generally counter to the expected flow of autumn migration. One of these three patterns occurred on 54.8 per cent of the nights during this study. Migrations of landbirds occurred under all three conditions and in each case flight directions were toward the north. The mean flight direction under Pattern II was 300° (s = 41.5°; r = 0.84) as shown in Figure 2. The flight directions of passerines under Pattern III are shown in Figure 3. Here the mean flight direction was 47° (s = 41.5°; r = 0.74). Northward flights with a mean direction of 7° (s = 28.3°; r = 0.88) occurred in weather typical of Pattern IV. These data are plotted in Figure 4.

The optimum conditions for direct bird flow from the northern Gulf coast to the tropics occur when Pattern V prevails, i.e., following the passage of a cold front far into the Gulf. On the three nights when these conditions occurred, overwater flights departed from the Louisiana coast. Indeed, trans-Gulf departures took place only under these conditions. The flight directions

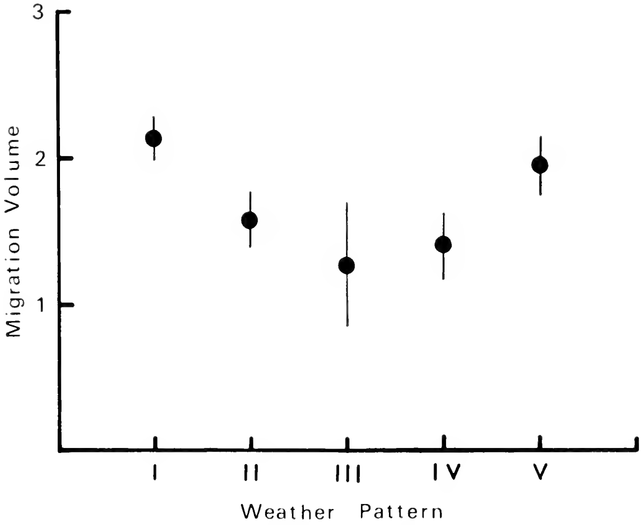

Fig. 7. The magnitude of migration under each of the five weather patterns. The dots and vertical lines show the mean nightly maximum traffic rate and its standard error under each condition.

of birds on these nights are plotted in Figure 5 where the mean direction is 207° (s = 19.2°; r = 0.94).

The relative magnitude of migration in different directions.—Among the diverse weather patterns which characterize the northern Gulf coast in fall, some are obviously more favorable for a direct movement to the wintering ground than others. We would expect, a priori, that passerine migrants would have evolved the ability to select optimum weather conditions in which to undertake long migrations. Most birds initiating a migratory flight from southwestern Louisiana in the fall will move in one of three general directions: 1) southwest on a circum-Gulf flight parallel to the coast; 2) southward directly across the Gulf to Yucatán; or 3) some direction generally counter to the normal flow of autumnal migration. The foregoing results and other data (Gauthreaux and Able, 1970, 1971; Able, 1971 and in prep.) show that passerine nocturnal migrants fly downwind even when this behavior carries them in apparent "nonsense" directions. It is, therefore, of considerable interest to know if migrations in seasonally appropriate directions are of disproportionately larger size.

The volume of migration under the five weather patterns is shown in Figure 7. The graph shows the mean maximum traffic rate recorded under each weather pattern. The means under Patterns II, III, and IV (those with

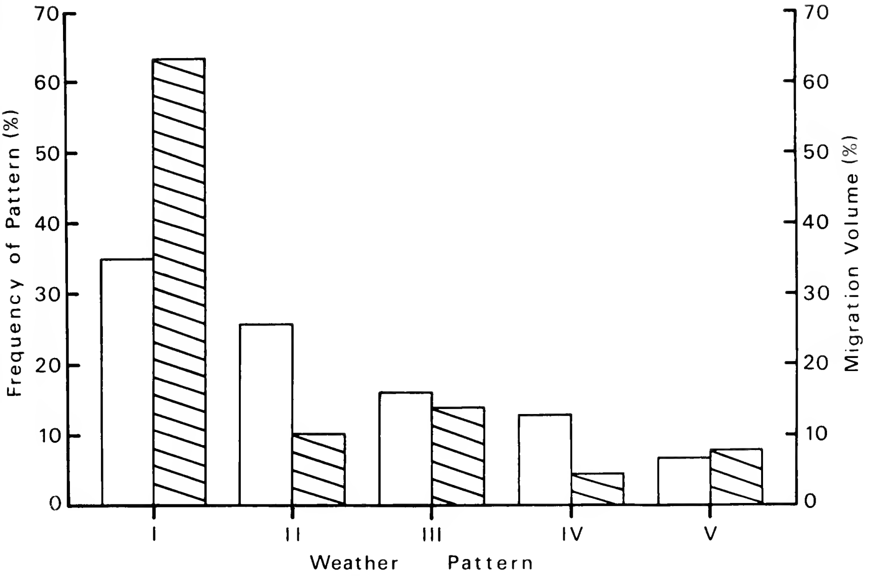

FIG. 8. The proportion of migration occurring under each of the five weather patterns. Open bars show the frequency of each weather pattern as a per cent of the total nights sampled. Hatched bars represent the per cent of the total migration volume (total nightly maximum traffic rates) observed under each condition.

generally southerly winds and "reverse" migrations) were significantly smaller than those under Patterns I and V (those generally favorable to fall migration) ($t_{29} = 14.42$; $P < 0.001$; two-tailed test). The histograms (Fig. 8) show the frequency of occurrence of each weather pattern and the proportion of the total migration volume (based on nightly maximum traffic rates) that took place under that Pattern. Only under Patterns I and V did more migration occur than would be expected on the basis of the frequency of occurrence of the condition. However, the differences were not great enough to yield a significant value of Chi Square. The volume of migration immediately following the passage of cold fronts (Pattern V) is surprisingly small, as this might be considered the optimum condition for migration. At least part of the reason for this anomaly is that the three cold fronts occurred late in the migration season after the bulk of birds had passed. Traffic rates in all weather conditions were considerably smaller toward the end of migration. In addition, October migrations contain a higher ratio of arriving winter residents to passage migrants than earlier flights and thus fewer birds would be likely to embark on trans-Gulf flights during post-frontal weather.

DISCUSSION

Trans-Gulf flights of considerable magnitude take place in fall, but in contrast to the spring migratory picture in the Gulf region, they are of irregular occurrence. The results of this study show that the direction of autumn passerine migration on the Louisiana coast conforms to the patterns of air flow in major weather systems. This was predicted by our finding that passerines at night fly downwind regardless of wind direction or speed (Gauthreaux and Able, 1970, 1971; Able, 1971). The correspondence of migratory flow to broad-scale weather patterns results in a fairly large net movement of birds on a circum-Gulf path.

Few other data are available with which my results may be compared. Lowery and Newman (1966) analyzed data from moon-watching on four consecutive nights. Trans-Gulf flights of considerable magnitude departed on two nights immediately following the passage of a cold front into the Gulf. Circum-Gulf flight directions were noticeable on the other two nights and at the eastern and western ends of the northern Gulf coast. Their data are thus in general agreement with mine.

On the north coast of Yucatán, Buskirk (1968) recorded at least small incoming flights of passerine migrants almost daily in fall. Heavy flights occurred only following the penetration of cold fronts into the Gulf. My observations at Lake Charles cannot account for the *regular* arrival of migrants in Yucatán in fall. However, predominant weather patterns often are favorable for flights from Florida or Cuba.

The major broad-front migration patterns can be explained on the basis of prevailing weather systems and the behavior of the birds. Large-scale wind patterns are probably strong selective forces in the evolution of passerine migration patterns, at least when these involve long overwater flights. The pattern of selective downwind flight described here assures that small landbirds will not embark on a hazardous overwater flight in unfavorable winds. On the other hand, the same behavior allows them to be opportunistic in taking advantage of northerly post-frontal winds when they occur in fall. In the Gulf region, birds embark on a water crossing in both spring and fall whenever winds are favorable. The major differences in the resultant seasonal patterns are due to the fact that the wind flow across the Gulf is roughly south to north during both seasons, while the main direction of bird flow is reversed. But, although southerly winds blow on a majority of days during the fall migratory period, a fairly strong net flow of birds in a southward direction results from downwind flight coupled with some behavioral selection of favorable synoptic weather situations.

All the data from the Gulf region show that passerine migrants will not depart on an overwater flight into head winds. However, the birds leaving Yucatán in spring or the northern Gulf coast in fall presumably cannot predict the presence of a cold front somewhere in the Gulf. We do not know specifically what happens when a mass of migrants flying in tail winds meets the front and its opposing winds over the water. However, when birds meet a cold front in the northern Gulf in spring, many abandon downwind flight and fight the head winds northward toward the coast. Since autumn cold fronts rarely reach Yucatán, the birds usually meet partially or completely opposing winds somewhere during the water crossing. Paynter (1953) and Buskirk (1968) observed birds arriving in head winds at Yucatán. On the contrary, Gauthreaux (pers. comm.) once observed the northward return of a fall migration which had departed from the Louisiana coast only to meet a retreating cold front not far offshore. These observations imply that the birds are employing some navigational ability ("map sense" of Kramer, 1953) and are somehow aware of their position in space relative to the geography of the Gulf. Once they have proceeded most of the way across the water barrier, they will abandon their customary downwind flight in order to reach the nearest shore if opposing winds are encountered.

SUMMARY

Passerine nocturnal migration was observed with radar and portable ceilometer on 34 nights during fall, 1969, at Lake Charles in southwestern Louisiana. Weather patterns over the Gulf in fall are generally similar to those of late spring and summer and are usually characterized by southerly winds. These conditions, which favor large-scale trans-Gulf migrations in spring, are opposed to such flights in fall. The daily weather patterns observed during this study were grouped into five basic types. Passerine migrants at Lake Charles flew with the wind, regardless of its direction. Because of the frequency of southerly winds, "reverse" migrations were common. However, a strong net flow of birds in a southwesterly direction resulted from prevailing northeasterly winds and the occurrence of disproportionately large migrations when air flow was favorable for movement toward wintering areas. Downwind flight assures that small landbirds will not embark on long overwater flights in unfavorable winds, but at the same time allows them to take advantage of northerly post-frontal winds when they occur.

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LITERATURE CITED

ABLE, K. P. 1971. Environmental influences on the nocturnal orientation and migration of birds. Ph.D. Thesis, Univ. Georgia. University Microfilms, Ann Arbor, Michigan.

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. AIBS Monograph, Washington, D.C.

BUSKIRK, W. H. 1968. The arrival of trans-Gulf migrants on the northern coast of Yucatán in fall. Unpubl. MS Thesis, Louisiana State University, Baton Rouge.

GAUTHREAUX, S. A., JR. 1969. A portable ceilometer technique for studying low-level nocturnal migration. Bird-Banding, 40:309–320.

GAUTHREAUX, S. A., JR. 1970. Weather radar quantification of bird migration. BioScience, 20:17–20.

GAUTHREAUX, S. A., JR. 1971. A radar and direct visual study of passerine spring migration in southern Louisiana. Auk, 88:343–365.

GAUTHREAUX, S. A., JR., AND K. P. ABLE. 1970. Wind and the direction of nocturnal songbird migration. Nature, 228:476–477.

GAUTHREAUX, S. A., JR., AND K. P. ABLE. 1971. Nocturnal songbird migration. Nature, 230:580.

GRISCOM, L. 1945. Modern bird study. Harvard Univ. Press, Cambridge.

KRAMER, G. 1953. Wird die Sonnenhöhe bei der Heimfindeorientierung ver wertet? J. Ornithol., 94:201–219.

LOWERY, G. H., JR. 1945. Trans-Gulf spring migration of birds and the coastal hiatus. Wilson Bull., 57:92–121.

LOWERY, G. H., JR. 1951. A quantitative study of the nocturnal migration of birds. Univ. Kansas Publ. Mus. Nat. Hist., 3:361–472.

LOWERY, G. H., JR., AND R. J. NEWMAN. 1966. A continent wide view of bird migration on four nights in October. Auk, 83:547–586.

PAYNTER, R. A. 1951. Autumnal trans-Gulf migrants and a new record for the Yucatan Peninsula. Auk, 68:113–114.

PAYNTER, R. A. 1953. Autumnal migrants on the Campeche Bank. Auk, 70:338–349.

PETTERSSEN, S. 1958. Introduction to meteorology. McGraw-Hill, New York.

SIEBENALER, J. B. 1954. Notes on autumnal trans-Gulf migration of birds. Condor, 56: 43–48.

WILLIAMS, G. C. 1945. Do birds cross the Gulf of Mexico in spring? Auk, 62:98–111.

WILLIAMS, G. C. 1947. Lowery on trans-Gulf migration. Auk, 64:217–237.

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RECOGNITION OF NEST, EGGS, NEST SITE, AND YOUNG IN FEMALE RED-WINGED BLACKBIRDS

Frank W. Peek, Edwin Franks, and Dennis Case

In general, birds which build nests recognize and respond to their nest sites and later their young but show little evidence of being able to specifically recognize their nests or eggs (see Nice, 1943; Tinbergen, 1953; Davies and Carrick, 1962; and Beer, 1970). In species which do not build nests, such as the Common Murre (*Uria aalge*), both the egg and the laying site are specifically recognized and responded to (Johnson, 1941). In the Tricolored Blackbird (*Agelaius tricolor*), which nests in dense colonies, the adults feed any young Tricolor placed in their nests and thus do not specifically recognize their own young (Emlen, 1941, and Lack and Emlen, 1939). In species in which parents recognize their own young the speed with which recognition develops appears to be faster the shorter the time the young spend in the nest (Davies and Carrick, 1962). The majority of the studies cited above and others in the literature were done with non-passerines and investigated only one or two factors of the nesting situation at only one period of the breeding cycle. The present study examines in a passerine, the Red-winged Blackbird (*Agelaius phoeniceus*), the responses of the female Redwing to the nest site, nest, eggs, and young throughout the entire nesting cycle.

METHODS

Experiments were carried out during May and June, 1968 and 1969 on a small (16.5 acre) fresh-water marsh near State College, Pennsylvania. The marsh contained 27 Redwing nests in 1968 and 12 in 1969. Observations were made with the aid of 7 × 50 binoculars and a 25× spotting scope from concealed locations at considerable distances from the nests. The data on nestling vocalizations were obtained from two Redwings taken from different nests in a marsh near St. Paul, Minnesota in July, 1970. Vocalizations were recorded on magnetic tape at 7½ ips using a Uher 4000 Report-L recorder and a Uher omnidirectional microphone.

RESULTS

Response to the nest.—Six experiments were conducted in which a female's entire nest along with its supporting vegetation was dug up and replaced with another Redwing nest from the same marsh. All nest substitutions were made while the female was off the marsh, and thus out of sight of her nest. All the original nests were constructed entirely of sedge (*Carex* sp.) and were situated on the tops of sedge tussocks. In the first three experiments the substitute nests closely resembled the originals in that they were also constructed of sedge and were situated on sedge tussocks. Each of the females upon returning to the substitute nest settled upon it without hesitation. In the fourth experiment the female also settled without hesitation upon a substitute nest which, though built on a sedge tussock, was largely constructed of cattail (*Typha* sp.). In the fifth and sixth experiments the substitute nests differed strikingly from the originals in that they were constructed entirely of cattail and were supported by cattails rather than sedge tussocks. Upon returning to these nests the females were at first quite distressed; however, both accepted the strange nests within 15 minutes. Holcomb (1971) has demonstrated that female Redwings tolerate considerable alteration of their nests without abandoning them. These observations are also consistent with those reported for other species. For example, Lashley (1915) found that Sooty Terns (*Sterna fuscata*) responded positively to any nest at the chosen site.

Response to eggs.—In these experiments the entire clutch of a female was replaced with eggs from another nest. Egg substitutions involved interchanging clutches containing the same number of eggs as well as clutches with different numbers of eggs and also with young. Birds readily accepted substitute clutches of eggs even though they invariably differed slightly in color and pattern from the original clutch. They also accepted both increases and decreases in clutch size (three eggs substituted for four, two for four, four for three, and four for two). These findings agree with those of Holcomb (1971) who found that female Redwings readily accepted artificial eggs similar to their own and tolerated both increases and decreases in clutch size. Females of the closely related Tricolored Blackbird also accepted eggs of other Tricolors and tolerated alterations in clutch size (Emlen, 1941). Under the criteria of these experiments the female Redwing does not discriminate between her own eggs and those of other Redwings or similar artificial eggs. She does, however, discriminate against eggs of the Brown-headed Cowbird (*Molothrus ater*). During the course of the present study, two Cowbird eggs were found covered over with nesting material. Friedmann (1963) also reported instances of Redwings building over Cowbird eggs.

Female Redwings clearly were aware of change when eggs were substituted for a mixture of day-old young and eggs, and vice versa; however, little else can be said on the basis of one observation of each manipulation.

As already mentioned, the ability to recognize eggs varies with the ecology of the species. Johnson (1941) interchanged the eggs of three Common Murres nesting near each other. When the birds returned, each went to its own egg and rolled it back to the original site. Murres lay their eggs on bare rock cliffs where they are likely to roll; hence individual recognition of eggs has adaptive significance.

Response to the nest site.—In one set of experiments five nests containing eggs were moved various distances (2, 3, 5, 7, and 10m) while the females were away. Each nest was moved only once and all movements were within the original territory. In all cases females returned to the original nest site before locating their displaced nests. On as many as 15 subsequent trips females returned to the original nest site before flying to the relocated nest. The nest displaced a distance of 10 m was abandoned.

These results show that female Redwings have an attachment to the site and return by "habit" to their own nest sites even when the nests have been removed. This is undoubtedly important in their willingness to accept even very dissimilar nests placed on the original nest site as discussed above. The cues which the bird uses to locate its nest site were not investigated.

These results agree with an experiment reported by Nero and Emlen (1951) in which a Redwing nest and eggs were moved for a second time a distance of 3 m while the female was absent. Upon returning she went first to the site where the nest had last been located and then to the site from which it has been moved the previous day. She finally located the nest on its new site and accepted it. Nero and Emlen also report a number of other experiments in which Redwing nests containing eggs and/or young were moved 1.5 or 2 m while the female watched. In these cases the females returned directly to their nests rather than to the former sites. In these experiments females even followed nests which were moved across territorial boundaries. In experiments with the Sooty Tern (Lashley, 1915) and House Sparrow (*Passer domesticus*) (Nice, 1943), however, birds returned to former nest sites rather than to nests displaced short distances.

A second set of experiments was done with two females whose nests, each containing three eggs, were built in sedge tussocks. While each female was away, her nest and eggs were moved to a position 4 m from the original nest site (within the same territory) and replaced with another nest (Cattail in both cases) also containing three eggs. The results were essentially the same for each bird. When the female returned to her nest site, she settled on the new nest, got off and returned by the same route several times during the next 3 hours. One bird also flew over to her own nest at the new site but finally settled on the new nest at the old site and remained there for a normal incubation bout (30 min average duration). The original nest and eggs were then moved back to within 0.5 m of the new nest. The female continued to return to the new nest on the original site for 2 hours despite the presence of her own nest and eggs 0.5 m away. The new nest and original nest were then interchanged; the original nest was now back on the original site. The female returned without hesitation to the original nest and site. The two nests were again interchanged after the female left and the female continued to return to the original nest site, now containing the new nest and eggs, for the rest of the afternoon. On the following day, both females were returning to

TABLE 1

RESPONSE OF FEMALE TO SUBSTITUTE NESTLINGS AND DISPLACEMENT OF OWN NESTLINGS

Female	Age of Nestlings Removed and Placed in a Nearby Nest (days)	Age of Substitute Nestlings (days)	Response of Female
1	1	2	settled on nest with no hesitation
2	2	1	"
3	2	3	"
4	3	2	"
5	3	4	"
6	4	3	"
7	6	7	"
8	7	6	accepted but showed distress
3	10	11	followed young to new nest
4	11	10	"
5	10	11	"
6	11	10	"
9	10	none substituted	"
10	11	"	"

their original nests, which were 0.5 m from the original sites. The replacement nests and eggs were still at the original sites. Both females eventually fledged young from their original nests.

These results show that the female is more strongly attached to her nest site than to her nest and eggs, but that she discriminates against a substitute nest and eggs if her own are not far removed from the original site.

Response to young.—The female Redwing's response to her young was investigated by replacing a female's own young with an equal number of nestlings from another nest (in two cases a female's young were moved and no replacement was made). The substituted nestlings were within a day of being the same age as the female's own young. In all cases the female's own young were placed in a nest 3 to 6 m away within the same territory. The reaction of the female depended upon the age of the nestlings at the time the manipulation was made (Table 1). If the female's own young were less than 7 days old, the female settled upon the nest with no hesitation. The female whose nestlings were 7 days old apparently had developed some degree of recognition of her own young and was disturbed by the interchange. By the time the young were 10 days old, the female specifically recognized her own young and followed them to their new location.

Females 5 and 6 (Table 1) were both nesting in the same male's territory, 6 m apart. Over a period of 14 days their nests, then their eggs, and then their young (at two ages) were interchanged. In agreement with results discussed above, interchanging nests and eggs had no measurable effect upon the females; both females readily returned to their original nest sites which contained either a different nest or different eggs. The first time the nestlings were interchanged at ages 3 and 4 days, both females readily accepted the foster nestlings. When the nestlings were again interchanged at ages 10 and 11 days, the females immediately switched nest sites, remaining with the nestlings they had cared for during the previous 7 days (these nestlings were not the young they had hatched and initially brooded for 3 and 4 days, respectively). The females thereafter stayed with the young they had followed to the alien nest site until they fledged 1 or 2 days later. The females had, during a 7-day period, formed a specific attachment to the 3 and 4 day-old foster nestlings. Females 3 and 4 (Table 1) were also nesting within one male's territory (4 m apart). Their young were successfully interchanged at 2 and 3 days of age. When the young were again interchanged at 10 and 11 days of age, the females switched nest sites, as did females 5 and 6, and remained with their young until they fledged.

These results agree with those discussed by Davies and Carrick (1962) for a number of gull species. The gulls learned to recognize their own young before the young left the nest. Nice's (1937) Song Sparrows (*Melospiza melodia*) behaved similarly. She found that parents did not recognize their own young under 7 days of age. Alley and Boyd (1950) found that parent European Coots (*Fulica atra*) gradually learned to recognize their own young over a period of 2 weeks after the young were able to swim and leave the nest. The following species have been shown not to recognize their chicks, at least in the nest: Kittiwake (*Rissa tridactyla*) (Cullen, 1957); Tricolored Blackbird (Emlen, 1941); and Black Phoebe (*Sayornis nigricans*) (Kinsey, 1935).

Beer (1970) has pointed out that experiments in which young are interchanged provide inconclusive evidence that parental recognition has occurred. The possibility exists in such experiments that the young might discriminate among adults or might react to being placed in a strange nest, with the result that their behavior (rather than any individual characteristics) marked them as foreign and caused the strange adults to reject them. However, specific recognition of young is demonstrated in the present study when females followed their own young to different nest sites.

The behavior of females which followed their young to new nest sites strongly suggested that they used the vocalizations of the young to find them.

After an interchange of young had been made, the females first hovered over their own nests for a short time, then flew directly to the nest which contained their own young, and eventually settled on it. Since the nests were situated deep in sedge tussocks, the young were concealed except from directly overhead, making it impossible for the female to see them until she was directly over the nest.

Observations were also made on two captive Redwings taken from different nests at age 10 days. In agreement with Nice (1950), these birds gave loud location notes at approximately hourly intervals, and ceased calling when fed. Tape recordings of their calls were made during their tenth and eleventh days of age. Sonagrams show that the character of the calls varied little within an individual but were distinctly different between individuals. The location call presumably enables the parent to recognize and find its young even though the latter are motionless and hidden in tall vegetation. The call may also stimulate the parent bird to feed the young.

CONCLUSION

Tinbergen (1953) introduced the terms "specific recognition" and "nonspecific recognition" when referring to responses of parent birds to factors in the nesting situation. Nonspecific recognition refers to those factors which are innately recognized as belonging to the species. For example, a wide range of Red-winged Blackbird eggs would be recognized nonspecifically by a female Redwing and therefore would be appropriate for incubation. Thus, a moderate range of eggs can satisfy her. Markedly differing eggs, such as those of cowbirds, are not accepted.

In the present study, female Redwings were found to recognize the nest, eggs, and young under 7 days of age nonspecifically. Replacements of any of these by counterparts from another Redwing nesting situation were quickly accepted.

Specific recognition of factors in the nesting situation must be learned. At least one factor or aspect of the nesting situation must be specifically recognized or parent birds would stop at the first conspecific nest encountered rather than returning to their own nests. Female Redwings were found to recognize specifically the nest site and young older than 7 days. Females returned to their specific nest sites, and after the young were about 7 days old, learned to recognize them or their calls specifically. At this time the female becomes more strongly attracted to the young than to the nest site, for she will abandon the site to follow the young. Since the female Redwing feeds her young after they fledge, this transfer of attachment must occur prior to the time the young leave the nest. The present study shows that this happens when the young are about a week old.

SUMMARY

Responses of female Red-winged Blackbirds to substitute nests, eggs and young, and to displacements of nests and young were investigated. Females show a strong attachment to nest sites throughout the nesting period. They preferred to remain at the nest site even though the nest, eggs, and young (under 7 days old) were replaced with counterparts from other Redwing nest situations. When young older than 10 days were displaced from the nest site, females abandoned the site and followed the young. Female Redwings therefore learn to recognize their young during the period they are in the nest. The earliest females were found to show signs of recognizing their young was 7 days post-hatching. This recognition is probably partly based upon the location call which is given only by older young. Though the structure of the location call remained the same from one utterance to the next for an individual, it differed markedly between individuals.

LITERATURE CITED

Alley, R., and H. Boyd. 1950. Parent-young recognition in the Coot *Fulica atra.* Ibis, 92:46–51.

Beer, C. G. 1970. Individual recognition of voice in the social behavior of birds. *In* Lehrman, D. S., R. A. Hinde, and E. Shaw, eds., Advances in the study of behavior, 3:27–74. Academic Press, New York.

Cullen, E. 1957. Adaptations in the Kittiwake to cliff-nesting. Ibis, 99:275–302.

Davies, S. J. J. F., and F. Carrick. 1962. On the ability of Crested Terns, *Sterna bergii*, to recognize their own chicks. Australian J. Zool., 10:171–177.

Emlen, J. T., Jr. 1941. An experimental analysis of the breeding cycle of the Tricolored Redwing. Condor, 43:209–219.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U. S. Natl. Mus. Bull., No. 233.

Holcomb, L. C. 1971. Nest building and egg laying by Redwinged Blackbirds in response to artificial manipulations. Auk, 88:30–34.

Johnson, R. A. 1941. Nesting behavior of the Atlantic Murre. Auk, 58:153–163.

Kinsey, E. C. 1935. Parental instincts in Black Phoebes. Condor, 37:277–278.

Lack, D., and J. T. Emlen, Jr. 1939. Observations on breeding behavior in Tricolored Red-wings. Condor, 41:225–230.

Lashley, K. S. 1915. Notes on the nesting activities of the Noddy and Sooty Terns. Carnegie Inst. Wash., 211:61–83.

Nero, R. W., and J. T. Emlen, Jr. 1951. An experimental study of territorial behavior in breeding Red-winged Blackbirds. Condor, 53:105–116.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Trans. Linnaean Soc. N. Y., 4:1–247.

Nice, M. M. 1943. Studies in the life history of the Song Sparrow. II. The behavior of the Song Sparrow and other passerines. Trans. Linnaean. Soc. N. Y., 6:1–328.

Nice, M. M. 1950. Development of a Redwing (*Agelaius phoeniceus*). Wilson Bull., 62:87–93.

Tinbergen, N. 1953. The Herring Gull's world. Collins, London.

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COMMUNAL WINTERING OF A SANDHILL CRANE WITH JAPANESE CRANES IN HOKKAIDO, JAPAN

Hiroyuki Masatomi

In the course of my ecological studies on the Japanese Crane, a Sandhill Crane (*Grus canadensis*) was found 18 January 1970 at Shimo-setsuri, Tsurui village, Kushiro district, Hokkaido, Japan, feeding with many Japanese Cranes (*Grus japonensis*) in a field where food was scattered for the cranes. This is the first record from Hokkaido, and the second for Japan, of this Nearctic species. This paper deals with observations made on the behavior and relationship of these two species, supplemented by additional records made by the people who daily feed grain to the birds.

COLORATION OF THE INDIVIDUAL OBSERVED

The plumage coloration of this Sandhill Crane changed gradually during the winter as follows:

> The head was still feathered in February. The forehead and lores became slightly bald in early April and more redness appeared in early May but was definitely not as pronounced as in adults. The chin and malar regions were more whitish than the sides of the neck. In February the back feathers had dark rachises, were gray, tipped with tawny. In April they appeared to be neutral gray without the tawny tips. However, most wing coverts retained tawny-colored tips up to early May. The abdomen was somewhat paler than the breast. The primaries were dark.
>
> The coloration in early February generally was similar to that of a hand-reared bird of about three months of age described by Walkinshaw (1949:16–20), but molting and the acquisition of the red forehead appeared about six months later. The red generally begins to appear during the first fall in some Sandhill Cranes but may not develop until spring with some others (Walkinshaw, pers. comm.). The redness or baldness of the foreheads of the Japanese Crane often is variable even among synchronously hatched individuals (Masatomi, unpubl.).
>
> The exposed culmen was blacker than those of the Japanese Cranes, but the basal half of the lower mandible was pale gray-olive. The entire bill and especially the lower mandible gradually became lighter colored. The legs were dark greenish-black or nearly black. The eyes were hazel.

ROOSTING AND FEEDING RANGE

It is not certain just when this bird arrived. In late September or early October 1969, one of the regular feeders of the Japanese Cranes noted a strange smaller dark crane feeding with four Japanese Cranes at Naka-setsuri, about 20 km north of Kushiro city (Figure 1,A). This was probably the first observation. In late November this Sandhill moved to Shimo-setsuri, 7 to 8 km south of the first location. Here many Japanese Cranes, stay in small

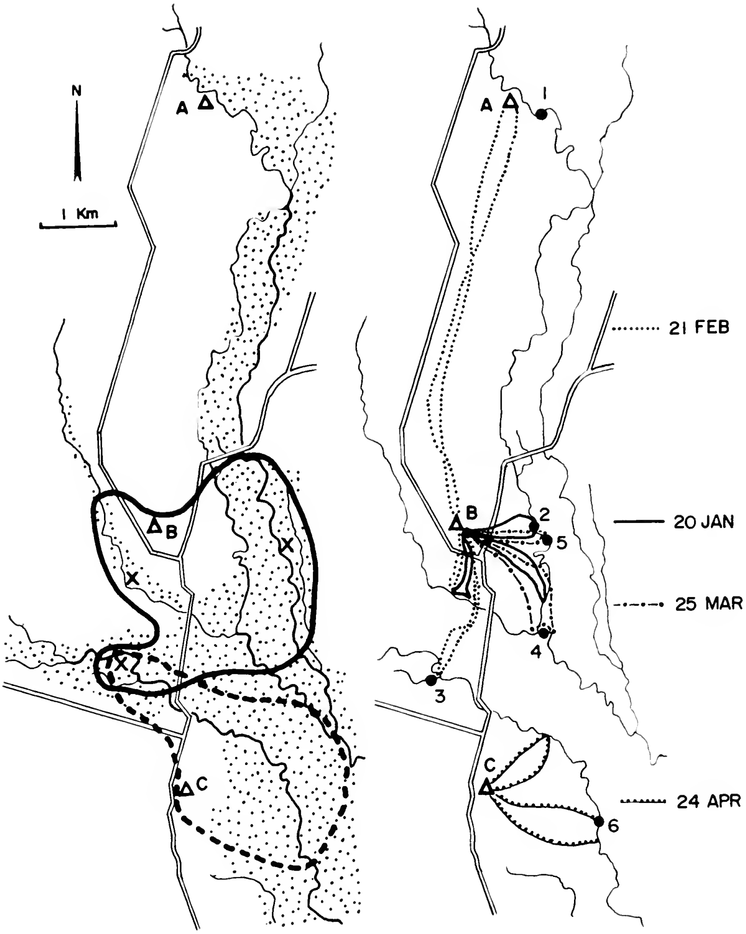

Fig. 1. (Left) Feeding ranges of flocks of Japanese Cranes in January to March (solid line) and in April (dotted one). X: roosting places used by the majority of Japanese Cranes wintering in this area. (Right) Some of the feeding ranges of the Sandhill Crane. Various lines show the Sandhill Crane's flight routes on each day. Circular dots: roosting points. Numbers given to each roosting point: change of settlements, 1. October, 2. January, 3. February, 4–5. March, and 6. April.

groups during the colder part of winter (Figure 1,B). After that the Sandhill Crane fed at Watanabe's feeding place at Shimo-setsuri, eating corn every day, until 17 April 1970 when it suddenly appeared at Narukawa's feeding place at Shimo-hororo, 3.5 km south of the second place (Figure 1,C). It arrived at this place at least once daily from then until 6 May. A similar bird seemed to be observed in May on the opposite side of the marsh, about 14

TABLE 1

FIRST ARRIVAL AND LAST DEPARTURE AT SHIMO-SETSURI FEEDING PLACE

	Arrival									
	Time		Sunrise	J.N.	M.M.	D.F.	Weather	Temperature °C	W.D.	Lux
18 Jan	—	—	06:49	—	—	—	—	—	—	—
19 Jan	—	—	06:48	—	—	—	—	—	—	—
20 Jan	09:40	(08:48)[1]	06:48	47	53	E	Cloudy	-6.5	N-1	8,500
22 Jan	10:35	(09:20)	06:46	34	54	E	Clear	-6.8	W-1	57,000
21 Feb	13:43	(09:35)	06:12	0	—	S	Clear	4.8	WNW-4	74,000
22 Feb	10:48	(09:50)	06:10	30	49	S	Cloudy	-4.0	S-1	62,000
11 Mar	14:30	(09:05)	05:43	2	—	E	Clear	2.8	S-2	102,000
24 Mar	08:32	(06:55)	05:19	27	33	E	Cloudy	-1.2	S-1	72,000
25 Mar	07:37	(06:50)	05:18	28	32	E	Clear	-8.0	NW-2	19,000
5 Apr	—	—	04:58	—	—	—	—	—	—	—
8[2] Apr	—	(14:10)	04:53	0	—	—	Clear	5.8	NW-5	95,000
17 Apr	—	—	04:38	—	—	—	—	—	—	—
24[3] Apr	—	—	04:27	—	—	—	—	—	—	—

Abbreviated head means: J.N.: Number of the Japanese Cranes aggregating before the Sandhill's arrival. M.M.: Maximum number of the Japanese Cranes gathered temporarily in the morning. R.N.: Number of the Japanese Cranes remaining behind after the Sandhill's departure. M.A.: Maximum number of the Japanese Cranes at pre-roosting assembly in the afternoon. D.F.: Direction of flight (W–E; at first west, then eastward). W.D.: Direction and degree of wind.

[1] Time in parentheses shows the first arrival and the last departure of the Japanese Cranes in flock.

[2] The record of Japanese Cranes, the Sandhill Crane not seen anywhere.

[3] At Shimo-hororo feeding place.

TABLE 1 Continued

	Time		Sunset	Departure			Weather	Temperature °C	W.D.	Lux
				R.N.	M.A.	D.F.				
18 Jan	16:27	(16:34)	16:15	2	53	E	Cloudy	–3.0	NW–1	55
19 Jan	16:30	(16:50)	16:16	18	33	E	Clear	–5.0	E–1	55
20 Jan	16:23	(16:48)	16:17	48	56	E	Cloudy	–3.3	E–2	95
22 Jan	16:38	(16:50)	16:20	22	46	W–E	Clear	–3.0	W–2	40
21 Feb	17:34	(17:42)	17:00	11	46	E–S	Clear	–3.8	E–1	10
22 Feb	17:23	(17:43)	17:01	16	45	SE	Clear	–7.0	NW–1	17
11 Mar	17:50	(—)	17:22	0	37	SE	Cloudy	–3.2	NE–1	5
24 Mar	18:11	(18:19)	17:37	11	37	E	Cloudy	–3.0	S–0	0
25 Mar	17:46	(18:05)	17:38	9	25	E	Snow	–4.7	NE–1	190
5 Apr	18:13	(—)	17:51	0	8	SE	Clear	–0.8	S–1	—
8 Apr	—	(16:06)	17:55	—	2	W	Cloudy	4.2	NW–4	3,300
17 Apr	18:00	(—)	18:05	—	4	—	Rain (Foggy)	—	S–1	—
24 Apr	18:20	(—)	18:13	0	7	SSE	Clear	4.8	SE–1	145

km east of Shimo-hororo. Thus this Sandhill Crane wintered in marginal regions of the Kushiro Marsh from early October 1969 until early May 1970, changing feeding regions at least twice.

As it changed its feeding regions, it also roosted in several different points along the Setsuri and Hororo rivers (Figure 1). Since the river never froze in many places, it was possible for the bird to feed in the river during the early mornings prior to its appearance at the feeding places. It also fed there on some evenings after returning. This bird roosted apart from the communal roosting region used by the majority of the Japanese Cranes, sometimes for several weeks or more, but often a pair of Japanese Cranes with their young will do the same. The Sandhill became affiliated with one of these groups and remained apart from the main group.

Because of the unusually deep snow at Shimo-setsuri (about 60 cm on 21 February, compared with 30 cm during normal years) the fields were snow-covered until mid-April. But the Setsuri River, 2 to 3.5 m wide at the roosting points did not freeze even in the coldest months (–20° C in February). The river here is shallow, wide and has embankments. The food of the Sandhill Crane was not known but some edible roots and rootlets as well as green parsley (*Oenanthe stolonifera*) and sticklebacks (*Pungitius pungitius*) were available in addition to the corn on the feeding stations.

DAILY ACTIVITIES AT FEEDING PLACES

Every morning at the night roost, the Sandhill searched for food or preened. Then when its adopted "family" of two adult and two young Japanese Cranes flew from the night roost, it joined them. Although it did not always go to the feeding stations in the very early morning it appeared there at least once daily during the winter. Records of earliest daily arrival and latest daily departure at the feeding regions are given in Table 1. The chronological sequence of its activities at Shimo-setsuri, on several different days are given in Figure 2.

On 25 March 1970 there had been a snowfall of 1 cm the previous night. The sky was clear, temperature –11.4° C at 07:00. Two Japanese Cranes flew from the Ashibetsu River to Shimo-setsuri feeding station at 06:50. Between then and 08:00, 32 Japanese Cranes, including five young of the year, assembled there, one after another. The Sandhill came from the east with its "family," landed, and fed for awhile. When nine Japanese Cranes came to the feeding place, the male of the "family," showed a threatening posture against them. The "family" gradually moved away 150 m eastward on foot. Sometimes the Sandhill rested, preened, fed, yawned, stretched its wings and legs, fluffed its feathers but then remained inactive until 09:55. At 09:59 the "family" flew to the region near the Setsuri River where they foraged. Heavy snow fell between 13:40 and 15:10. At 15:50 the birds came flying back in the following order- male-female-young-Sandhill-young.

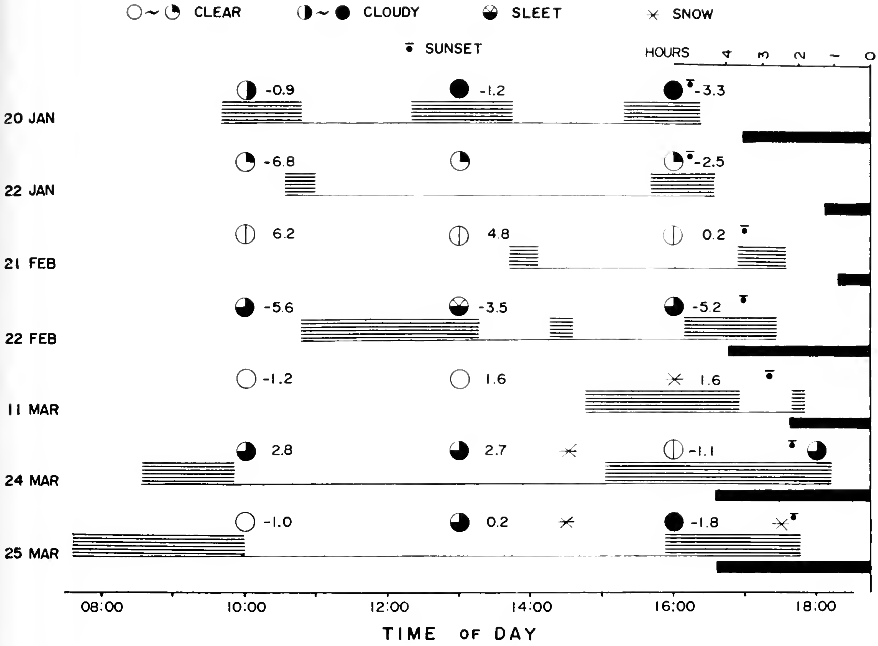

FIG. 2. Chronological sequence of the Sandhill Crane at Shimo-setsuri feeding place. Horizontal hatching: stay at feeding place. Number at each weather mark is temperature (°C). Histogram at right shows the total duration of stay at feeding place.

Approaching the feeding station, they landed then, walked the last short distance where they fed on corn. Later they sauntered to the east end of the field, preened, and rested. Later they joined other cranes and all began to dance, chasing each other, jumping high into the air. The Sandhill did not dance, but rested and watched nearby. At 16:55 all birds went to the west side of the field where much corn had been scattered. The Sandhill began feeding at 17:10, then rested, standing on one leg. Heavy snow fell again from 17:20 to 17:40. At 17:46 the male of the "family" group flew to the roosting ground, followed by the three members of his family. The Sandhill was feeding so eagerly, that it did not notice they had departed for a moment. But soon it took off after them.

The flight order was variable. Sometimes the Sandhill was in the center, sometimes behind. Excluding several double trips to Naka-setsuri from the Shimo-setsuri feeding place, its daily feeding ranged little as shown in Figure 1. Most of the Japanese Cranes gathered at the Shimo-setsuri feeding station, flew southwest or west to drink or to rummage out food along the Ashibetsu River, but the "family" seldom flew to the region. Therefore, the feeding range of the Sandhill in Figure 1 is identical with that of the "family," during January, February, and March, and of the young when they were chased away by their parents in early April.

At the earliest arrival each morning a photometer registered between 8,500 and 72,000 lx and at evening departure time registered under 190 lxs. But as spring approached, the Sandhill came earlier and remained later. The temperature at departure time was between –3° C and –7° C between January and March (Table 1). The morning departure seemed later than that recorded during the same months by Walkinshaw (1949:36–42) at Roswell, New Mexico but this was probably because of lower temperatures at Shimo-setsuri. Japanese Cranes tend to waste much time on the roosting place after sunrise during severe cold mornings (Masatomi, unpubl.). The time of evening arrival on the roosting region in January varied little from Walkinshaw's observations. The Sandhill usually joined the "family" directly on the roosting spot, after sunset. (The sun set 20 minutes earlier behind the west ridge than official sunset.)

RELATIONS WITH JAPANESE CRANES

Relation with the "family" members.—The Sandhill relationship with the "family" members can best be described in three stages:

a) Formation of interspecific association: How the Sandhill joined with this family of *G. japonensis* consisting of a pair and their two young cannot be explained. When it was first observed, it already was with the group at Naka-setsuri, so it apparently joined them even in September or early October. Unfortunately it was considered to be an undergrown young *japonensis* or a Gray Heron (*Ardea cinerea*) until I encountered it on 18 January 1970. Japanese Cranes are considered as residents in Hokkaido but there may be a movement of some birds between Kushiro and Nemuro. It is thus not completely impossible that the Sandhill met the family while migrating westward in Nemuro, but this is probably only conjecture.

b) Maintenance of the relationship with a definite "family": The Sandhill associated with the "family" of the Japanese Crane in all activities-roosting, feeding, flying, resting, etc. until 7 April. Nevertheless, it seemed that they, especially the parents, did not treat the Sandhill as a genuine member or young of the family, no matter how rarely they turned on it by a threatening posture, by chasing or other hostile activities. If it was threatened or chased, the same as their own young, the male responded by counterattacks against the attacking bird. Some birds approached it with light threatening posture and were immediately attacked by one of the "family" adults, but it was difficult to distinguish between these attacks and weak aggressions frequently expressed only to maintain interindividual distance or to defend a good feeding spot.

The parents never flew without their youngsters until the new breeding season approached, but the Sandhill was sometimes tardy as described above.

It also separated several times from the "family" during February and March. At the Shimo-setsuri feeding station, the members, especially the male, of the "family" occasionally approached the Sandhill with or without, light threatening postures, and the latter always withdrew. Such approach-avoidance, however, was not restricted for it was rather common between *G. japonensis* in a feeding flock. Although generally *G. canadensis* avoided *G. japonensis*, one young jumped aside two or three meters with half-spread wings when the former approached it with light threatening posture on 22 February. The male of the "family" approached in threatening posture toward the Sandhill in late March. The Sandhill ran away with the first threat, but I never saw the male attack the Sandhill as he did his own young when the breakdown of family ties was made in late March and early April.

c) Relationship with the post-juveniles driven away by the parents: According to the feeders, the "family" came on 7 April to the Shimo-setsuri feeding station at 11:00. Later, only the Sandhill, fed between 14:00 and 17:00. The next day I found only two adults there and after 9 April, three young, (i.e. the Sandhill, and two Japanese Cranes.) They came once or twice daily. Young *G. japonensis* sometimes danced, facing each other on the feeding grounds after March and the Sandhill joined in these dances, somewhat different from the regular courtship display, in April. On 17 April, during the afternoon, after two young Japanese Cranes had been dancing, the three young of the "family" began dancing after they had eaten. They bowed, bounced up and down, stabbed the ground, ran about flapping their wings, all in one section of the feeding region which still was covered with patches of snow. The Sandhill danced very similarly to *G. japonensis*, either with the young birds or alone. It stabbed the ground, at times picked up objects which it threw into the air. After bowing once or more it bounced 30 to 50 cm into the air, but not as high as described by Walkinshaw (1949:32–36), with legs held stiffly, and wings flapping. When it danced with young Japanese Cranes, it bowed repeatedly, tried to attack one of them, then they both jumped into the air facing each other similar to comrades of *japonensis*.

At the third feeding station such a dance was observed until early May when the three began separating. Often, each flew alone, so that it was impossible to differentiate the "family" young from others also abandoned by their parents. All young of the year often assembled into a temporary flock immediately after being abandoned. On 3 May the Sandhill took off with two Japanese Cranes for the roosting site and four days later it disappeared.

Relations with other Cranes.—Japanese Cranes forming the winter flock seemed to take no special interest in the Sandhill. They were not familiar neighbors, nor were they strong opponents. But when foraging over the feeding grounds, during the colder months, the Sandhill usually avoided them.

especially when they approached him. In contrast, however, they often showed decisive resistance against other neighbors who drew too near when they were eating. The Sandhill stretched its neck forward, pointing it's bill against the other bird and called a shrill *Bui-puy-puy-puy-puy-puy*. It then raised its body, stood in an upright position, and by this posture caused the other birds to retreat hastily away. A similar behavior was observed the next day when the bird stood in nearly erect posture, and called *Gui-puy-puy-puy-puy-puy* toward a Japanese Crane which passed slowly alongside it. The *japonensis* was startled slightly. A few approaches and more avoidances were observed in April. The Sandhill became much more self-reliant at this time.

On 24 March the Sandhill leaped half-heartedly three times into the air as if fleeing from two year-old opponents who began dancing in the flock. Occasionally he danced with young *japonensis* at the third feeding ground, but it was uncertain whether they were its former "family" mates or not.

DISCUSSION

Although a specimen of *Grus canadensis*, without date and locality was described from Japan by Temminck and Schlegel (1849:117–118) as *la grue commune a long bec* (*G. cinerea longirostris*), this record was not adopted in any authoritative list of Japanese birds (such as Austin and Kuroda, 1953; Ornithol. Soc. Japan, 1958) because of the poor data of the specimen (cf. footnote in the latter paper).

There was no record of this species for over 100 years until Takano (1964) unexpectedly found a Sandhill Crane wintering with White-naped Cranes (*Grus vipio*) and Hooded Cranes (*G. monacha*) at Arasaki, Kagoshima, Kyushu on 9 December 1963. This crane was an adult, but of unknown age. It remained there from 10 November 1963 until 26 February 1964.

Although the present case is the first Hokkaido record, the bird may have wandered in more often and was mistaken for a heron, a small Japanese Crane or a Common Crane (*G. grus*).

Several color slides taken by me were examined by Walkinshaw. He wrote "This bird from its size, very short bill and tarsi, must be a Lesser Sandhill Crane (*G. c. canadensis*) . . ." The Kyushu bird was similar to the one in Hokkaido but its subspecific identity was not determined.

According to Takano (1964) the Sandhill at Arasaki always moved in association with *G. vipio*, a larger species. But it often drove away *G. monacha* which is much more like it in size and color, when they accidently approached it. Moreover, even in flocks of *G. vipio* it was alone and often pecked at by *vipio* (Ogasawara, 1970:7). On the other hand the 1970 Sandhill always behaved as though it were a member of the "family" of *japonensis* and its activities were synchronized with the movements of this family. It might be in the category stated by Rand (1954) as "casual associations of no benefit," but the Sandhill probably received benefits from *japonensis* by joining them on both roosting and feeding regions.

In appearance the "family" adopted the young Sandhill Crane as their member but apparently, from their behavior, not as a genuine member. They were indifferent to it but tolerated it and showed no definite hostility towards it. Yet, in late March and early April they acted as though it was a stranger. Leadership of the group was retained in all cases by *G. japonensis*, chiefly the male. Hence the association must have been made and maintained by the Sandhill from the tendency for intense gregariousness of the species. The tendency of some birds to associate with, and be tolerated by birds larger than they, in non-breeding flocks is not uncommon. For instance, several sandpipers (Nichols, 1931), Bean Geese (*Anser fabalis*) with White-naped Cranes (Shimomura, 1955), and a Sandhill Crane with White-naped Cranes (Takano, op. cit.).

The Sandhill Crane that wandered into Kyushu did not associate with *G. vipio* as intensely as did the bird in Hokkaido did with *G. japonensis*, but the difference may have been because of the difference in ages. The bird in Kyushu was not a bird of the year as was the one in Hokkaido. The Whooping Crane (*G. americana*), very similar in size to *G. japonensis*, does not tolerate spoonbills, herons, or egrets within several hundred yards of the nest location while these birds are tolerated in established territories in winter although Sandhill Cranes are not (Allen, 1952:145, 188–191). However, at times Sandhill and Whooping Cranes gathered at fresh water on Aransas Refuge without indications of fighting at all. On the other hand *G. japonensis* pays no marked attention to other birds on either winter or summer territories, except birds of prey. Eastern Gray Herons (*Ardea cinerea jouyi*), Whooper Swans (*Cygnus cygnus*), and other birds forage or roost within the same territory of *G. japonensis* (Masatomi, 1970). Emlen (1952) pointed out that the form characteristics of homogeneous bird flocks were determined by the interplay of positive and negative forces associated with gregariousness and intolerance. Such tolerance (as described above) of the Japanese Cranes might be one of the causes which made unusual association between two different species possible.

The Sandhill Crane stayed longer in Hokkaido than did the one in Kyushu. Possibly because Kushiro is 1,800 km northeast from Arasaki. Since this Nearctic species breeds in northeastern Siberia, it was once recorded on 20 May on Commander Islands and observed at Nizhne-Kamchatsk in Kamchatka (Dement'ev et al., 1969:133–134) indicating possible migration of Asiatic stragglers.

SUMMARY

A young-of-the-year Sandhill Crane (*Grus canadensis* probably *canadensis*) wintered with a "family" of Japanese Cranes (*G. japonensis*) consisting of a pair and two young, near Kushiro, Hokkaido, Japan. The group formed part of a wintering flock of the latter species. This is the second record of this species for Japan, the first for Hokkaido.

The Sandhill and it's associated "family" of Japanese Cranes changed their feeding range twice or more during the winter, and correspondingly changed their roosting sites.

In the spring, when the family broke down, the Sandhill associated with the two young. At times it danced lightly with them. Some behavioral associations between the family and the Sandhill or its relationship with others in the flock are given and discussed briefly. The attitude of the "family" and other cranes was generally indifferent to it. Therefore, the formation and maintenance of this association depended on the Sandhill's positive attachment to the "family" and the general tolerance of *G. japonensis* to smaller birds. But the actual process of attachment and time of arrival were not known.

ACKNOWLEDGMENTS

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LITERATURE CITED

ALLEN, R. P. 1952. The Whooping Crane. Natl. Audubon Soc. Res. Rept., 3:1–246.

AUSTIN, O. L., JR., AND N. KURODA. 1953. The birds of Japan, their status and distribution. Bull. Mus. Comp. Zool., 109:279–637.

DEMENT'EV, G. P., AND N. A. GLADKOV (Ed.). 1969. Birds of the Soviet Union, Vol. 2. Jerusalem, Israel Progr. Sci. Transl.

EMLEN, J. T., JR. 1952. Flocking behavior in birds. *Auk*, 69:160–170.

MASATOMI, H. 1970. Tancho no seikatsu ni okeru sho-mondai 1. J. Bibai Agri. Engineer. Coll., 1:37–45.

NICHOLS, J. J. 1931. Notes on the flocking of shorebirds. *Auk*, 48:181–185.

OGASAWARA, A. 1970. Yacho no shiki. Tokyo, Asahi Shinbun.

ORNITHOLOGICAL SOCIETY OF JAPAN. 1958. A Hand-list of the Japanese birds. Herald Co., Tokyo.

RAND, A. L. 1954. Social feeding behavior of birds. Fieldiana, 36:1–71.

SHIMOMURA, K. 1955. Bird report from Arasaki, Kagoshima, Kyushu. Tori, 14:33–36.

TAKANO, S. 1964. Arasaki ni kanada-zuru torai su. Yacho, 29:21.

TEMMINCK, C. T., AND H. SCHLEGEL. 1849. Aves, *in* Siebold's Fauna Japonica (photo copy). Tokyo.

WALKINSHAW, L. H. 1949. The Sandhill Cranes. Cranbrook Inst. Sci. Bull., 29. 1–202.

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AN EVALUATION OF WINTER BIRD POPULATION STUDIES

Richard Brewer

The only large body of data on population sizes of birds in winter is that contained in the winter bird population studies published annually since 1948 in *Audubon Field Notes* (now *American Birds*). The method used in these studies (Kolb, 1965) is that an observer traverses an area of known size six or more times (hereafter termed "visits") during the winter and records all birds observed. After the last visit, the total number of individuals recorded is divided by the number of visits to give an average. This number is then multiplied by the appropriate factor to express results in birds per hundred acres. The same calculations may be made for individual species.

The method appears to have been developed more as a device to make wintertime use of plots established for breeding bird censuses than for any other reason; however, no discussion of the development of the method has been published so far as I know. In the course of conducting such studies it became clear that interpretation of the results was uncertain. This same conclusion has been reached by other workers and, in fact, the difficulty of analysis and comparison has been a persistent theme in the comments by the editor of the winter bird population studies (Kolb, 1961, 1962).

This paper reports results from a model devised to assess the meaning of the figures resulting from the use of the *Audubon Field Notes* (hereafter "AFN") method of studying winter bird populations. I take as a starting point the view that the most desirable datum is density, that is, the number of birds per unit area. For any given area, density changes more or less continually as birds enter the area or leave it. If we visualize a tract of 20 acres on which 10 birds occur but all of which have some portion of their home range lying outside the boundaries of the tract, it is clear that the instantaneous density of the tract can vary between 0, when all of the birds are in those portions of their home ranges off the tract, and 10 when all by chance happen to be on the tract. These figures have some interest but a more valuable figure is some appropriate average of the instantaneous densities. If the average fraction of the home range of the 10 birds included on the study tract was 0.6, then the average density would be 6 birds per 20 acres (assuming that a bird spends equal time in all areas of its home range). An accurate estimate of density would be provided by the AFN method if each bird were recorded on the fraction of visits corresponding to the fraction of its home range included on the tract.

Scientific names of birds mentioned in later sections are Ruffed Grouse, *Bonasa umbellus*; Red-bellied Woodpecker, *Centurus carolinus*; Hairy Woodpecker, *Dendrocopos villosus*; Downy Woodpecker, *D. pubescens*; Blue Jay, *Cyanocitta cristata*; Black-capped Chickadee, *Parus atricapillus*; Tufted Titmouse, *P. bicolor*; White-breasted Nuthatch, *Sitta carolinensis*; Brown Creeper, *Certhia familiaris.*

THE MODEL

The basic method used was this: a board was constructed on which were drawn to scale a census tract of 23 acres and the home ranges of eight birds with varying fractions of their home ranges included on the tract. The whole board was the equivalent of about 275 acres and was covered by a grid with coordinates the equivalent of 100 feet apart. The census tract was divided into a grid by lines 200 feet apart (corresponding to every other 100-foot coordinate in the section of the board occupied by the census tract). A simulated observer moved systematically over the tract following the 200-foot coordinates at the same time that a simulated bird (represented by a transparent plastic disk of known diameter) moved within its home range. If the plastic disk touched or overlapped a point occupied by an observer, the bird was considered to be observed and was counted.

Although some simplifications were necessary, the model was made as realistic as possible. Because a primary aim was the eventual assessment of studies conducted from 1966 to 1970 on five study tracts in oak and oak-pine forests of Allegan County, Michigan, the features of the model were based as far as possible on the biological features of the bird community of those areas. On these areas, which varied in size from 9.6 to 18.4 acres, about 20 species of birds were observed on more than 150 visits between November and March. Only 7 species were seen on all five tracts. Populations were low, AFN estimates being in the range from about 5 to 8 birds per study tract or about 30 to 55 birds per hundred acres. Black-capped Chickadee was the most common species with an AFN estimate of about 20 birds per hundred acres. White-breasted Nuthatch, Blue Jay, and Tufted Titmouse were the next most common species.

Specific features of the model were as follows:

1. Home range sizes varied from 9 to 76 acres, with six between 22 and 38 acres (Table 1). These are reasonable sizes for home ranges of forest birds based on our unpublished determinations and the literature (see, for example, Butts, 1931; Fitch, 1958; Kilham, 1969; Robins and Raim, 1971). The percentages of the simulated home ranges lying on the tract varied from 4 to 100 per cent.

2. The initial position of the observer at the beginning of a trial, or simulated visit, was at the southeast corner of the tract. His movement was then systematically across the tract. Systematic movement along coordinates was

TABLE 1

RESULTS OF THE MODEL EVALUATING AFN WINTER BIRD STUDY METHODS. Trials = 25 except as indicated.

Home range	Percentage on tract	Size (acres)	Occurrence (Percentage of trials recorded)		
			36′ radius	75′ radius	250′ radius
Normal speed					
J	4	34	0	7	12
A	14	37	4	22*	48
C	30	76	20	56*	92
G	45	38	32	56*	88
D	65	22	24	63*	96
E	65	35	36	64	84
H	100	8.6	24	89*	100
B	100	23	24	68	100
Half-normal speed					
J	4	34		8	
A	14	37		32	
C	30	76		48	
G	45	38		44	
H	100	8.6		64	
Twice-normal speed					
J	4	34		12	21**
C	30	76		76	93**
G	45	38		88	100**
D	65	22		64	100**
E	65	35		88	100
H	100	8.6	60***	92	100**

* 27 trials
** 14 trials
*** 20 trials

the method employed in the field by us and by many participants in the AFN studies, but it is not a requirement of the method (Kolb, 1965).

3. The initial position of the bird was determined by the use of randomly chosen numbers indicating a coordinate position on the board. The direction of the bird's first movement was determined randomly from among the eight primary compass directions. After the first movement, the three opposing directions were eliminated for subsequent movements. For example, if the first movement was east, then west, northwest, and southwest were eliminated. The possible actions for the bird on its second movement were six of equal probability: north, northeast, east, southeast, south, and no movement. Tests in the development of the model showed that if all eight directions were re-

tained the simulated bird tended to stay in a restricted area near its initial position rather than to move over its home range in a manner corresponding more closely to the actual movements of birds in the field.

Eventually movement of the simulated bird might bring it to the edge of its home range. At this point all directions were again made available and the no-movement possibility was eliminated. Certain movements, those which would take the bird outside its home range, were impossible in this situation and were rejected; other movements would move the bird along the edge of its home range. The first move which took it away from the edge into its home range was used as a new direction and the procedure of discarding the three opposing points of the compass was again followed (and the no-movement possibility re-instated).

The paths taken by the simulated birds under these procedures seemed realistic when compared with our maps of actual paths taken by birds in the field.

4. Three different speeds of movement of the bird relative to the speed of the observer were used. These were approximately one-half the speed of the observer (termed "normal speed"), one-fourth the speed of the observer (half-normal speed), and the same as the speed of the observer (twice-normal speed). In our censusing of oak forests, the actual speed of the observer (median values) varied by area from about 56 to 69 feet per minute (fpm), or about 0.6–0.8 miles per hour (mph). In subsequent sections 67 fpm is used as the speed of the observer. Although slightly faster than our actual overall average, it is convenient as a rate taking exactly 3 minutes from one stake to the next.

The actual movements on the board were as follows: For half and full speeds the observer went from one grid intersection to the next (200 feet) in two moves of 100 feet (that is, from one board coordinate to the next). The bird took one move (normal speed) or two moves (twice-normal speed) for each move of the observer. The moves of the bird were one-half square. Going north, south, east, or west, one move of the bird was 50 feet; going one of the four intermediate directions it was about 71 feet. For half-normal speed the observer went from one grid intersection to the next (200 feet) in a single move and at the same time the bird took one move.

At any time the possibilities for movement for the bird were 3 50-foot moves, 2 71-foot moves, and no movement. Consequently, the average distance per move was about 49 feet. Twice-normal speed for the bird, accordingly, was about 65 fpm, normal speed 33 fpm, and half-normal speed 16 fpm.

There is relatively little information in the literature on the rate of travel of birds. Yapp (1956) commented that he had timed feeding winter tit flocks at speeds from one-eighth to two mph (that is, about 10–175 fpm). Odum

TABLE 2

RATE OF MOVEMENT OF THREE SPECIES OF OAK FOREST BIRDS, ALLEGAN COUNTY, MICHIGAN, FEBRUARY–MARCH, 1969.

Species	Number of observations	Total minutes	Feet per minute	
			Range	Median
Downy Woodpecker	7	140	12–71	23
White-breasted Nuthatch	14	229	9–122	30
Black-capped Chickadee	9	149	15–64	42

(1942) reported rates of movement of Black-capped Chickadees, based on all-day observation of flocks, from 18 to 40 fpm. He observed that speeds varied by time of day and by weather conditions and commented that movement was not uniform, periods of rapid movement (up to 350 fpm) alternating with periods of little or no movement.

Our own observations made on one of our study areas at Allegan (the Small Oak area) in February and March 1969 generally agree with these findings. The observations were made (in connection with studies designed to determine home range boundaries) by following birds for as long as possible and mapping the observations. Measurement of distance was along the actual path followed and speed was calculated using the time elapsed from the first to the last observation of the bird. Obtaining data on speed that are unbiased is difficult. For example, the speed of birds which travel by moving slowly through the forest and then taking a long flight to another area beyond the range of observation will be generally underestimated because the long flights will be omitted from the sample. Also it is important that short observations as well as lengthy ones be included, inasmuch as observations of greater duration may be of birds traveling slowly enough that they can be readily followed. I used a lower limit of four minutes for the practical reason that estimates of speed based on shorter durations might be too inaccurate owing to our recording times only to the nearest minute.

The data seem to indicate that birds may travel at speeds from less than 10 to more than 100 fpm and that variability is appreciable (Table 2). They indicate also that for the time and place they were gathered speeds of three important species of the forest are in the range between 20 and about 40 fpm.

5. Differences in conspicuousness were taken into account by using plastic disks of three radii corresponding to 36, 75, and 250 feet. The circle of 36-foot radius represents a very inconspicuous species, the circle of 250-foot radius, a very conspicuous one. If the disk touched or overlapped the point occupied by the observer or his path in moving from one point to the next.

the bird was counted. This corresponds to a situation in which a bird is totally observable up to a given distance from an observer and is never censusable beyond that distance (curve 1 in Fig. 2 of Eberhardt, 1968), an obviously unrealistic situation. It also corresponds, however, to a situation in which the radii represent median distance of observability (defined as probability of observation). For example, the 75-foot circle represents a situation in which the number of birds nearer than 75 feet that are missed is the same as the number of more distant birds that are observed.

The relationship in the field between observability and distance from the observer is difficult to approach directly. We may visualize the observer in the center of a space that can be subdivided by circles drawn at equal distances going outward from him. The area of the concentric rings so produced increases outward. For example, if 50-foot intervals are used, the ring from 50–100 feet away is larger than the circle from 0–50 feet and the ring from 100–150 feet is larger still. Assuming a homogeneous distribution of birds in the space, the number of birds present in each ring will, accordingly, increase going outward. The increase in area of the concentric rings is linear and so, consequently, is the increase in number of birds present at given distances from the observer. Discussions germane to these ideas but developed in connection with strip censuses are given by Anderson and Pospahala (1970) and Emlen (1971).

If there were no decrease with distance in the ability of an observer to detect birds, the number of birds seen at increasing distances would increase, following curve A in Fig. 1. In fact, we expect observability to decline with distance. Curve B represents a linear decline in observability from 100 per cent at the point occupied by the observer. In this case, the number of birds actually observed would be related to distance from the observer as shown in curve C.

A linear decline in observability with distance is not an unreasonable assumption but other reasonable relationships can be envisaged. I approached the question indirectly in the following manner. During routine visits to the oak forest study areas in the winter of 1968–9, the observer recorded the distance from each stake on each plot at which any bird could be observed by sight or sound. Estimating distances in the field is not easy but was facilitated by the observers' familiarity with the study areas, by the areas being staked at 200-foot (in some cases, 100-foot) intervals, and by the use of maps showing any prominent topographic and vegetational features. Data deemed sufficient for analysis were obtained for the White-breasted Nuthatch (Table 3) on one study area, the Black-capped Chickadee on three study areas, and the Ruffed Grouse on one study area (Table 4).

Grouping of observations by distance (observations falling at a class

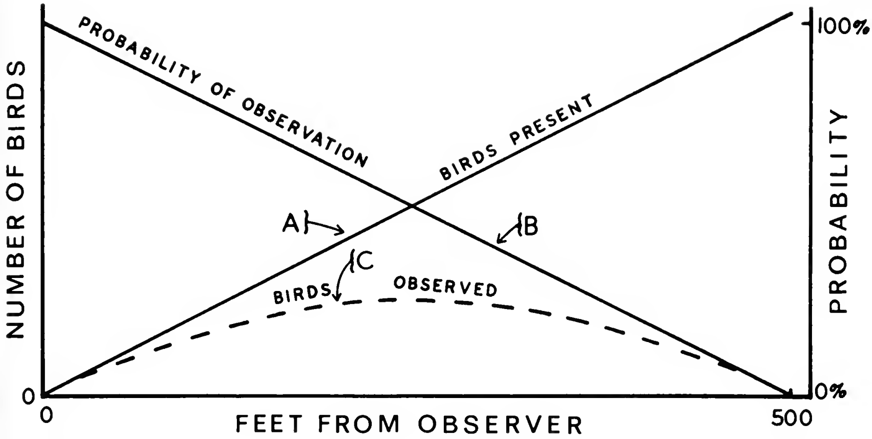

FIG. 1. Relationship between the number of birds present, their probability of being observed (observability), and the number of birds actually observed in ten concentric zones centered on the observer. A linear decline of observability from 100 per cent at distance 0 to 0 per cent at 500 feet is assumed.

boundary, as for example at 100 feet in Table 3, were counted as one-half observation in each class) and plotting the result gives curves corresponding to C in Figure 1. Making the assumption that observation is 100 per cent efficient in the closest zone, the actual number of birds present in each zone can be calculated as in Table 3 (cf. Anderson and Pospahala, 1970: 142–145,

TABLE 3

RELATIONSHIP OF NUMBER OF WHITE-BREASTED NUTHATCHES OBSERVED AND PROBABILITY OF OBSERVATION TO DISTANCE FROM OBSERVER (LARGE OAK AREA, ALLEGAN CO., MICHIGAN, WINTER 1968–9).

Number of birds estimated as actually present in each zone is calculated by determining density for zone 1 (0.00077 per square foot in this case) and multiplying this value by the area of the other zones.

Zone (Distances in feet)	Area of zone (square feet)	No. of observations	No. birds calculated as present	Probability of observation
1 (0–100)	31416	6	6	100
2 (100–200)	94248	5.5	18	31
3 (200–300)	157080	5	30	17
4 (300–400)	219912	2.5	42	6
5 (400–500)	282744	1	54	2
6 (500–600)	345576	0	66	0
7 (600–700)	408408	1	78	1

TABLE 4

RELATIONSHIP OF NUMBER OF BLACK-CAPPED CHICKADEES AND RUFFED GROUSE OBSERVED AND PROBABILITY OF OBSERVATION TO DISTANCE, ALLEGAN CO., MICHIGAN, WINTER 1968–9.

	Black-capped Chickadee						Ruffed grouse	
	Large Oak		Small Oak		Large Pine		Small Pine	
Zone (distances in feet)	No. Obs.	Prob.	No. Obs.	Prob.	No. Obs.	Prob.	No. Obs.	Prob.
1 (0–40)	2	100	5	100	6.5	100	4	100
2 (40–80)	5	83	7	47	11.5	60	6	50
3 (80–120)	1	10	5	20	2.5	8	1.5	8
4 (120–160)	1	7	2	6	1.5	3	0.5	2
5 (160–200)	0	0	—	—	—	—	—	—
6 (200–240)	1	4	—	—	—	—	—	—

and Emlen, 1971: 329–333). If these figures were plotted they would correspond to curve A of Fig. 1. Dividing the number of birds observed by the number calculated to be present gives a curve relating probability of observation of distance (Table 3), corresponding to curve B of Figure 1. The assumption of 100 per cent efficiency in zone 1 is probably erroneous (see, for example, Enemar, 1959: 78–89, and Emlen, 1971), but this will not affect the shape of the probability curve derived. The shape would be affected if the distribution of birds were not homogeneous around the observer; bias might be serious if the presence of the observer affected the distribution by attracting birds or driving them away. My impression is that for winter studies in oak forest this was not a serious problem in that any such movements tended to be within zone 1 rather than between zones.

The results suggest that probability of observation declines rapidly at first and then more slowly (Tables 3 and 4). It is clear that a straight-line relationship does not hold over the whole distance from zero to the limits of observation. A negative exponential relationship like that suggested by Gates et al. (1968) for the flushing of Ruffed Grouse is a possibility, but it is also possible that the relationship is a reversed sigmoid curve like curve in Fig. 2 of Eberhardt (1968), with a short upper limb hidden within zone 1.

I return now to the suggestion that the radius used for the plastic disk simulating a bird should represent the median distance of observability. This distance, at which the number of near birds missed is equal to the number of far birds seen, shifts depending upon the observability curve. Calculation of the median distance of observability appears to require a knowledge of this curve, information which, as I have indicated, is not readily obtained. One can, however, fairly readily obtain actual distances of observation in

TABLE 5

DATA FOR COMPARISON OF MEDIAN DISTANCE OF OBSERVATION AND MEDIAN DISTANCE OF OBSERVABILITY, USING AN ARBITRARY DENSITY OF 0.0026 BIRDS PER SQUARE FOOT AND AN ARBITRARY REVERSE SIGMOID RELATIONSHIP BETWEEN PROBABILITY OF OBSERVATION AND DISTANCE FROM OBSERVER.

Distance from observer (feet)	Number of birds present	Probability of observation	Number of birds seen	Cumulative numbers		
				Birds seen	Near birds missed	Far birds seen
0–50	2	0.99	2	2	0	27
50–100	6	0.95	6	8	0	25
100–150	10	0.75	7.5	15.5	2.5	19
150–200	14	0.30	4	19.5	12.5	11.5
200–250	18	0.15	3	22.5	27.5	7.5
250–300	22	0.07	1.5	24	48.0	4.5
300–350	26.5	0.05	1	25	73.5	3
350–400	31	0.03	1	26	103.5	2
400–450	35	0.02	1	27	137.5	1
450–500	39	0.01	0	27	176.5	0

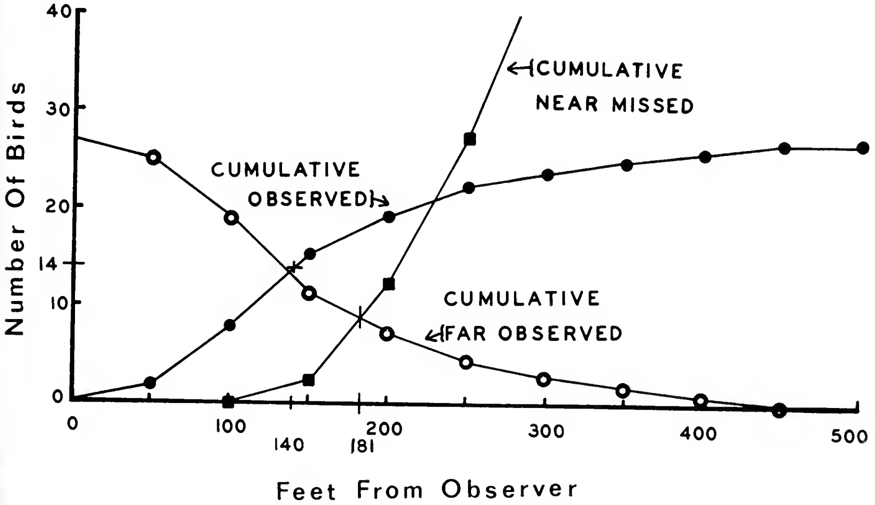

FIG. 2. Comparison of median distance of observation and median distance of observability for data in Table 5. Median distance of observation is the distance below which and above which half of the birds were observed. A total of 27 birds was observed; consequently, the median is the distance at which the 14th bird was seen, or about 140 feet. Median distance of observability is the distance at which the number of near birds missed is equal to the number of far birds observed, or about 181 feet.

some manner such as that described on page 266; from such data one can calculate a median distance of observation. The median distance of observation is the distance below which and above which half of the actual observations lie. I have investigated the relationship between the median distance of observation and the median distance of observability using models based on various observability curves. Table 5 and Fig. 2 illustrate the method for an arbitrary reverse sigmoid relationship between observability and distance. Graphical solution (Fig. 2) indicates that the median distance of observation is about 140 feet and the median distance of observability is about 181 feet. All of the observability curves which I have tested, including most of the biologically reasonable ones, yielded a similar relationship of the median distance of observation lying within the median distance of observability; the quantitative relationship between them, however, varied considerably depending on the exact nature of the observability curve. For birds in oak forests the median distance of observation lies between 40 and 200 feet and several are clustered between 50 and 100 feet (Table 6; see also the appropriate species in Table 9 of Kendeigh, 1944. The latter figures apparently are means rather than medians; because of the occasional bird observed at a great distance, the mean will usually exceed the median for data of this sort.) Presumably these medians are all in some degree underestimations of the median distance of observability. In sum, the oak forest data seem to justify the radii of 36 feet as a very inconspicuous species, 250 feet as a very conspicuous one, and 75 as a species of average conspicuousness.

6. As soon as a given simulated bird was tallied, the trial was discontinued; this corresponds to a situation in which an observer can invariably avoid counting the same bird more than once on a visit. This is undoubtedly unrealistic, but I have no information on the frequency with which birds are counted more than once, nor on how often birds are not counted in the belief that they had already been recorded.

Fourteen to 27 (mostly 25) trials, or simulated visits, were used for each home range under each set of radius/speed conditions. In all, 1000 simulated visits were used (Table 1).

RESULTS

The relationship of basic importance is that between the percentage of visits on which a bird is recorded (hereafter this percentage is called "occurrence") and the percentage of the bird's home range lying on the study tract. For the AFN method to indicate accurately the contribution of a given individual bird to the density of birds on the tract, the two values must agree. This relationship is indicated by the diagonal line in Figs. 3 and 4.

For all conditions occurrence was positively related to the percentage of

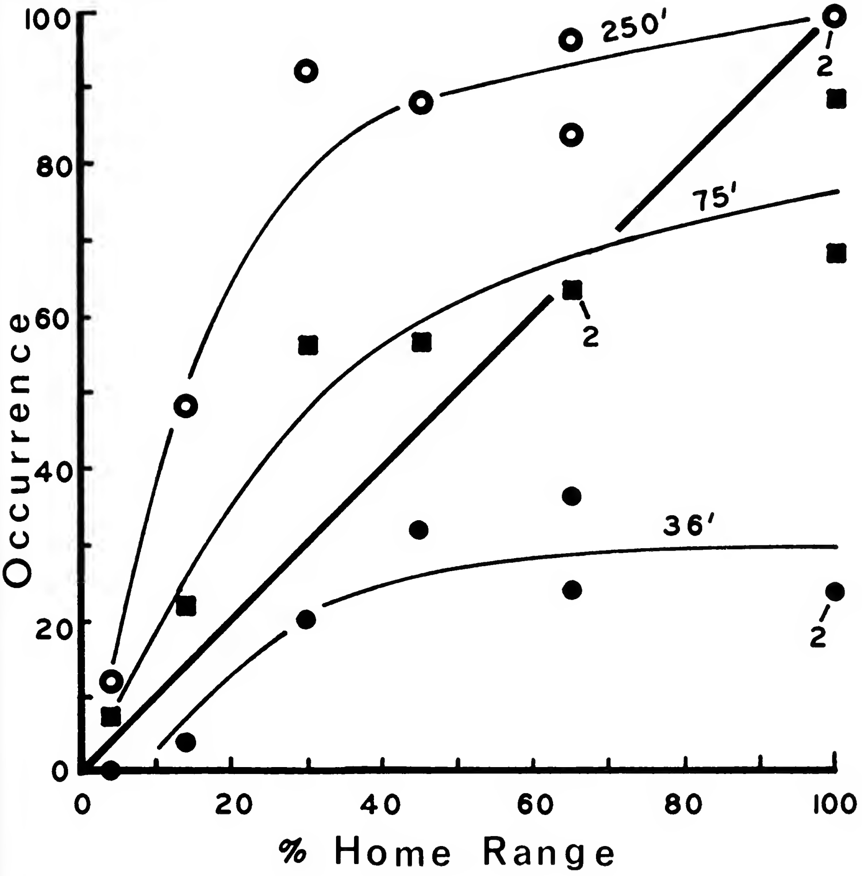

Fig. 3. Relationship between occurrence (percentage of simulated visits on which a bird was counted) and percentage of the bird's home range on the study tract (birds moving at normal speed) for highly conspicuous birds (circle, 250-foot radius of observability), moderately conspicuous birds (squares, 75-foot radius), and inconspicuous birds (dots, 36-foot radius). Lines were fitted by eye.

the home range on the tract. In no case, however, did the curve relating occurrence to home range follow the required diagonal (Figs. 3 and 4, Table 1). Both conspicuousness of the bird and its speed relative to that of the observer influenced occurrence. The closest approach to the diagonal and, thus, the closest approach to an accurate reflection of density was given by the combination of a 75–foot median distance of observability and normal speed. All of the other combinations gave curves lying further from the diagonal.

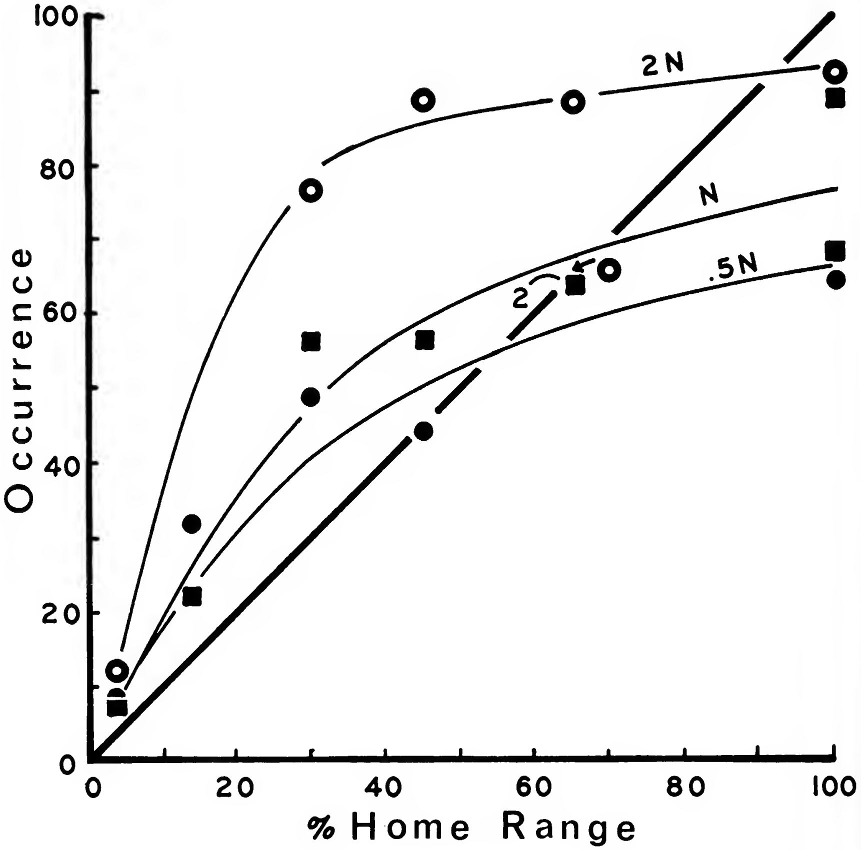

Fig. 4. Relationship between occurrence (percentage of simulated visits on which a bird was counted) and percentage of the bird's home range on the study tract for birds (moderate conspicuousness) moving at normal speed (squares), twice-normal speed (circles), and half-normal speed (dots). Lines were fitted by eye.

For any conspicuousness: speed combination the basic curve relating occurrence to per cent home range on the tract showed a fairly sharp initial rise and then tended to level off (Figs. 3 and 4, Table 1). The AFN method, accordingly, is relatively insensitive to changes in percentage of home range on the tract from 30 or 40 to 100 per cent.

Occurrence increased with increased conspicuousness but the exact relationship was complex. The same increase, either actual or proportionate, in median distance of observability was more effective in increasing occurrence when the increase was in the range from 36 to 75 feet than when in the range from 75 to 250 feet (Table 1). Also, the increase in occurrence was greater for a given increase in median distance of observability for birds with large percentages of their home range on the tract than for those with small (Table 1).

Occurrence increased with increased speed of the bird relative to that of the observer (Fig. 4, Table 1). Increasing to twice-normal the speed of birds with a median distance of observability of 75 feet moved their curve far above the diagonal into about the same position occupied by highly conspicuous birds (250-foot radius) traveling at normal speed.

There was no consistent indication that size of home range had an effect on occurrence (cf. home ranges D with E and H with B in Table 1).

DISCUSSION

It is clear that the AFN method fails in most situations to indicate accurately the contribution of an individual bird to the avian population of a study tract. To recapitulate, the relationship between occurrence and percentage of home range on the tract is non-linear, such that occurrence increases only slightly for home ranges 100 per cent on the tract compared with those 40 per cent on the tract. Occurrence is also affected by the conspicuousness of the bird and the speed of the bird relative to that of the observer.

Other things being equal, the 75-foot radius of observability gave best results. I suspect that this is true because this value, among the three used, most nearly approximates half the distance between census-plot coordinates. With the 36-foot radius a bird may be within a square adjacent to the observer and escape observation. With the 250-foot radius, a bird may be beyond the adjoining coordinate and still be observed; consequently, if the bird has any substantial part of its range on the tract, the probability of tallying the bird at some time during the visit becomes very high, approaching 100 per cent once half or more of the home range is included on the tract (Table 1, Fig. 3). It is a matter of some interest that, with the 75-foot radius, even birds whose home ranges are wholly on the tract, whether contained within it or coincident with it, were not invariably encountered on a visit (Table 1). This was made possible by the movements of the bird producing a path that avoided the observer.

Presumably a bird which remained stationary for the length of a visit and which was of sufficient conspicuousness to be seen from one point on the tract, if it were on the tract, would be recorded on the number of trials corresponding to its percentage of home range on the tract. Increasing the speed of the bird increases its exposure to the observer, at least for home ranges having a small percentage of their area on the tract and, thus, results in these birds being observed too often. Allowing birds with a very high percentage of their home range on the tract to move, however, introduces the possibility of their eluding the observer, as described above. It is unclear whether birds moving at one-fourth the speed of the observer are censused much more poorly than birds moving at one-half the speed of the observer (Table 1, Fig. 4) ; it is, however, clear that birds moving at the same speed as the observer are generally observed far too often.

The aim of the AFN method is to estimate abundance—ideally density—of the total bird community and its constituent species. This is slightly different from the question of how well the method assesses the contribution to density of an individual bird and is worth examining directly. To begin with, very conspicuous birds and birds having speeds equal to that of the observer will almost invariably be overestimated. The Blue Jay is probably an example of a species which will be overestimated. Very inconspicuous birds (the Brown Creeper, perhaps) will invariably be underestimated, possibly excepting cases in which they are very fast moving.

Birds of medium conspicuousness and moving at speeds one-half to one-fourth that of the observer will produce estimates that may be close to the actual density on the tract. The occurrence curve for such birds cuts the diagonal in such a way that birds having a small percentage of their home range on the tract will be overestimated and birds having a large percentage will be underestimated. If birds of both categories occur on the tract, the errors will be in opposing directions. It would be too much to expect that the errors would cancel one another but the tendency would be in this direction. Unfortunately, the extent and direction of the final error will be impossible to calculate.

Possibly some species of birds of the oak forests fit reasonably well the conditions of conspicuousness and speed which allow fair estimates of density (Tables 2 and 6). More information on conspicuousness and speed could be used, however, before drawing such a conclusion. These topics are worth some further research. Persons making AFN studies could contribute data on conspicuousness and help to interpret their own figures by recording distances at which birds are observed. It is certain that variations in speed and conspicuousness will affect estimates greatly; consequently, if a bird is fast moving at one period of the year and slow at another, or if it is more conspicuous in one vegetation type than another, the figures derived in these separate situations will not be comparable.

One important consideration in the winter study of populations not dealt with directly in the model is the tendency of many species to occur in flocks. If only mathematical considerations were involved, the effect would be simply to increase variability over the situation in which each bird moves independently. This is undoubtedly one of the reasons for the visit-to-visit vari-

TABLE 6

MEDIAN DISTANCE OF OBSERVATION FOR SEVERAL OAK FOREST BIRDS. THE STUDY AREAS WERE LARGE OAK (LO), SMALL OAK (SO), LARGE PINE (LP), SMALL PINE (SP), AND GREENBRIER (GB).

Species (Study Area)	No. of observations	Median distance (feet)
Brown Creeper (LP)	3	40
Brown Creeper (SO)	3	90
Ruffed Grouse (SP)	12	50
Black-capped Chickadee (LP)	22	60
Black-capped Chickadee (SO)	19	60
Black-capped Chickadee (LO)	10	50–75
Tufted Titmouse (GB)	5	70
Tufted Titmouse (LO)	9	100
White-breasted Nuthatch (GB)	7	70
White-breasted Nuthatch (LO)	21	200
Blue Jay (LO)	15	175
Red-bellied Woodpecker (LO)	9	200

ability in actual counts which, in my field experience, is substantial. In light of this variability, the six visits minimally required by the AFN method may, by chance, give very atypical results and will give a variance so large that statistical demonstrations of any except enormous differences between years or areas may be impossible. Other, biological, considerations may, however, also be involved. Probably the presence of a bird in a flock increases its likelihood of being seen. This is so because the flock tends to be more conspicuous than a single bird and once any member of a flock is detected, the observer is likely to observe most or all of the other members. Individual conspicuousness and flock conspicuousness may, then, be different things. Values such as those given in Table 6 will, however, tend to reflect the conspicuousness of the usual unit (flocks for chickadees, individuals for creepers, twosomes for nuthatches) so that we are led again to the conclusion that the most important effect of conspecific flocking on AFN results will be to increase variability.

Because of the severe biasing effect of bird speeds that are high relative to the observer's speed, I would recommend that in conducting AFN studies the observer move at the most rapid pace compatible with his ability to detect birds in his vicinity. Doubtless this pace will vary among habitats. It is perhaps worth emphasizing that this recommendation is designed to increase the likelihood that AFN figures will approximate densities; if the aim is to include as many as possible of the birds whose ranges touch the tract, an extremely slow pace would be best but the estimates derived will then be overestimates for all except the very inconspicuous species.

This discussion has emphasized the fact that AFN figures are full of imponderables. It may be desirable to conclude with a point that, if not optimistic, is at least moderately firm. In the special situation in which the study tract is so isolated or circumscribed that all birds have their home ranges entirely within it, all species except the most conspicuous ones will be underestimated.

SUMMARY

A model was designed to evaluate estimates of bird numbers derived by methods employed in *Audubon Field Notes* winter bird population studies. Strictly accurate estimates of density would result if the percentage of visits to a study tract on which a bird was seen (called "occurrence") was the same as the percentage of that bird's home range lying on the tract. This linear relationship was not found; instead occurrence tended to level off at percentages above 40. Occurrence was also affected by the conspicuousness of the bird and by the speed of movement of the bird relative to that of the observer.

It was concluded that in field situations fulfilling the conditions of the model very conspicuous birds would be overestimated and very inconspicuous birds underestimated. Estimates for species of medium conspicuousness might be fair approximations of actual density, owing to the tendency of the method to underestimate the contribution to density of birds with a high percentage of their home range on the tract and to overestimate the contribution of birds with a low percentage. These conclusions hold for birds moving slowly relative to the observer. Density of birds moving as fast as the observer will be drastically overestimated, except for very inconspicuous species.

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LITERATURE CITED

Anderson, D. R., and R. S. Pospahala. 1970. Correction of bias in belt transect studies of immobile objects. J. Wildl. Mgmt., 34:141–146.

Butts, W. K. 1931. A study of the chickadee and White-breasted Nuthatch by means of marked individuals. Parts II and III. Bird-Banding, 2:1–26, 59–76.

Eberhardt, L. L. 1968. A preliminary appraisal of line transects. J. Wildl. Mgmt., 32:82–88.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk, 88:323–342.

ENEMAR, A. 1959. On the determination of the size and composition of a passerine bird population during the breeding season. Vår Fågelvärld, suppl. 2:1–114.

FITCH, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. Univ. Kansas Publ. Mus. Nat. Hist., 11:63–326.

GATES, C. E., W. H. MARSHALL, AND D. P. OLSON. 1968. Line transect method of estimating grouse population densities. Biometrics, 24:135–145.

KENDEIGH, S. C. 1944. Measurement of bird populations. Ecol. Monogr., 14:67–106.

KILHAM, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. Wilson Bull., 77:134–145.

KOLB, H., JR. 1961. Winter bird-population study. Audubon Field Notes, 15:358–359.

KOLB, H., JR. 1962. Winter bird-population study. Audubon Field Notes, 16:367.

KOLB, H., JR. 1965. The Audubon winter bird-population study. Audubon Field Notes, 19:432–434.

ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee—3. Auk, 59:499–531.

ROBINS, J. D., AND A. RAIM. "1970" (1971). Late winter movements and social behavior of the Black-capped Chickadee. Jack-Pine Warbler, 48:66–72.

YAPP, W. B. 1956. The theory of line transects. Bird Study, 3:93–104.

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PUBLICATION NOTES AND NOTICES

OBSERVATIONS ON DUCK HUNTING IN EASTERN CANADA IN 1968 AND 1969. By H. Boyd. Occasional Paper No. 12, Canadian Wildlife Service, 1971: 6½ × 9 in., paper covered, 24 pp. No price given.

(From the author's abstract) "Observations of hunter performance provide information on specific differences in crippling losses and on factors governing the choice by hunters of what ducks they shot at, how effectively they shot at different times during the season and in various kinds of weather and what proportions of the ducks brought down were retrieved and kept."—G.A.H.

ACTIVITY PATTERNS OF CANADA GEESE DURING WINTER

Dennis G. Raveling, Wendell E. Crews, and W. D. Klimstra

It is common knowledge that activity patterns of wild geese are correlated with weather conditions. Geese usually fly to feeding areas in the early morning and late afternoons but undertake increased flight activity throughout the day when it is stormy. In conjunction with a study of social behavior and local movements of Canada Geese (*Branta canadensis*) during winter (Raveling, 1969*a–c*; 1970) exact times of flight activities of a large wintering flock were recorded almost daily for two seasons. Specific records of times of flights were also available from radio-marked geese of known age, sex, and social class (i.e., family, pair, single). This paper documents the activity rhythms of a large winter flock of Canada Geese and of some specific individuals within that flock, and the environmental features associated with goose activity. Such knowledge is necessary for understanding the ecological relationships associated with an animal's activity and can usually be utilized in management of exploited species.

METHODS

Observation of the times of flight and activities of the flock were made almost daily from late September to mid-March in 1963–64 and 1964-65 at Crab Orchard National Wildlife Refuge, Williamson County, Illinois. Approximately 40,000 Canada Geese (*B. c. interior*; see Hanson and Smith, 1950:77) spent the major portion of the winter period on and near this refuge. The inviolate portion of the refuge used by the geese included 2,600 acres of Crab Orchard Lake where the birds roosted, and 5,000 acres of cropland (corn and soybeans) and 2,800 acres of pasture where the geese fed.

The geese roosted mainly at the lake (Raveling, 1969*b*). Observers were usually in the same locations each day and in position to note accurately the time at which the first geese flew (either out from or back to the lake) and when flights were "heavy." The notation of heavy flight was relative to total numbers of geese in the area. This could be as few as 10,000 in October or March and as many as 60,000 in January. The start and ending of a period of heavy flight represented judgments of the time periods in which many flocks were leaving or arriving from different areas at the same time. In general, the period of heavy flight included movement of an estimated 75+ per cent of the geese present.

During the two winters, 77 Canada Geese were color-marked and outfitted with miniature radio transmitters. These included parts or all members of 10 families, 2 pairs, and 35 yearlings. Data recorded regularly from transmitter-marked geese included: lake locations before flight in the morning and afternoons, times of flight out from and back to the lake and changes in feeding areas, and locations in fields. Flight times of radio-marked geese were easily determined by continuous scanning of the frequency range receiving their signals. The instant these birds flew, large increases in auditory signal

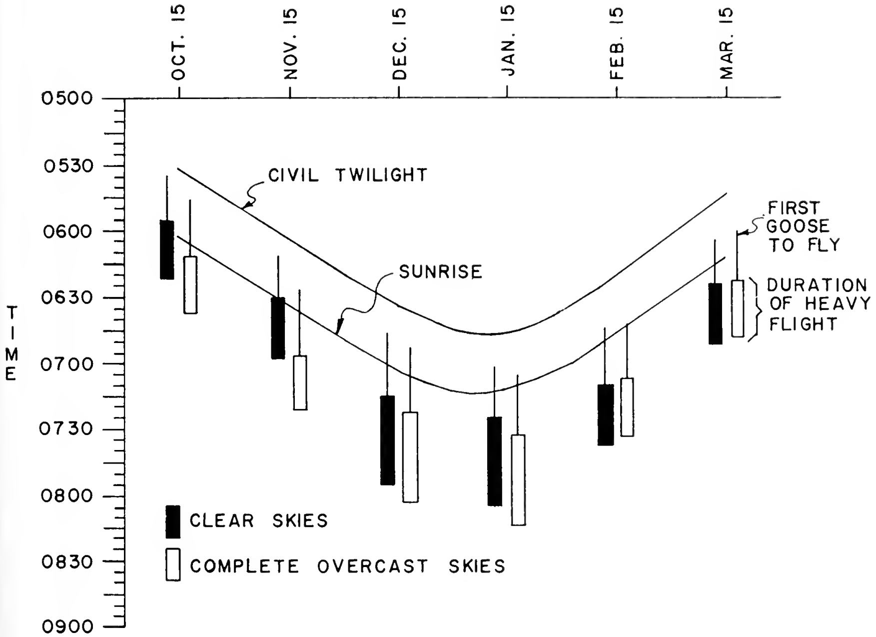

FIG. 1. Generalized average morning flight pattern of Canada Geese from the roost lake under clear and complete overcast skies (civil twilight and sunrise from U. S. Naval Observatory, 1961, 1962, 1963).

strength occurred which then faded suddenly or disappeared at the termination of a flight. Details on the techniques of radio-tracking and color-marking, and recognition and permanency of families of geese and other social classes are provided in Raveling (1969*a*).

Temperature and humidity were recorded on a hygrothermograph at the refuge. Notes were kept on cloud cover, wind direction, precipitation, and disturbances affecting the movements and locations of geese. Cloud cover was recorded as none, partly (< 50 per cent), mostly (> 50 per cent), or complete.

MORNING FLIGHTS FROM THE LAKE

Initiation.—At the latitude of Crab Orchard, civil twilight occurs within 26 to 29 minutes before sunrise and after sunset and the increase and decrease of light intensity during these minutes is approximately eighty-fold (Kimball. 1916). With the exception of the coldest days in winter, morning goose activity began within this period of rapidly increasing light (Fig. 1).

In October and November under clear or partly cloudy skies, the first geese to fly did so within 10 minutes after dawn civil twilight; from December into March, when temperatures were above 20° F, the first flying geese were re-

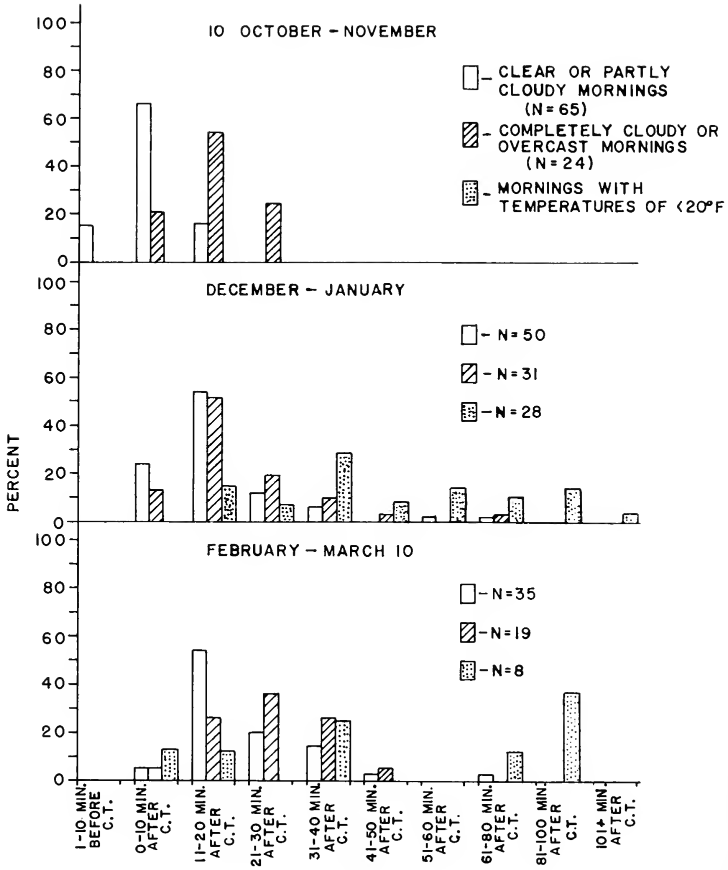

FIG. 2. Time period in which the first geese flew in relation to dawn civil twilight (C.T.).

corded somewhat later, usually within 20 minutes after civil twilight (Fig. 2). Completely cloudy conditions usually delayed the time of first flight by approximately 10–15 minutes. Flight times were less predictable under cloudy conditions. The delay of the first geese to fly during the darker, cloudy mornings was more pronounced during periods when the first geese had been leaving near the time of civil twilight rather than a few minutes later.

The time lag between the first geese to fly and the start of the heavy flight was relatively constant regardless of variations in time of first flight and the cloud cover (Fig. 3). Concentrated flights usually began between 10–30 minutes after the geese flew. When a dense fog occurred the heavy flight was delayed up to 1.5 hours after the time the first geese flew. In general, the

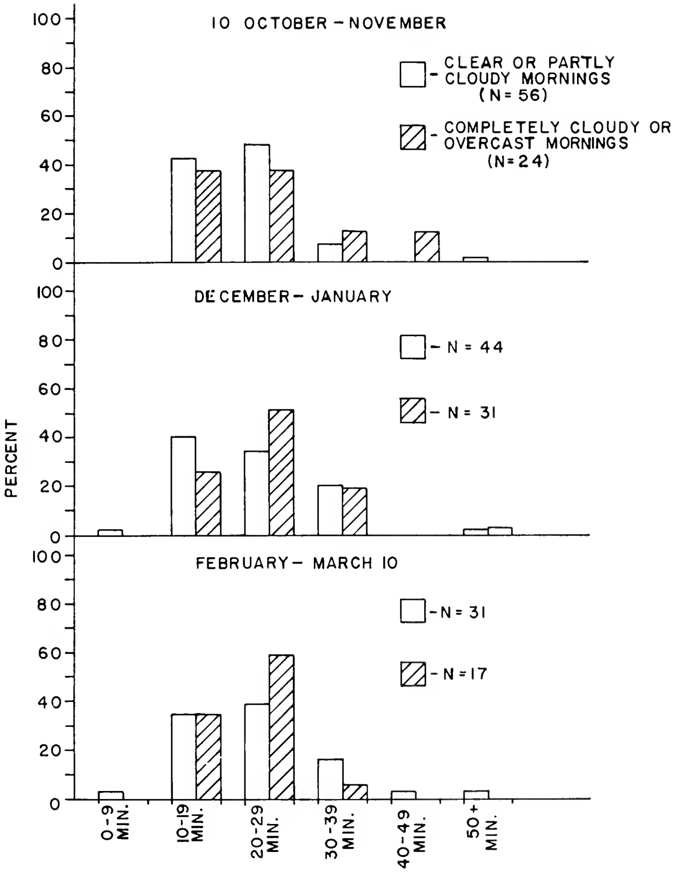

FIG. 3. Time lag between first geese to fly and the start of the heavy flight in the mornings.

factors causing later initial flight also caused a corresponding time lag in the flock as a whole. This suggests that the activities of the birds themselves were also of importance in synchronization of flight times of the majority of the flock.

Temperature.—The most striking factor influencing both the time and the magnitude of morning flights was temperature (Table 1). When temperatures were below 15° F at sunrise there usually was no heavy flight. On the coldest days only a few or often no geese would fly out to feed. When temperatures were between 16° and 20° F there occasionally was no heavy flight, but more often a partial flight or a normal flight occurred. Above 20° F there almost always was a heavy flight of geese in the morning.

TABLE 1

EFFECTS OF TEMPERATURE ON THE MAGNITUDE OF THE MORNING FLIGHT OF CANADA GEESE IN SOUTHERN ILLINOIS IN THE WINTERS OF 1963–64 AND 1964–65.

Sunrise temperature (° F)	Number of days within each temperature range	Number of days in which no heavy morning flight occurred	Number of days in which morning flight was intermediate*	Number of days in which morning flight was normal**
–5 to 5	12	12 (100%)	0	0
6 to 10	10	9 (90%)	1 (10%)	0
11 to 15	13	11 (85%)	1 (7.7%)	1 (7.7%)
16 to 20	23	5 (22%)	8 (35%)	10 (43%)
21 to 25	33	0	1 (3%)	32 (97%)
26 to 30	34	1 (3%)	1 (3%)	32 (94%)

* Many geese flew but many did not (40–60% flew or remained).
** Great majority of geese flew (>90%).

Temperatures between 16° and 20° F represent a relatively narrow threshold at which these Canada geese did or did not fly in large numbers. Below 15° F the geese spent a great amount of time apparently sleeping with the bill placed under the scapular feathers and the feet and tarsi drawn into the flank feathers. Activity was minimal and the tendency to flee from predators or other disturbances was markedly reduced.

This notable response to environmental temperatures was rather precise but is variable within the species as correlated with body size (Table 2).

TABLE 2

RELATIONSHIP BETWEEN ENVIRONMENTAL TEMPERATURES AT WHICH THREE SUBSPECIES OF CANADA GEESE BECOME INACTIVE AND THE PREDICTED LOWEST LONG-TERM TEMPERATURE AT WHICH THE IMMATURE FEMALE OF EACH RACE COULD SURVIVE FOR EXTENDED PERIODS.

Subspecies	Temperature at which inactivity begins (° F)	Source	Predicted lowest long-term existence temperature (° F)	Source
maxima	0° to –5°	Personal observations	+5°	Birkebak et al. (1966*a*)
interior	15°	This paper	14°	This paper (following methodology of Birkebak, et al., 1966*b*)
parvipes	ca. 30°	L. A. Mehrhoff, Jr. (personal communication)	32°	Birkebak et al. (1966*a*)

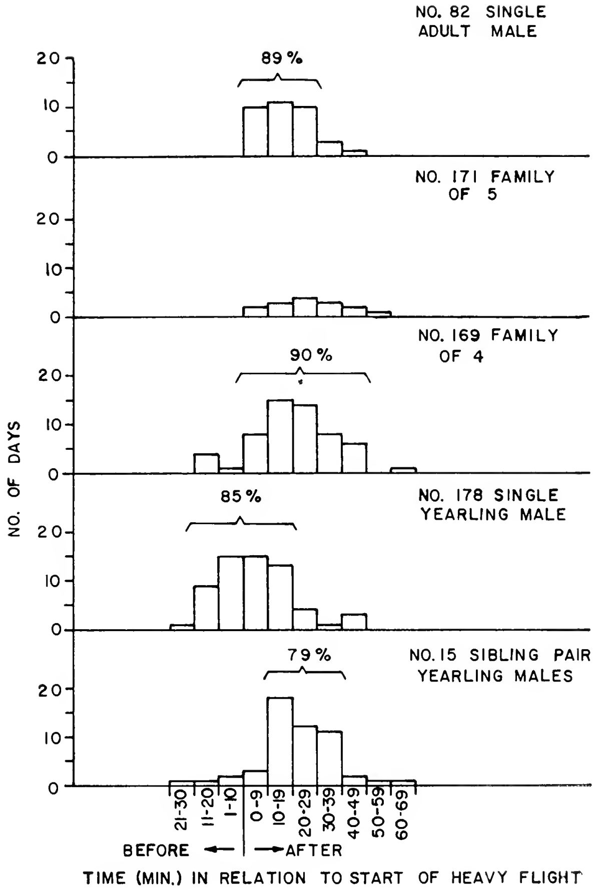

Fig. 4. Times of morning flights away from the roost lake of radio-marked Canada Geese in relation to times of initiation of heavy flight of the entire flock.

Maxima is the largest race of Canada goose (Hanson, 1965:13–41) while *parvipes* (*hutchinsii-parvipes* complex of MacInnes, 1966) is one of the smallest and *interior* is intermediate between the two (Hanson, 1951).

Flight Pattern of Radio-marked Geese.—The fact that the flock as a whole exhibited marked regularity in relation to civil twilight and sunrise in the times of first flights and initiation of heavy flights suggested that individual birds and families might initiate flight in a pattern of constancy with respect to light and the flight pattern of the entire flock. Comparison of flight times of transmitter-geese with the patterns for the entire flock revealed that for certain periods (up to six consecutive days) some marked geese were pre-

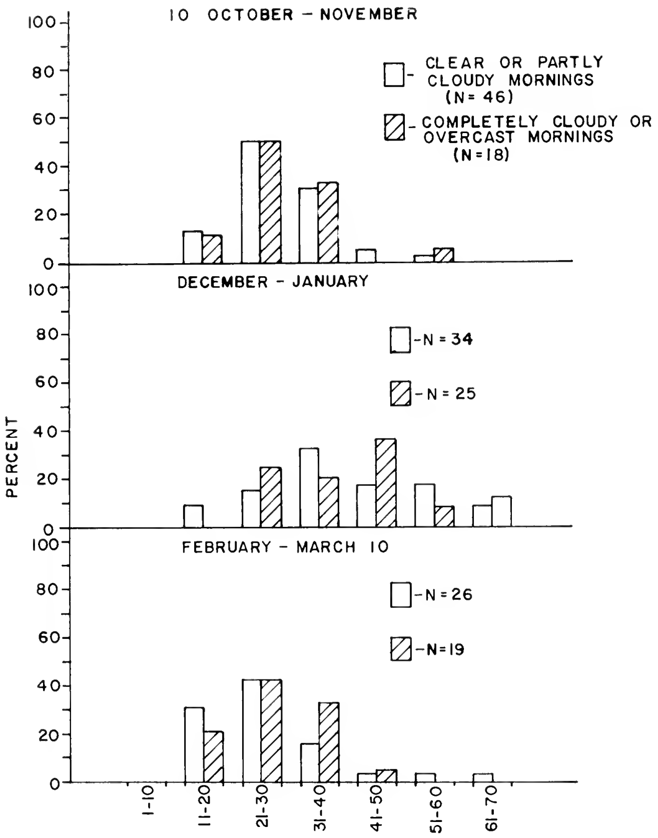

Fig. 5. Duration (minutes) of the heavy morning flight.

dictable within 5 minutes as to when they would fly in relation to the initiation of heavy flight. At other times the same birds were unpredictable and variable in the times at which they flew. When radio-tracked over a period of weeks, it was demonstrated that any individual or family might fly at almost any time within the period of heavy flight of the flock as a whole (Fig. 4).

Duration.—During October and November the heavy flight usually lasted from 20–40 minutes (Fig. 5). The duration of heavy morning flight in December and January was longer and more variable than at other times. This may be a reflection of greater numbers of geese at the refuge and also colder average temperatures which may delay or prolong activity. Heavy flights in February and March usually lasted from 15–40 minutes. Cloud cover had little, if any, effect in prolonging the morning flight once it was started even though it may have initially delayed it. The last geese to depart from the lake

TABLE 3

LENGTH OF TIME (MINUTES) THAT RADIO- AND COLOR-MARKED CANADA GEESE REMAINED IN FEEDING FIELDS IN THE MORNINGS UNDER DIFFERENT CLOUD CONDITIONS AND AT DIFFERENT PERIODS OF THE WINTER (1963–64 AND 1964–65).

	Sky Conditions		
Time of year	Clear or partly cloudy	Mostly cloudy	Complete overcast
15–31 October	134 ± 8* (N = 20)	154 ± 11 (N = 14)	192** (N = 4)
1–15 November	147 ± 6 (N = 32)	152 ± 10 (N = 9)	231 ± 14 (N = 15)
16–30 November	138 ± 17 (N = 14)	164 ± 12 (N = 14)	203 ± 7 (N = 18)
1–31 December	165** (N = 5)	142 ± 7 (N = 10)	210 ± 20 (N = 10)
1–30 January	121 ± 11 (N = 16)	169 ± 17 (N = 17)	254 ± 16 (N = 33)

* Mean ± standard error.
** Variation about mean not calculated because of insufficient sample size.

in the morning usually did so from 10 to 30 minutes after the heavy flight had ended.

MORNING FEEDING PERIOD AND MIDDAY ACTIVITY

When clear weather prevailed during October and November and almost all the geese were feeding on the refuge near the lake, the flight pattern back to the lake after feeding was almost as regular as the early morning departure. The sight and sound of flying geese appeared to stimulate nearby geese on the ground to fly also and this resulted in regular mass return flights to the roost lake. The geese spent an average of just over 2 hours in the fields (Table 3). On completely cloudy days geese remained in fields over twice as long as on clear days after their initial flight from the roost lake and then scattered segments of the flock moved back and forth from the lake all day.

As the season progressed and available food at Crab Orchard Refuge was exhausted (i.e., late December), the geese flew out farther (up to 10 miles and occasionally more) and split into more widely separated subflocks (see Raveling, 1969*b*). These subflocks usually returned to Crab Orchard at different times, especially if they were separated in their feed-field locations far enough apart not to hear or see other subflocks returning to the lake. When this pattern prevailed, it was impossible to record beginnings and endings of a heavy flight that represented meaningful averages for the entire flock.

TABLE 4

LENGTH OF TIME (MINUTES) THAT RADIO- AND COLOR-MARKED CANADA GEESE REMAINED IN FEEDING FIELDS IN THE AFTERNOON UNDER DIFFERENT CLOUD CONDITIONS AND AT DIFFERENT PERIODS OF THE WINTER (1963–64 AND 1964–65).

	Sky Conditions		
Time of Year	Clear or partly cloudy	Mostly cloudy	Complete overcast
15–31 October	55 ± 5* (N = 19)	71** (N = 4)	80** (N = 3)
1–15 November	77 ± 5 (N = 32)	65 ± 6 (N = 11)	—
16–30 November	74 ± 12 (N = 15)	—	—
1–31 December	64** (N = 6)	102** (N = 3)	92** (N = 3)
1–15 January	70 ± 5 (N = 30)	—	111** (N = 8)
16–30 January	65 ± 7 (N = 20)	81** (N = 7)	63** (N = 4)

* Mean ± standard error.
** Variation about mean not calculated because of insufficient sample size.

Data on the length of morning feeding periods of the radio-marked individuals demonstrate that, under equal cloud conditions, geese did not remain out for a longer time during the colder mid-winter or when they had to fly farther to feed (Table 3).

AFTERNOON FLIGHTS AND FEEDING PERIODS

Afternoon flight times of the geese from the roost lake to feeding areas were more variable than in the morning, especially on cloudy days. Even on clear days, small groups of geese left the lake from 1 to 3 hours before the time when the heavy flight occurred as the light level was fading. The correlation of goose activity to light intensity was less prominent in the afternoon than in the morning and this seems to be true for many birds (Armstrong, 1954); but, there remained a predictable flight time for the majority of geese during clear weather. As in the morning, the amount of time spent in feeding areas in the afternoon under clear skies was relatively constant throughout the winter and averaged about 1 hour (Table 4).

The evening flight from feeding areas to the roost lake varied widely (Fig. 6). This variation was due largely to completely cloudy conditions. Data on the start of the heavy flight on cloudy afternoons were often missing

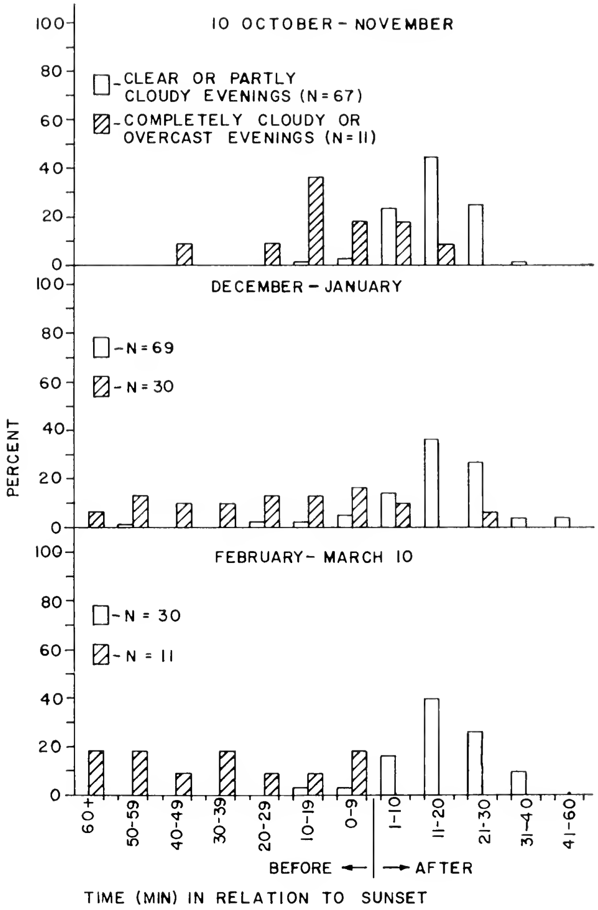

FIG. 6. Time period in which the heavy flight to the roost lake started in the afternoons in relation to sunset.

because the geese arrived over a longer time and often no definite peak flight was observed. During clear weather the heavy flight usually began between sunset and civil twilight; times later than this usually represented evenings when a full or nearly full moon was visible at sunset. When cloudy, the evening flight to the lake almost always occurred before sunset.

Once flight back to the lake was initiated, it quickly became heavy and lasted for 15 to 40 minutes when skies were clear (Fig. 7). As with the morning flight out (Fig. 5), duration of the evening flight back was 5 to 10 minutes longer in December—January than earlier or later in the winter. This probably represents the effects of greater numbers of geese.

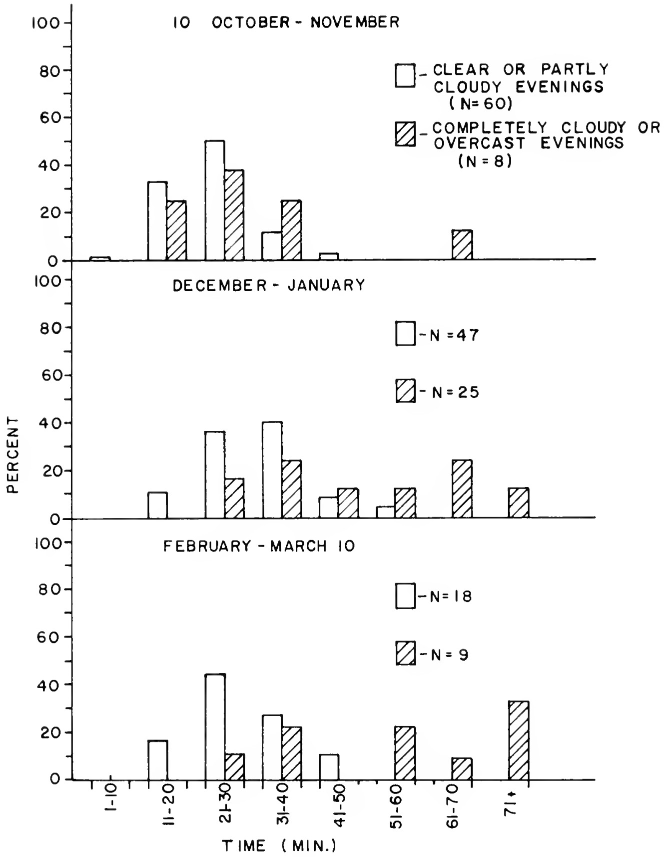

Fig. 7. Duration of the heavy evening flight.

The last geese to return to the lake usually did so within 5 to 20 minutes after the heavy flight ceased. The last returning geese were often from 10 to 30 minutes or occasionally more after civil twilight. Evening feeding periods were shorter and goose activity was more intense than during morning feeding periods. The majority of geese stopped feeding and flew back to the lake in in the evening at light levels lower than prevailed when they flew out in the morning (compare relation of flight to civil twilight, Figures 1 and 8). The earlier evening flights during cloudy weather and the often later flights when a moon was showing again demonstrated the rather critical responsiveness of geese to prevailing light (Fig. 8).

Since temperature always increased above 15° or 20° F in midday, even

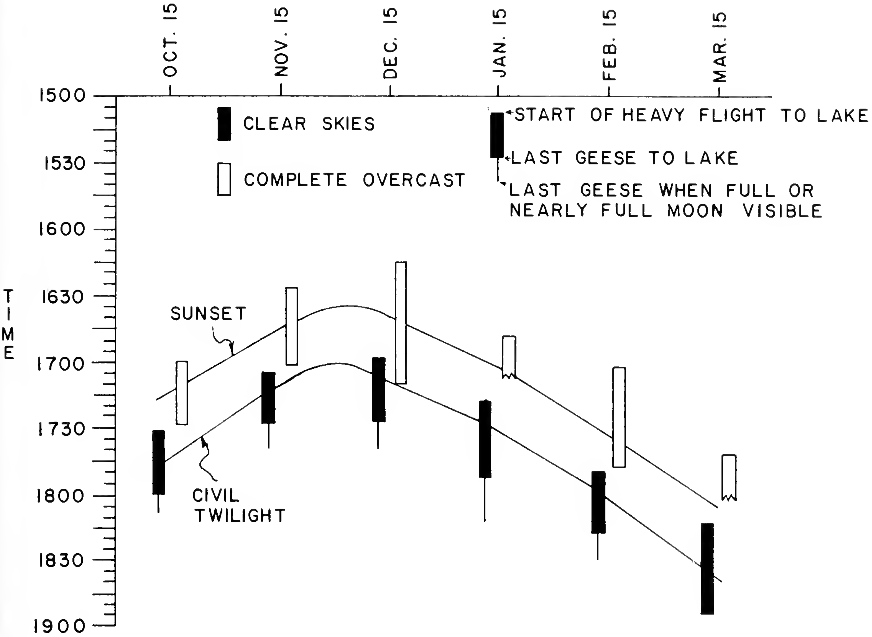

FIG. 8. Generalized average flight pattern of Canada Geese to roost lake under clear and complete overcast skies (sunset and civil twilight from U. S. Naval Observatory, 1961, 1962, 1963).

on the coldest days, temperature never caused a cessation of flight in the afternoon as occurred in the morning.

As in the morning, some records of afternoon flight times of radio-marked geese indicated short-term regularity of time of flight with respect to the initiation of the heavy flight during clear weather. Most records, however, revealed that the time of flight of an individual or family was not predictable within the 30 to 40 minute time span in which the majority of geese flew back to the lake.

NOCTURNAL ACTIVITY

Little time was spent by the investigators at Crab Orchard during the night. However, personnel residing at the refuge informed us when, on rare occasions, night flights and feeding activity occurred (excluding migration). When night activity occurred, effects were noticeable during the day because some geese stayed out far beyond their regular time of return to the lake in the evening or were encountered in fields prior to dawn civil twilight. Extensive activity at night was encountered only during one period in this study. This occurred when snow covered over 75 per cent of the ground and at the time of a full and nearly full moon from 13 to 19 February 1965. The reflection of moonlight off the snow caused brighter than usual conditions and the majority of geese remained out after 19:00 and continued feeding. The usual daily patterns of flight and activity were noticeably changed.

In contrast to the rarity of night activity at Crab Orchard, it was relatively common at Horseshoe Lake and Union County Refuges, also in southern Illinois (refuge personnel, pers. comm.). Such activity seemed to be related to heavy hunting pressure. Again, geese demonstrated their plasticity and ability to change normal regular patterns when extreme conditions prevailed. Markgren (1963:369) noted that Bean Geese (*Anser fabalis*) were normally diurnal but could change to almost complete night activity when affected by disturbance.

DISCUSSION

Initiation of Morning Flight.—Measurements of light levels were not performed in this study but can be estimated from other data. Canada Geese initiated morning flight in Saskatchewan when light intensity was 32 foot-candles as measured with a light meter pointing east (or 11 foot-candles with the meter pointing north) (A. Dzubin, Canadian Wildlife Service, in litt.). These geese began flight 15 minutes before sunrise under clear skies, as did the geese at Crab Orchard (Fig. 2).

Schreiber (1967) presented data on the rate of change of light intensity under clear and cloudy skies. From this it can be estimated that it takes 15 minutes longer to reach 25 foot-candles intensity (overhead reading) under cloudy skies than under clear skies. This delay in reaching the approximate threshold reacted to by the geese as recorded by Dzubin equals the delay of flight initiation observed under cloudy skies in this study. Beyond this low threshold value, the length of time required to reach higher light intensities shows wider differences between cloudy and clear sky conditions (Schreiber, 1967). Thus, the first geese to fly did so at approximately the same light intensity regardless if it was cloudy or clear, but the majority of geese flew under darker sky conditions on cloudy mornings than on clear mornings. Therefore, light acted as a trigger but not as a graded controlling factor.

Birds awaken in a rhythm even in constant light (Palmgren, 1949). Light is correlated with and probably influences the beginning, length of, and ending of many activities. Dawn and dusk represent the times at which external physical factors influencing synchronization of social flocks is probably easiest (Wynne-Edwards, 1962:326). Several studies have demonstrated the sensitivity of waterfowl to dawn or dusk light changes (Bossenmaier and Marshall, 1958; Winner, 1959; Martin and Haugen, 1960; Hein and Haugen, 1966).

No generalizations can be made as to the tendency of a particular single or family to be constant in initiation of morning flight as they tended only to be predictable within the 30 to 40 minute time span in which the majority of the flock flew. Many factors can influence the time at which geese fly; nearness to other birds taking off, presence or absence of disturbing factors (e.g., predators), synchronization of a pair or members of a family (Raveling, 1969*c*), and many unknowns (e.g., hunger, sleep, time since awakening, etc.). Apparently, all these factors contribute to variability in flight initiation of individuals and families.

Temperature.—Birkebak et al. (1966*a*) calculated the magnitude of heat loss for varying temperatures for *maxima* and *parvipes* utilizing a methodology verified by Birkebak et al. (1966*b*). LeFebvre and Raveling (1967) related these heat loss calculations to winter distribution of each race. The data in Table 2 demonstrate that Canada Geese become inactive at temperatures almost identical to those predicted to be the minimum at which they could survive for extended periods (i.e., up to 15–20 days) while utilizing almost all their energy metabolism for maintenance at a moderate work level of metabolism (see LeFebvre and Raveling, 1967). These relations suggest that inactivity is the most adaptive response to severe cold and functions to conserve energy and is an important factor determining northern limits of distribution in winter. Markgren (1963:325) noted comparable inactivity of Bean Geese during the coldest days of winter.

Feeding Periods and Midday Activity.—Cold per se seemed to have little or no influence on the length of the feeding period but instead caused a cessation of activity. Canada Geese at Crab Orchard were in good physical condition as judged by body weights during the winter of 1964–65 (Raveling, 1968). If the geese were requiring more food during mid-winter, it appears that ample time was afforded by the normal 2 to 2½ hour morning feeding period and the one hour evening feeding period to obtain that extra food. Geese did not spend a majority of their feeding period actually feeding; much time was also spent in alertness, loafing, and sometimes in aggression. Increased cloudy weather in mid-winter rather than cold temperatures led to geese remaining away from the lake for longer periods of time and provided further opportunity for spending more time feeding.

Geese that returned to the roost lake on cloudy days often flew out again within 1 or 2 hours. Geese apparently avoided the large lake during completely cloudy weather and sought water during bright clear periods. When a strong wind created noticeable waves or small "whitecaps," geese moved into nearby sheltered bays or flew from the lake in large numbers, even during clear weather. Cloudy weather was often associated with stormy conditions, rain, and wind. It appears that selection or conditioning or both have produced a state of fear in geese associated with such weather.

When the main roost lake(s) is small and ponds or other small water areas are available in feeding areas, then large numbers of geese regularly day-roost in the fields on or near these small water areas. This situation prevailed at Union County and Horseshoe Lake Refuges. Markgren (1963:372) observed a comparable pattern in Bean Geese.

We suggest that fear of predators by geese is an important factor influencing habitual utilization of water areas during non-feeding periods in calm, clear weather. When on water, geese are almost completely safe from mammalian predators. Geese spent the night on the water, but very often loafed on the bank during the day. Even on land, Canada Geese did not readily flee from mammalian predators, but rather they "mobbed" them by walking parallel to the predator while honking continuously. The near presence of a Golden Eagle (*Aquila chrysaetos*) or a Bald Eagle (*Haliaeetus leucocephalus*), however, occasioned rapid and somewhat disorganized flight back to the roost lake or nearest water if the geese were in fields. If an eagle approached them on water, however, the geese resorted to diving and rapid movements on the surface of the water, but they usually did not fly back over land. We suggest that this resort to water and diving in the presence of an eagle is adaptive and prevents successful attack by an eagle. Thus, fear of predators influences the geese to be on or near water during non-feeding periods of the day, whereas fear of rough water and stormy conditions influences the geese to remain on land.

Another important factor influencing length of time spent in fields during cloudy weather is that the goose's "sense of time" seems to be impaired. This was most noticeable and revealing on days when the sun finally appeared through the cloud cover at a time after which the geese would normally have gone back to the lake if the sun had been visible all morning. Within 5 to 15 minutes after such a "sunflash," thousands of geese that had still been feeding or were loafing began a mass flight back to the lake. Their cessation of feeding and other activities was almost immediate and they began the alertness and characteristic Head-tossing (Raveling, 1969*c*) that precedes flight. It seems that the azimuth position of the sun as well as increasing and decreasing light intensity at dawn and dusk, is an important factor regulating the onset, duration, and cessation of daily activities of Canada geese.

Several species of birds have been demonstrated to possess a sun orientation mechanism of time sense (see reviews by Kramer, 1961; Schmidt-Koenig, 1965).

Management Implications.—Knowledge of the usual rhythm of daily activities of geese under a variety of conditions has been and will be useful in manipulating shooting hours during the hunting season. For example, in the area containing the refuges in southern Illinois, goose hunting is not legal after 15:00. Thus, during clear weather, the heavy flight of geese in the afternoon is allowed to leave the refuge and be relatively unharrassed during their feeding period. Although many goose hunters in southern Illinois believe that the geese "learn that it is safe" to come out at 1500 hours, comparison of the length of the evening feeding period (Table 4) to the time at which geese return in the evening (Fig. 6) shows that this is the usual pattern of a relatively undisturbed flock. There were relatively light effects of hunting pressure at Crab Orchard as compared to other refuges because of the size of the refuge and its relation to numbers of geese. However, where hunting pressure is extreme, geese may become conditioned to time periods when they are not pursued.

Various other manipulations of shooting hours have been tried at other locations, e.g., no shooting before 09:00 or after 14:00 (cf. Hunt, et al. 1962). Such manipulations can achieve many effects, e.g., increased or decreased kill and wider dispersion of the harvest. Each situation should be studied as an individual case.

SUMMARY

Based on daily observation of the activities of a large wintering flock of Canada Geese and specific records of radio-marked families and individuals, the times and nature of flight patterns of these geese are described along with the environmental variables associated with these patterns. Characteristics of flight patterns were: regularity of onset of morning and evening flights in relation to light intensity under similar weather conditions; regularity of onset of the heavy flight with respect to the first geese which flew and the prevailing light levels, usually at or just after sunrise in the mornings and between sunset and civil twilight in the evenings; variability of individuals and families within the regularity exhibited by the flock as a whole; delay of flight under completely cloudy conditions; longer periods of time spent in feeding areas when cloudy, but not when cold provided it was not too cold to prevent flight; considerable delay in flight time or usually cessation of flight when below 15° F. The motivation and probable adaptive nature of goose responses to roosting on or near water during clear weather or in fields during stormy weather and their cessation of activity in cold periods are discussed.

ACKNOWLEDGMENTS

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LITERATURE CITED

ARMSTRONG, E. A. 1954. The behaviour of birds in continuous daylight. Ibis, 96:1-30.

BIRKEBAK, R. C., E. A. LEFEBVRE, AND D. G. RAVELING. 1966*a*. Estimated heat loss from Canada Geese for varying environmental temperatures. Minnesota Mus. Nat. Hist. Tech. Rept., No. 11.

BIRKEBAK, R. C., C. J. CREMERS, AND E. A. LEFEBVRE. 1966*b*. Thermal modeling applied to animal systems. J. Heat Transfer, 88:125–130.

BOSSENMAIER, E. F., AND W. H. MARSHALL. 1958. Field-feeding by waterfowl in southeastern Manitoba. Wildl. Monogr., 1.

HANSON, H. C. 1951. A morphometrical study of the Canada Goose, *Branta canadensis interior* Todd. Auk, 68:164–173.

HANSON, H. C. 1965. The giant Canada goose. South Illinois Univ. Press. Carbondale.

HANSON, H. C., AND R. H. SMITH. 1950. Canada Geese of the Mississippi Flyway: with special reference to an Illinois flock. Illinois Nat. Hist. Surv. Bull., 25:67–210.

HEIN, D., AND A. O. HAUGEN. 1966. Illumination and wood duck roosting flights. Wilson Bull., 78:301–308.

HUNT, R. A., J. G. BELL, AND L. R. JAHN. 1962. Managed goose hunting at Horicon Marsh. N. Amer. Wildl. and Nat. Res. Conf. Trans., 27:91–106.

KIMBALL, H. H. 1916. The duration and intensity of twilight. Monthly Weather Rev., 44:614–620.

KRAMER, G. 1961. Long-distance orientation. Chap. 22 *In* Marshall, A. J., Ed., Biology and comparative physiology of birds. Vol. 2. Academic Press, N. Y. pp 341–371.

LEFEBVRE, E. A., AND D. G. RAVELING. 1967. Distribution of Canada Geese in winter as related to heat loss at varying environmental temperatures. J. Wildl. Mgmt., 31: 538–545.

MARTIN, E. M., AND A. O. HAUGEN. 1960. Seasonal changes in wood duck roosting flight habits. Wilson Bull., 72:238–243.

MACINNES, C. D. 1966. Population behavior of eastern arctic Canada Geese. J. Wildl. Mgmt., 30:536–553.

MARKGREN, G. 1963. Studies on wild geese in southernmost Sweden. Part I. Acta Vertebratica, 2:299–418.

PALMGREN, P. 1949. On the diurnal rhythm of activity and rest in birds. Ibis, 91: 561–576.

RAVELING, D. G. 1968. Weights of *Branta canadensis interior* during winter. J. Wildl. Mgmt., 32:412–414.

RAVELING, D. G. 1969*a*. Social classes of Canada Geese in winter. J. Wildl. Mgmt., 33:304–318.

RAVELING, D. G. 1969*b*. Roost sites and flight patterns of Canada Geese in winter. J. Wildl. Mgmt., 33:319–330.

RAVELING, D. G. 1969*c*. Preflight and flight behavior of Canada Geese. Auk, 86:671–681.

RAVELING, D. G. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour, 37:291–319.

SCHMIDT-KOENIG, K. 1965. Current problems in bird orientation. *In* Lehrman, D. S., R. A. Hinde, and Evelyn Shaw, Eds., Advances in the study of behavior. Academic Press, N. Y., pp 217–278.

SCHREIBER, R. W. 1967. Roosting behavior of the Herring Gull in central Maine. Wilson Bull., 79:421–431.

UNITED STATES NAVAL OBSERVATORY. 1961. The nautical almanac for the year 1963. U. S. Govt. Print. Off. Washington.

UNITED STATES NAVAL OBSERVATORY. 1962. The nautical almanac for the year 1964. U. S. Govt. Print. Off. Washington.

UNITED STATES NAVAL OBSERVATORY. 1963. The nautical almanac for the year 1965. U. S. Govt. Print. Off. Washington.

WINNER, R. W. 1959. Field feeding periodicity in Black and Mallard Ducks. J. Wildl. Mgmt., 23:197–202.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Hafner Co., New York.

COOPERATIVE WILDLIFE RESEARCH LABORATORY, SOUTHERN ILLINOIS UNIVERSITY, CARBONDALE, ILLINOIS (PRESENT ADDRESSES: (RAVELING) DEPT. OF ANIMAL PHYSIOLOGY, UNIVERSITY OF CALIFORNIA, DAVIS, DAVIS, CALIFORNIA, 95616; (CREWS) U. S. FISH AND WILDLIFE SERVICE, BLACKWATER NATIONAL WILDLIFE REFUGE, CAMBRIDGE, MARYLAND 21613). 3 NOVEMBER 1971.

THE NEOTROPICAL NEST REGISTRY

A Nest Registry system has been formed to record in a systematic fashion information on the breeding biology and nesting of neotropical birds. A detailed discussion of the rationale for and the difficulties associated with such a registry appears in *American Birds* for February, 1972 (vol 26, pp. 18–20). Contributions from Mexico, Central and South America, and the West Indies, are needed, and nest reports for primarily neotropic species elsewhere would also be valuable. Contributions need not be in the form of a standard nest record card, although entries typed on 4 × 6 index cards, one card per species, would be desirable. Information to be published by the contributor will, of course, be respected. In lieu of submitting detailed nest records, a statement of for what species and in what countries, nest information exists, would help keep the Registry file complete. Part of the Registry file will consist of a library of reprints containing papers on life history studies or on specific aspects of reproductive biology of neotropical birds. Send requests for information, or contributions of nest data or reprints to Michael Gochfeld, Department of Ornithology, American Museum of Natural History, New York, New York 10024.

REPRODUCTIVE BEHAVIOR OF THE COMMON LOON

Sverre Sjölander and Greta Ågren

There is comparatively little known about the behavior of the loon family, Gaviidae. The Common Loon (*Gavia immer*) is the species most extensively treated in the literature, especially in the comprehensive report by Olson and Marshall (1952), but nevertheless several important behavioral features still remain unknown, especially those pertaining to courtship and mating. As a part of a more extensive comparative study on the behavior of the Gaviidae the Common Loon was studied during the summer 1970 on Iceland, where it was possible to obtain most of this missing information.

MATERIAL AND METHODS

Between 27 May and 5 September, a total of 391 hours of observation were recorded on five pairs of *G. immer* in four different lakes. The lakes were: Selvatn on the Skagi peninsula, Holmavatn by the town Blönduos, Midfjadarvatn near the town Hvammstangi and Holtavörduvatn in the mountain pass south of Hrutarfjördur. All these pairs were followed from the arrival in spring until September. A number of additional observations were also made, on several localities spread over the whole of Iceland.

In pairs where copulation was observed and the sexes thus could be determined, the male was seen to be distinctly larger, with a heavier head and neck, and it was therefore possible to distinguish and identify these birds during later stages of reproduction.

Table 1 shows the distribution of the observations regarding different types of behavior. All the types of behavior described here have been filmed unless stated otherwise in the description, and sounds were tape-recorded using an Uher 4400 recorder. Most observations were made from the car, a Land-rover, using binoculars or from blinds.

RESULTS

Arrival.—Most authors on the subject, e.g. Bent (1919), Yeates (1950) and others, agree that *G. immer* arrives paired in spring as soon as the ice on their nesting lakes has thawed. Our observations are in accordance, since the pairs in all lakes arrived in this way, as far as could be ascertained. In one case (Selvatn) the two pairs arrived on 30 May, when the ice had left the shores, and the first egg was laid only 5 days later, on 4 June, a remarkably short time but well in accordance with data on other loons (Sjölander, 1968; Lehtonen, 1970).

Territorial behavior.—The fact that all loons are extremely territorial has been noted by most authors, as well as the fact that the Common Loon chooses a large oligotrophic lake as a nesting place. The fact that the territory is large (up to 25 ha) might be explained by its use as the main source of food, and this also leads to the well known sparse occurrence of loon pairs.

TABLE 1

THE NUMBER OF OBSERVATIONS OF SOME BEHAVIORS AND/OR THE NUMBER OF PAIRS INVOLVED IN THESE ACTIVITIES. BEHAVIORS OBSERVED MORE THAN 100 TIMES ARE GIVEN AS 100+.

Behavior observed	Number of observations	Number of pairs
Raised neck	100+	5
Bill-dipping	100+	5
Splash-dive	100+	5
Circle dance	24	5
Rush	21	2
Upright	15	1
Courtship	33	2
Copulation	6	2
Nest search		3
Nest choice		2
Nestbuilding		2
Incubating		3
Relieving	8	2
Feeding the young	100+	4
Riding on parent	30	2
Resting ashore	9	2

Perhaps the best known territorial behavior is the crying of the loon, as described by e.g. Olson and Marshall (1952). The yodeling cry was the type most clearly used as a territorial marking in all the birds we studied. It was heard only from owners of territories and occurred most frequently during the first phase of reproduction. The "wail" was observed in the same situations as the "yodel," and seemed a low-intensity form of this cry. The "tremolo call" was the cry used in all situations of agitation. i.e. disturbances by man, overflying birds, other loons directly intruding etc. Spectrograms of these calls are shown in Figure 1.

When intrusion by other loons and in some instances other species occurred, several types of defense reactions were shown. *Bill-dipping*, as illustrated in Figure 2 (15, 21, 38, etc) is the most common reaction in all situations where the birds are agitated, and might be regarded as a typical example of a displacement activity (and thus not necessarily a defense reaction). A

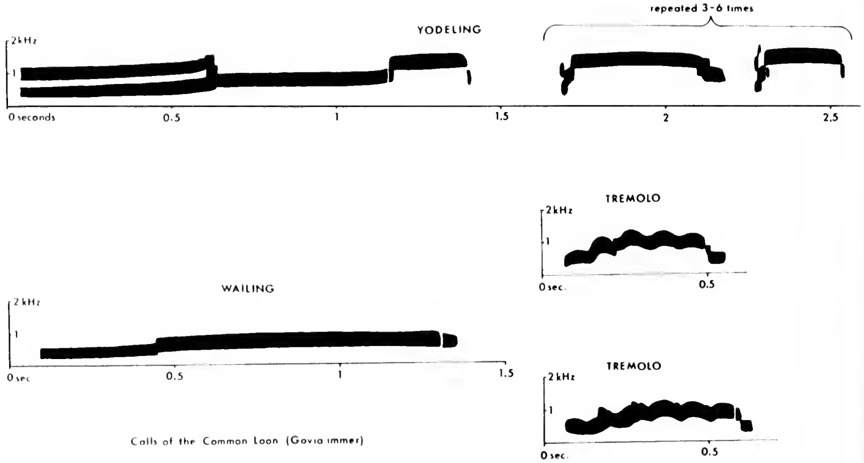

Fig. 1. Spectrographs of some calls, of the Common Loon.

raised neck position was another very common reaction, where the neck and breast are raised. At higher intensities and in aggressive situations the front plumage is lifted as well. This position is illustrated in Figure 3 (0) and in Figure 2 (26, 85, 131, etc). It is very often accompanied by the tremolo call. A *circle dance*, as illustrated in Figure 2, where the birds slowly circle around another with raised necks, bill-dipping and diving, is a common occurrence in all confrontations, especially when several birds meet. These behaviors mostly precede the *splash-dive*, where the bird gives a strong kick upwards when diving, as in Figure 4 (8). At more intense stages of territorial defense the bird raises to an *upright* position, when the body is held almost or quite vertical, with the wings folded, (Fig. 3–8), or spread (Fig. 3–54). The bird may even jump clear out of the water. This reaction is often preceded or followed by long *rushes* with flapping wings over the water (Fig. 3–121). This is not a pursuit but is mostly performed by a single bird.

Real fighting was not observed, except in one case where one bird of a pair with young attacked a floating paper bag, spearing with the bill and hitting with the folded wing, i.e. corresponding to the behavior in the vicious and occasionally deadly fights known in *G. arctica* (Sjölander, 1968). All these reactions, with the exception of the raised neck, have been reported earlier by different authors, e.g. Munro (1945), Yeates (1950), Olson and Marshall (1952) and others, though not always in connection with territoriality.

Courtship.—Since the territorial behavior of loons is so spectacular and the behavior most likely to be seen by the observer, it is easily understandable

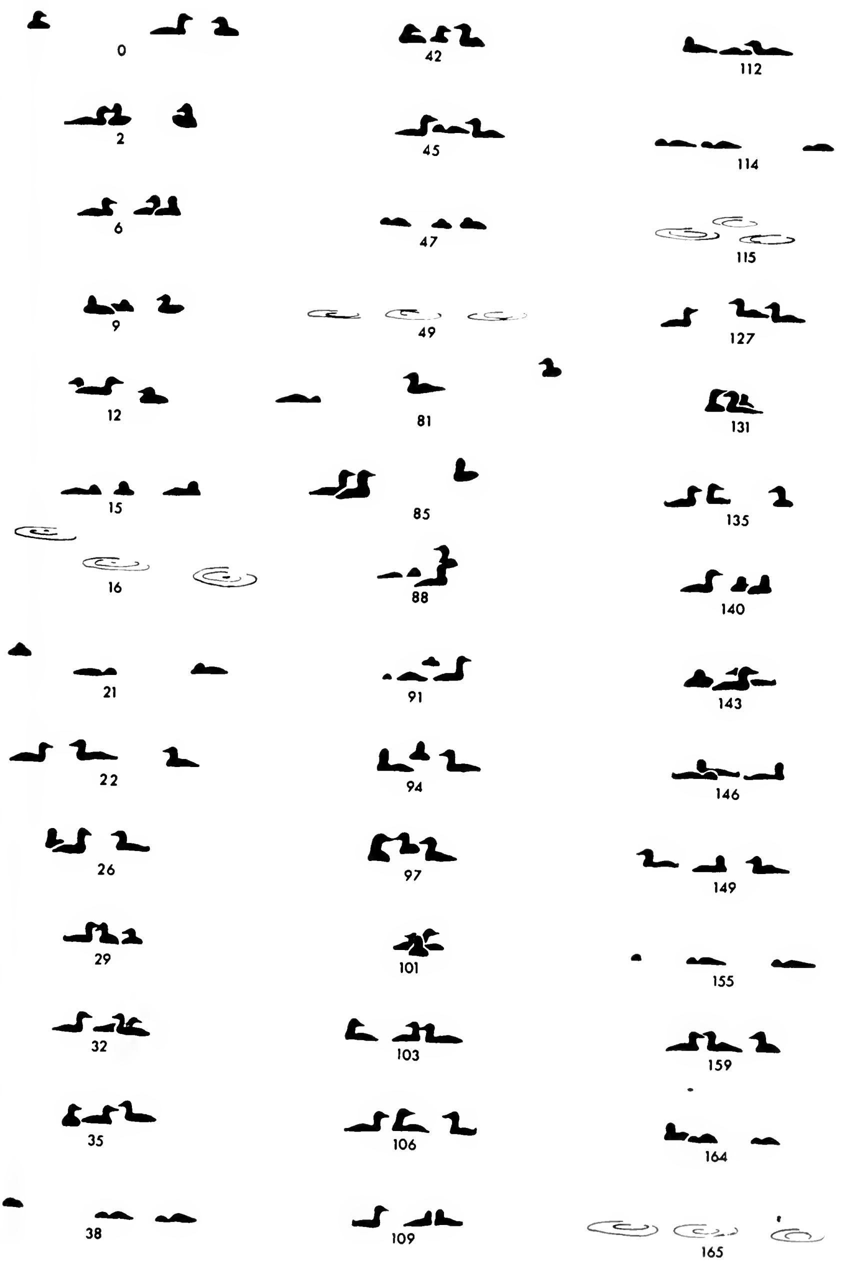

FIG. 2. Circle dance, performed by a territorial pair and an intruder. Numbers as in Fig. 3. Drawing directly from a film.

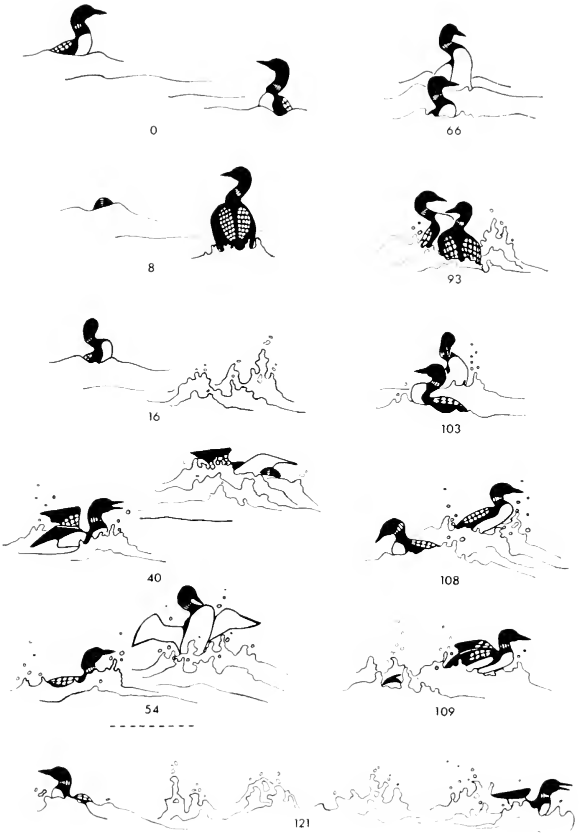

FIG. 3. Behavior towards an intruder in the territory of a pair with young. Defender to the right in 0, 8, 16, later indistinguishable from intruder. The numbers indicate frames of film at 18 frames per second, from an arbitrarily chosen zero, the drawing being made directly from a film.

that it has been interpreted as courtship by many authors (e.g. Huxley, 1923 for *G. stellata*). A number of authors, e.g. Munro (1945), Olson and Marshall (1952), Niethammer (1966), and others have described behavior regarded as courtship in *G. immer*, but all these descriptions seem to refer to territorial behavior. Our observations indicate, however, that there is very little courtship in *G. immer*, if by courtship is meant a special behavior preceding and leading to copulation. This is easily explained since the very probable life-long pairing in all loons makes the need for an elaborate courtship small. The only specialized behavior regarded as courtship in the pairs

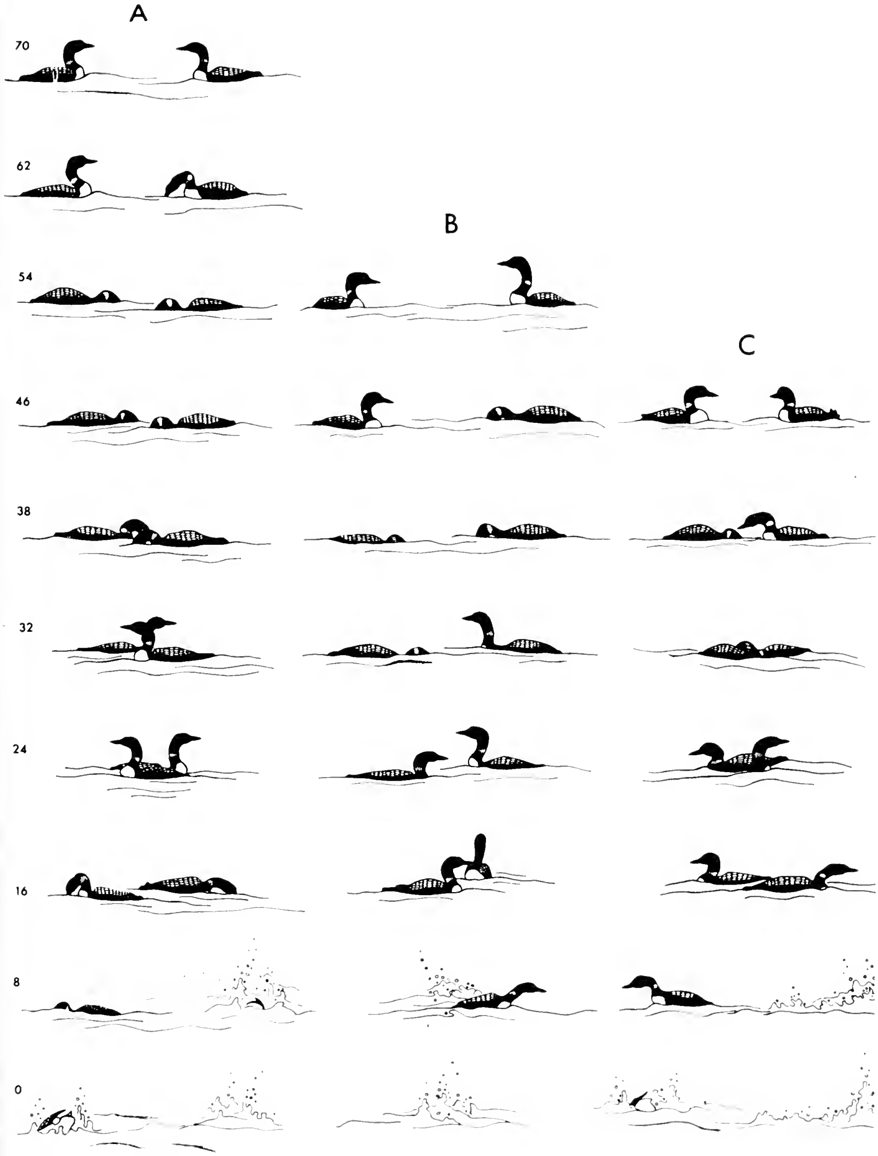

Fig. 4. Courtship, three different examples performed by the same pair. Numbers indicate frames at 18 frames per second, counted backwards from a zero chosen at the splash dive. Drawing directly from a film.

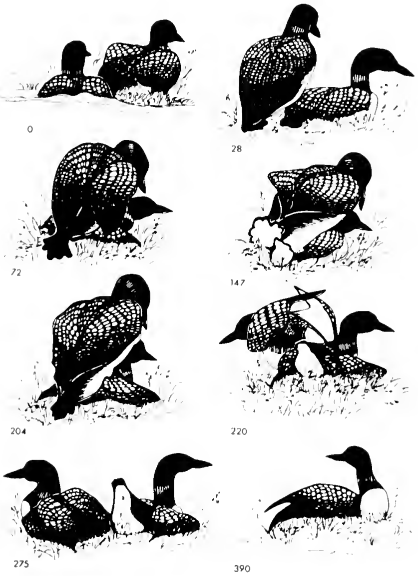

Fig. 5. Copulation. Frame numbers as in Fig. 3. Drawing directly from a film.

we studied was a formalized bill-dipping followed by a mutual splash-dive, as illustrated in Figure 4. This behavior only occurred as an immediate preliminary to copulation, or copulation attempts, and was easily distinguished from threat to intruders.

Copulation.—The copulation, which is not always preceded by any courtship, is initiated by the female who begins to seek a suitable place to go ashore anywhere in the territory. During this search-swimming both birds have very short necks. The male follows her closely. When she finds a place where she can climb up on land she goes up and awaits and male. He was in all cases very reluctant to follow, and especially in the days preceding egg-laying very often did not follow at all. If he decides to join the female he climbs up behind or next to her and immediately attempts to copulate. The copulation takes place as illustrated in Figure 5, i.e. corresponding to the same behavior in other loons.

Immediately after the copulation the male leaves the shore, whereas the female usually waits some minutes before following. The duration of the copulation is short, as can be gathered from Figure 5 (about 20 seconds from contacting the female to leaving her). Five of six copulations observed, as well as 22 out of 33 courtship displays, took place between 03:00 and 09:00.

The behavior, including attempts, was seen daily from the day of arrival until 2–4 days before egg-laying. The maximum number of copulations on one day was two.

Thus, the copulation closely resembles the same behavior in other loons as described by Huxley (1923) for *G. stellata* and Sjölander (1968) for *G. arctica*, as might well be expected. There seems to be no published description of this behavior, apart from a single observation by Tate (1969) and a report by Southern (1961). The latter report, however, describes a behavior where one bird chased another and then climbed on top of it, on the water, and thus in all probability refers to a territorial fight. It may also be noted that we found no evidence of the existence of a copulation platform, as mentioned by Tate (1969) and Tate and Tate (1970). Such platforms seem not to be used by the other loons either.

Nest choice.—In the two cases where it could be ascertained, the male chose the nest site. During the last 2 days preceding egg-laying he began to go ashore and make nest-building movements on different locations in the territory, soon settling for one of them. At the same time, the female in both pairs was still inviting; and on several occasions the two birds could be seen ashore on different places, the female inviting, the male building on the future nest. The female joined the male in nest-building on the day preceding egg-laying. In the two cases where the nest-building could be followed, the ultimate nest site was decided and the building of the real nest started on the day of the egg-laying (which as far as can be ascertained took place during the dark hours).

Nest building.—Both birds took part in the nest-building, but as soon as the female had accepted the male's choice she stayed on the nest and thus did the greater part of the building. The movements used were the same as in comparable birds, i.e. pulling material over the shoulder, drawing it near the body, scratching with the feet and wagging the body. In both observed cases the nest was built in less than 20 minutes, though added to sporadically during the incubating period. In one case these later additions combined with egg-turning moved the whole nest a distance of 1.4 m away from the first site, apparently since the place first chosen was unsatisfactory (reached by waves in strong winds).

Incubating.—Despite some reports to the contrary, several authors have noted the fact that both parents take part in the brooding, e.g. Bent (1919). In all the pairs we studied, the female took the greater part in the incubating. The periods between changing varied between less than one hour and 16 hours, with changes becoming less frequent towards the end of incubation. Especially in the beginning, there was a competition between the parents to incubate, where the incubating bird refused to leave its place to the other parent, although the latter had already climbed up to the nest. When being relieved, the leaving bird in the majority of cases started building, i.e. picking up material and drawing it in (or making the building movements without material) and continued this behavior while leaving the nest for several minutes (in one case 42 min), even out on the water. The relieving bird usually turned the eggs before laying down, and then made some building movements after settling on the eggs. Apart from the turning of the eggs at relief, the eggs were seldom turned, and during most sessions not at all.

Hatching.—The exact incubation time could only be determined in one case, and was 28 days. In this case, the single young (the other egg was not developed) stayed on the nest 20 hours before leaving it. It was fed on the nest during this time, and made two short excursions to the water.

Parental behavior.—Altogether six pairs with young were observed of which only one had two young. The survival of only one young seems to be a very common, even normal, condition in all loons, which may at least for *G. stellata* be explained by competition between the young for the food brought by the parents, and the aggressiveness between the young (von Braun, Hessle, and Sjölander, 1968). Two of the six pairs were studied more closely, and the main bulk of observations refers to these pairs.

Most of our observations coincide well with the reports by Olson and Marshall (1952), Dunlop (1915), Wilson (1929), and others. It might be pointed out, however, that the defense of the young is very difficult to distinguish from the normal territorial defense, and so a special defense of the young might not exist. When the birds are disturbed, the young normally leave the parents and hide near the shore, while the parents show the normal behavior towards the intruder, as described by e.g. Dunlop (1915). The young and parents were thus separated for rather long times (maximum observed 85 minutes).

A behavior not previously reported in this species, but well known from *G. stellata* (von Braun, Hessle, and Sjölander, 1968), is that the birds go ashore to warm the young, not necessarily on the nest but using any suitable place. This was observed nine and two times respectively in two pairs, the time spent ashore being from 11 min to 3 hours. The initiative to go ashore came from the young in one case, but in the others from the parent.

A difference noted between the description of the feeding behavior given by Olson and Marshall (1952) and our observations was that the former authors state that the parent dips the food into the water and splashes it around before it is handed over to the young, but in the several hundred instances we observed of feeding this was not seen. The young often miss the food and drop it, and the parents then pick it up again, which might create an impression of splashing. Both parents fed the young in all observed pairs, and the behavior described in Palmer (1962), i.e. one parent handing the food over to the other prior to feeding, was never observed.

The young were fed at approximately one hour intervals the longest pause at night being 6 hours. The number of feedings during each bout varied from one to 63, the duration of the bouts from less than one minute to 50 minutes. In practically all cases it was impossible to ascertain the type of food given, but in a few instances fishes were clearly recognized.

The young spent a considerable time riding on the back of either of the parents, up to 50 per cent of the time during the first 3–4 days, a notable difference from other loons, where riding seems less frequent (von Braun, Hessle, and Sjölander, 1968; Sjölander, 1968; Lehtonen, 1970). They were also warmed under the wing of either parent while floating. No riding was observed after the young were 16 days old.

Behavior of young.—Our observations of the behavior of the young are well in accordance with e.g. the report by Beebe (1909). The first dives were observed at four days of age, but the diving ability is not well developed until an age of about two weeks. Consequently, the young are an easy prey for such predators as the Great Black-backed Gull (*Larus marinus*), especially when the young leaves the parents during disturbances. The young bird moves easily on land, and might well be able to cover great distances in case of need, as reported for *G. stellata* (von Braun, Hessle, and Sjölander, 1968), a valuable ability if the nesting lakes freeze early.

Our observations give no clues as to the onset of independence, since all young stayed with their parents during our observation period, and were also fed (the oldest being 101 days old).

DISCUSSION

Even if a definite proof is yet lacking there are many reasons to believe that loons pair for life. The facts that they arrive in pairs immediately as the ice on the lakes thaws; that the number of pairs in a lake and even the nest sites remain the same throughout the years, as well as the lack of lengthy and spectacular courtship and the short time between arrival and egg-laying, all point to this conclusion.

We know practically nothing of the formation of these pairs, but the sparse occurrence of lone, calling birds in spring (observed in *G. arctica*) would point to the speculation that young males look for territories and then call for unpaired females, in which case the territorial cry could also be attributed a sexual significance. On the other hand, a pair formation in the spring flocks on the coasts might also be possible. Obviously, different loon species might differ in the method used, but this seems improbable in view of the many similarities in the reproductive behavior.

The courtship remains a disputable question. Very few authors on the subject have ever seen copulation, which has been described by Zedlitz (1913), Huxley (1923), and Keith (1937) for *G. stellata*, by Sjölander (1968) for *G. arctica*. There are no reports for the remaining two species except the previously mentioned report by Southern (1961) (obviously referring to a fight) and the observation by Tate (1969). In the descriptions of what has been regarded as courtship, there is therefore seldom if ever a connection stated between the reported behavior and copulation. A closer study of the territorial behavior of the loons leaves little doubt that the behavior described by different authors as courtship is really territorial, and only indirectly, if at all, connected with the mating.

The opinion given in this report, that the courtship consists of the relatively simple movements described above, gains further support from a comparision with *G. arctica* and *G. stellata* which show the same type of behavior preceding copulation, although there are notable differences in their territorial behavior (and thus in the behavior described as courtship in earlier reports).

Even if the pairs and copulations observed here are comparatively few, the fact that the behavior is about the same as in *G. stellata* and *G. arctica* strongly suggests that the observed cases were representative. Further, a copulation on the water as reported by Southern (1961) seems highly improbable since the loons lack a pseudopenis.

The significance of the building movements shown at relief by *G. immer*, in the same way as in *G. arctica* and *G. stellata*, remains uncertain, since it is the relieved parent that shows the most building, which makes a signalling interpretation difficult. A possible explanation might be that activity near the nest by the other parent stimulates an otherwise suppressed building, since inactivity on the nest is important to make the bird less conspicious, and thus a concentration of different activities from the conspicuous but necessary relieving might be advantageous.

Our observations on the behavior of parents and young do not differ from the reports by other authors except on some minor points. The warming of the young on the shore is probably a normal behavior, since it is well known especially in *G. stellata*, but since it does not seem to occur very often the fact that earlier observers have not seen it in *G. immer* is easily explained. This is also true for the differences noted in the feeding behavior, where the earlier observations are rather scanty.

On the whole, the observations in this report point to a strong similarity between *G. immer* and especially *G. arctica*, since the territorial behavior, courtship, copulation, nesting behavior, incubation, and parental behavior are very much the same. The explanation of such similarities and differences can, however, only be had in the context of a study of the behavior of the whole family Gaviidae, which is as yet incomplete.

SUMMARY

During the summer 1970, the authors studied a number of pairs of the Common Loon (*Gavia immer*) with respect to the reproductive behavior, on Iceland. The birds were studied from spring arrival till September, and the territorial behavior, courtship, copulation, nest choice, nest-building, incubation, and parental behavior was observed and filmed. The territorial behavior was observed and filmed rather extensively, and a description of the different movements is given. Of the several vocalizations the yodel is regarded as a territorial call, the wail as a low-intensity form of the yodel, the tremolo as a warning and agitation call.

The courtship observed was very much like the behavior in *G. arctica* and *G. stellata*, but differs from earlier reports of *G. immer*. This seems to stem from the description of territorial behavior as courtship by many authors. The copulation, which took place ashore, was similar to the copulation of *G. arctica* and *G. stellata*, as might be expected.

The nest site was chosen by the male, the main nest-building done by the female. Additional nest-building was observed when the parents relieved each other on the nest. The incubation period was 28 days. The parental behavior was as described in earlier reports, but differences noted in the feeding behavior (both parents feeding, no splashing or dipping of the food). The young were sometimes warmed ashore. A number of comparisons with *G. arctica* and *G. stellata* are made.

ACKNOWLEDGMENTS

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LITERATURE CITED

Beebe, C. W. 1907. Notes on the early life of loon chicks. Auk, 24:34–41.

Bent, A. C. 1919. Life histories of North American diving birds. U.S. Natl. Mus. Bull., 107:47–62.

Braun, C. von, A. Hessle, and S. Sjölander. 1968. Smålommens (*Gavia stellata*) beteende under ungvårdnadstiden. Zool. Revy, 30:3–4, 94–95.

Dunlop, E. B. 1915. Notes on the Great Northern Diver. Brit. Birds, 9:142–147.

Huxley, J. S. 1923. Courtship activities in the Red-Throated Diver, together with a discussion of the evolution of courtship in birds. J. Linnaean Soc. Zool., 35:253–292.

Keith, D. B. 1937. The Red-Throated Diver in North East Land. Brit. Birds, 31:66–81.

Lehtonen, L. 1970. Zur Biologie des Prachttauchers (*Gavia a. arctica* L.). Ann. Zool. Fennici, 7:25–60.

Munro, J. A. 1945. Observations of the loon in the Caribou Parklands, British Columbia. Auk, 62:42–46.

Niethammer, G. 1966. Handbuch der Vögel Mitteleuropas. Frankfurt am Main. 1: 61–69.

Olson, S. T., and W. M. Marshall. 1952. The Common Loon in Minnesota. Occ. Papers Minnesota Mus. Nat. Hist., 5:1–77.

Palmer, R. S. 1962. Handbook of North American birds. Yale Univ. Press, New Haven & London. 1:9–10.

Sjölander, S. 1968. Iakttagelser över storlommens (*Gavia arctica* L.) etologi. Zool. Revy, 3:89–93.

Southern, W. E. 1961 Copulatory behavior of the Common Loon. Wilson Bull., 73: 280.

Tate, J. D. 1969. Mating of the Common Loon. Proc. Nebraska Acad. Sci., 79:50.

Tate, D. J., and J. Tate. 1970. Mating behavior in the Common Loon. Auk, 87:125–130.

Wilson, F. N. 1929. The loon at close range. Bird-Lore, 31:95–103.

Yeates, G. K. 1950. Field notes on the nesting habits of the Great Northern Diver. Brit. Birds, 63:5–8.

Zedlitz, O. von. 1913. Ein Beitrag zur Biologie von Polartauchers, *Urinator arcticus*. J. Ornithol., 61:179–188.

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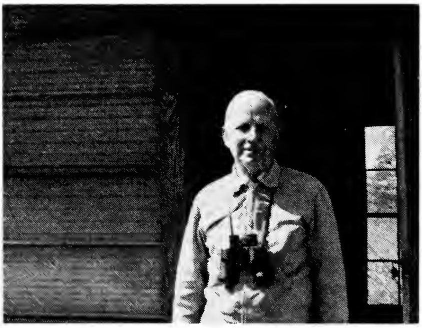
NEW PATRON



The latest addition to the list of Patrons of the Wilson Society is Dr. Paul A. Stewart of Oxford, North Carolina. Dr. Stewart, who is a research entomologist with the U.S. Department of Agriculture, holds three degrees from The Ohio State University. He has published about 100 papers on birds, 20 on insects, and 2 on mammals. One of his major pieces of research has been a thorough study of the life history of the Wood Duck, and his other interests in ornithology extend to the ecology of blackbird congregations, the evolution of bird migration, and the role of birds in the control of undesirable insects. He is a member of the AOU, the BOU, the Cooper Society, Ecological Society of America, Northeastern Bird-Banding Association, Inland Bird-Banding Association, and American Society of Mammalogists. Dr. Stewart is married and has two sons.

RESPONSES OF ADELIE PENGUINS TO COLORED EGGS

Leigh H. Fredrickson and Milton W. Weller

Adelie Penguins (*Pygoscelis papua*) normally lay one or two greenish-white eggs. Males, less commonly females, occupy old nest depressions from which they display and attract former or new mates (Sladen, 1958). Nest sites usually are occupied for several weeks before the laying of the first egg and either sex may sit in the incubating position on the nest bowl. Both sexes incubate, but males start intensive incubation first when females leave to feed after laying (Penney, 1968). The incubation drive is very strong, and nest defense can be intense.

As part of a study involving measurement of variations in incubation behavior, and recording temperatures of incubating birds, by means of thermistors placed in artificial eggs, we wanted to determine: 1) the ability of penguins to recognize their own eggs, 2) the likelihood of ejection of unlike eggs, and 3) possible measures of incubation intensity. Field studies of incubation behavior of Adelie Penguins provide an insight into how a species can maintain itself in this adverse environment.

PROCEDURES

Weller experimented with 13 pairs of Adelie Penguins at Hallett Station, Antarctica, during early November in 1969, and Fredrickson studied 23 pairs between 31 October and 20 November 1970. Birds studied during 1969 were of unknown age except for one female which had been banded as a breeding adult in 1959. Four birds banded in 1969 returned to the colony and were retested in 1970. The sexes of all pairs were determined in 1970, but only seven of 13 pairs were sexed in 1969. Sexed birds were color-marked with paint for rapid determination of the individual on the nest.

Plastic, hollow "Easter eggs" were used because of their availability, bright colors, and the fact that ballast (sugar and salt were used) could be placed inside to duplicate the weight and balance of real eggs. Plastic eggs of two sizes were used: 45 × 63 mm in 1969, and 57 × 83 mm in 1970. One size was smaller and the other larger than real Adelie Penguin eggs (56 × 70 mm for 126 eggs at Hallett, J. Weinrich, unpubl. data).

In this study, eggs were introduced into the nest bowl. This method is inferior to the choice of two nests method used for Herring Gulls (*Larus argentatus*) by Tinbergen (1961:151), but the minimal nest spacing and aggressive behavior of colonial Adelie Penguins would not permit such experimentation.

PRE-LAYING STAGE

In 1969 Pair 1 in the pre-laying stage was exposed to white, blue, and yellow plastic eggs for 2 minutes each. Each egg presented was accepted and incubated in the nest with the exception of the blue egg which was found out of the nest. Normally, penguins do not retrieve even their own eggs (Penney,

TABLE 1

NUMBER OF COLORED PLASTIC AND BLOWN PENGUIN EGGS EJECTED FROM ADELIE PENGUIN NESTS PRIOR TO LAYING. HALLETT STATION, ANTARCTICA, 1970.

Days prior to laying	Number of eggs ejected					
	Colored plastic eggs			Blown eggs		
	By male	By female	By pair	By male	By pair	
1	2/9*	0/9	0/9	0/2	0/2	
2	2/3	0/3	0/3	0/3	0/3	
3	0/8	0/8	1/8	0/2	0/2	
4	0/12	0/12	0/12	0/2	0/2	
5	2/6	0/6	0/6	0/3	0/3	
6	1/4	1/4	0/4	1/3	1/3	
7	1/8	0/8	1/8	1/2	0/2	
8	5/9	1/9	0/9	1/3	0/3	
9	0/3	0/3	0/3	0/1	0/1	
10	1/1	0/1	0/1	0/0	0/0	
11	0/2	0/2	1/2	0/0	0/0	
13	0/2	0/2	2/2	0/1	1/1	
15	0/1	0/1	0/1	0/0	0/0	
Totals	14/68	2/68	5/68	3/22	2/22	26/90

* In 9 trials, 2 eggs were ejected by a male.

1968). A pink plastic egg then was left for 20 minutes, and this time subsequently was used for tests of all birds in the pre-laying stage. Three other pairs in the pre-laying stage were tested with eggs of these four colors and all accepted each egg and incubated for 20 minutes each. Eggs were presented in different sequences of color.

Then, two highly aggressive pairs were used, including one banded female estimated to be in excess of 13 years of age. In both cases, the female was standing over the egg but the male pecked at the egg viciously until it was ejected from the nest. In both nests, all four test eggs were pecked until ejected from the nest bowl at which time they were ignored. This striking difference in behavior suggests that physiological state and perhaps experience may influence acceptance of any egg in the nest bowl. In another experiment, a blown, weighted Adelie Penguin egg was viciously pecked by both members of another pair but was finally accepted and incubated for several days.

In 1970, birds were tested from 1 to 15 days before laying with blue, pink, yellow, and natural colored, blown and weighted Adelie Penguin eggs. Eggs were pecked until ejected from the nests in 26 of 90 tests (Table 1). Males accounted for 17 of the ejections compared to only two ejections

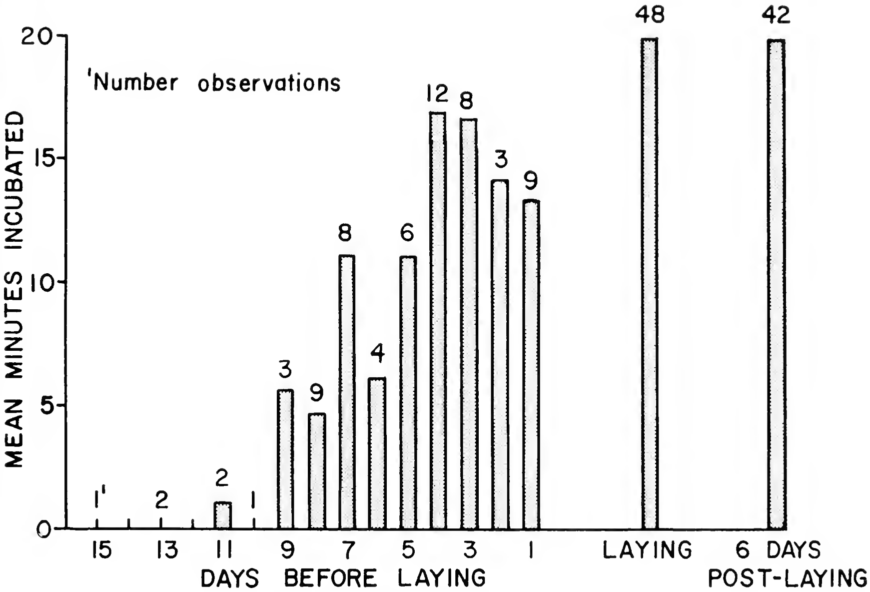


FIG. 1. Summary of responses to colored plastic eggs placed in nest bowls of Adelie Penguins prior to, during, and after laying. Hallett Station, Antarctica, 1970.

by females. In seven tests, both members of the pair actively ejected eggs. At no time did females eject blown, weighted Adelie eggs from the nest bowl. Females ejected colored plastic eggs at 6 and 8 days before laying, but one male ejected colored eggs the day before eggs appeared in the nest. In five of 22 tests, when blown and weighted Adelie Penguin eggs were ejected from nests, all rejections were 6 or more days before laying.

In six tests made from 15 to 7 days before laying the penguins either peered at the experimental eggs or ignored them, but the eggs were not incubated during the 20-minute test period. Four of these six tests were with colored eggs and two were with blown Adelie Penguin eggs.

Four penguins marked in 1969 were tested 12 times in 1970 during the pre-laying stage. These birds accounted for eight of 26 tests in which eggs were ejected from the nest. Six of these eight rejections were with colored plastic eggs. In three other tests from 15 to 6 days before laying, these birds failed to incubate eggs.

As laying nears, Adelie Penguins become increasingly broody (Fig. 1). Of nine tests 1 day before laying, all but one bird incubated at least 18 minutes. The mean incubation of 13.5 minutes shown in Figure 1 for a 20-minute test on the day before laying resulted from one particularly aggressive male, which ejected colored eggs during two tests the day before laying.

LAYING—INCUBATION STAGE

To test the responses of birds known to be broody in the laying or post-laying stage in 1969, three nests were selected with two, one, and one eggs, respectively. Pair 7 had two eggs and accepted a white plastic egg in place of one of its own eggs. Then a pink egg was presented to test both a smaller and strikingly different colored egg. It accepted the egg without hesitation and incubated for 10 hours, at which time the original egg was replaced.

The two pairs with one egg each were given a yellow or a blue egg in place of their own egg. In each case the egg was accepted as though it were its own, and incubation of the plastic egg continued for 10 hours at which time the original egg was replaced.

Briefer experiments of a similar nature were conducted on four pairs which had two, one, one, and two eggs, respectively. In nests of two eggs, one of the two was replaced by a plastic egg; real eggs were removed from nests of one egg. All of the birds readily accepted the pink, blue, and yellow substitutes even when in the nest bowl with a real egg. The behavior of several individuals suggested recognition of the colored eggs by their hesitancy and peering but the relative roles of color, sheen, size, and other factors in recognition cannot be clearly evaluated. However, in most cases responses other than incubation were masked by the external and internal stimuli that cause birds to incubate their eggs.

On 11 November 1969 Pairs 5 and 6, which had refused to accept plastic eggs, were tested again when they had two eggs. Each was given the one pink plastic egg for 20 minutes in place of one of its own. The male of Pair 5 was alone and was less aggressive but more broody than previously. This male examined the one pink and one normal egg for 3 minutes and then incubated for the 20-minute test period.

Pair 6, however, did not change in their response to the foreign eggs. The female accepted the egg by standing over it but the male pecked it out of the nest; thereafter, its second egg was returned.

In 1970, all pairs accepted the colored eggs and incubated them during laying and 6 days post-laying. Of 48 tests during laying and 42 tests post-laying (Fig. 1), one pair incubated a yellow egg 19 minutes instead of the 20 minutes observed in the other 89 tests.

DISCUSSION

Antarctic weather dictates the need for intensive incubation behavior if eggs of Antarctic species are to develop properly in sub-freezing temperatures. Because Adelie Penguins have strong attachments to nest sites before egg laying, the species provides unique opportunities for study of the external and internal factors related to development of incubation behavior.

There seems to be no evidence that penguins lack color vision, and the fact that several species have colored bills and feathers suggests strongly that they can differentiate colors. Moreover, Levick (1915) did experiments with colored rocks which suggested that Adelie Penguins preferred red. The ability of several individuals to quickly perceive and eliminate colored eggs from the nest supports the idea that color vision is present, but characteristics of these test eggs such as sheen, size, or the crack in the egg were not properly evaluated in these tests. There is little doubt, however, that the plastic eggs were recognizable as unlike their own when in the same nest bowl with a real egg.

It is well known that birds are not very selective in egg color or size (Tinbergen, 1961:144–159), but some birds which are parasitized regularly readily reject eggs unlike their own (Swynnerton, 1918). Ducks are more likely to reject unlike experimental eggs during laying than during incubation, presumably because the brooding drive is less strong (Weller, 1959:352).

Although the nest bowl is clearly important as a pair center for Adelie Penguins, they must become physiologically ready to accept an egg when it appears in the nest. Apparently there is no innate recognition of color or size of the egg. We infer from these brief experiments that Adelie Penguins, as in many other birds, incubate objects of any color which appear in the nest. The rejection behavior of several highly aggressive males in 1969 and 1970 may reflect lack of development of the incubation drive in males at this stage and longer experience in nesting. The external and internal factors that cause the change from aggressive to incubation behavior remain unknown.

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LITERATURE CITED

Levick, G. 1915. Natural history of the Adelie Penguin. British Antarctic "Terra Nova" Expedition, 1910–1913. British Mus. Nat. Hist., London. Natural History Rept. Zool., 1:55–88.

Penney, R. 1968. Territorial and social behavior in the Adelie Penguin. *In* Austin, O. L., Jr. (Ed.), Antarctic bird studies. American Geophysical Union, Washington, D. C. Antarctic Research Series, 12:83–131.

Sladen, W. J. L. 1958. The Pygoscelid penguins. Falkland Islands Dependencies Survey Sci. Rept., 17:1–97.

SWYNNERTON, C. F. M. 1918. Rejections of birds of egg unlike their own with remarks on some of the cuckoo's problems. Ibis, 6:127–154.

TINBERGEN, N. 1961. The Herring Gull's world. Basic Books, Inc., New York.

WELLER, M. W. 1959. Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. Ecol. Monogr., 29:333–365.

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NEW LIFE MEMBER

A recent addition to the list of Life Members of the Wilson Society is Dr. James A. Pittman. Dr. Pittman earned his bachelor's degree at Davidson College, and his M.D. at Harvard Medical School and is currently Head of the Office of Research and Education, Veteran's Administration as well as Professor of Medicine at Georgetown University. He is the author of over 150 papers in the medical and physiological literature, particularly thyroid physiology. His interests in ornithology also involve avian endocrine physiology. Dr. Pittman says that his interest in birds, in biology, and in The Wilson Society were aroused and stimulated by George Sutton and Franklin McCamey in Orlando, Florida in the latter days of World War II. Dr. Pittman is married (Mrs. Pittman is also a Professor of Medicine) and has two children.

VARIATION IN THE POSTERIOR BORDER OF THE STERNUM IN SOME TREE-TRUNK FORAGING BIRDS

Alan Feduccia

THE posterior border of the avian sternum varies considerably in various taxa but no one to date has been able to offer a convincing correlation between form and function of this complex character. Those correlations of sternal anatomy with functions which have been attempted and which have some credence are summarized by Heimerdinger and Ames (1967), but all are tenuous at best. This paper examines the form and possible function of the posterior border of the sternum in several unrelated groups of birds which are comprised both of forms which forage by creeping up vertical surfaces, and those which forage from the normal perching fashion.

THE STERNUM IN OVENBIRDS AND WOODHEWERS

Woodhewers (Dendrocolaptidae) (tree-trunk foragers) and ovenbirds (Furnariidae) ("normal foragers") are very closely related, and therefore offer the opportunity to discover specific adaptations associated with the tree-trunk foraging habit.

The variation in the notches of the posterior border of the sternum in oscine and suboscine passerine birds has been reported by Heimerdinger and Ames (1967). They examined almost a thousand specimens and divided the sternal types into six categories (see Fig. 1), grading from those with no notches (type 1), to those with four complete notches (type 6). Heimerdinger and Ames (op. cit.) discovered the greatest amount of variability within the Dendrocolaptidae, and found that of 173 specimens in nine genera, the majority possessed two-notched (type 3) sterna; types 2, 3, and 4 were sometimes found in the same species, but no specimens were described as possessing type 5 or 6. Woodhewers possess rather solid sterna, with one specimen of *Xiphocolaptes promeropirhynchus* having a sternum devoid of any perforations (type 1).

Ovenbirds typically possess a two-notched (type 3) sternum, but some specimens exhibit the more perforate types. Heimerdinger and Ames (op. cit.) discovered type 5 sterna (with a lateral notch and a large medial fenestra on each side) in five of 199 specimens examined, including certain specimens of *Xenops rutilans*, *Pygarrhichas albogularis*, *Sclerurus rufigularis*, and *S. guatamalensis*.

I have attempted to show general trends in the sternum by condensing data from Heimerdinger and Ames (1967) in tabular form (Table 1). When the data are presented in such a manner certain things become apparent. The

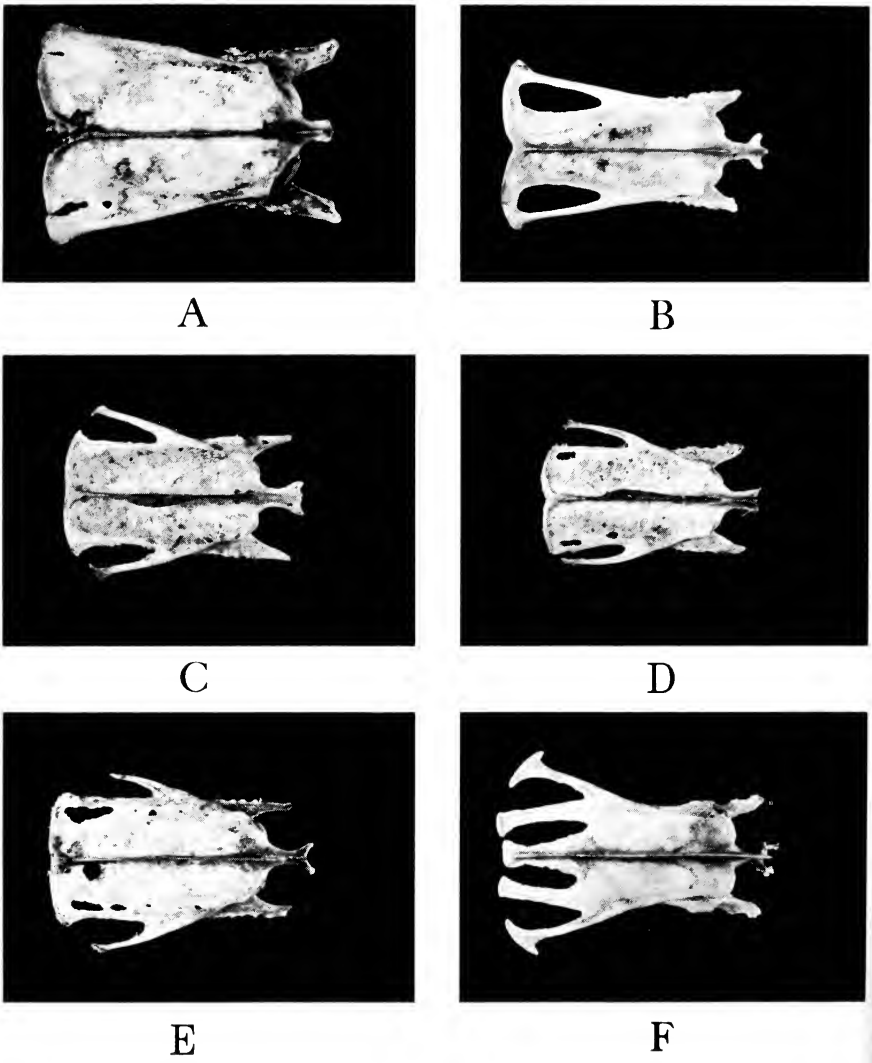

Fig. 1. Photographs of the sternal notch types: A, *Xiphocolaptes promeropirhynchus*: Dendrocolaptidae (type 1 approaching type 2); B, *Xiphorhynchus guttatus*: Dendrocolaptidae (type 2); C, *Automolus ochrolaemus*: Furnariidae (type 3); *Cinclodes fuscus*: Furnariidae (type 4 approaching type 5); E, *Sclerurus guatemalensis*: Furnariidae (type 5); F, *Dendrocopus villosus*: Picidae (type 6). Photographs made to approximately same scale.

TABLE 1

DISTRIBUTION OF STERNAL NOTCH TYPES FOUND WITHIN OVENBIRDS AND WOODHEWERS. (Data primarily from Heimerdinger and Ames, 1967).

The numbers under each sternal type represent the number of specimens examined within each genus. The species within each genus may be found in Heimerdinger and Ames (op. cit.).

	Sternal Notch Types							
	1	2	2–3	3	3–4	4	4–5	5
Geositta				5	1	2		
Upucerthia				7	1			
Ochetorhynchus				2		1		
Eremobius				1				
Cinclodes				7	3	4	1	
Furnarius				15				
Sylviothorhynchus				1				
Aphrastura				4		2		
Phleocryptes				1	1			
Leptasthenura				6				
Schizoeaca				1				
Schoeniophylax				2				
Synallaxis				34	1			
Certhiaxis				2				
Cranioleuca				5				
Asthenes				11				
Phacellodomus				3				
Coryphistera				3				
Anumbius				2				
Margarornis				7		1		
Premnoplex				2	1	2		
Pseudocolaptes				3				
Pseudoseisura				4		2		
Hyloctistes				2				
Syndactyla				3				
Anabacerthia				8		1		
Philydor				4				
Automolus				12	1			
Hylocryptus				2				
Xenops				7				1
Pygarrhichas						2		1
Sclerurus								3
Lochmias						1		

TABLE 1
Continued

	Sternal Notch Types							
	1	2	2–3	3	3–4	4	4–5	5
Dendrocincla				8	1			
Deconychura				3				
Sittasomus				18		1		
Glyphorhynchus				10				
Xiphocolaptes	1	3	1	5				
Dendrocolaptes		1	1	8	3	1		
Xiphorhynchus		10	4	37	5	3		
Lepidocolaptes		7	1	34		2		
Campylorhamphus				4				
Dendrexetastes				1				

ovenbirds and woodhewers possess a basic sternal type, which is type 3. These type 3 sterna tend to be more open (to the left-hand side of table 1), or more closed (to the right-hand side of table 1), than typical type 3 sterna. When they are more open they become types 3–4, 4, 4–5, and 5, and when they are more closed they become types 2–3, 2, and 1. The ovenbirds tend to have type 3 sterna, but with a considerable degree of opening; whereas, the woodhewers are the only forms which show closure. In fact, the only genera which show closure are *Xiphocolaptes*, *Dendrocolaptes*, *Xiphorhynchus*, and *Lepidocolaptes*. These data indicated to me the possibility that closure of the posterior border of the sternum might be associated with the tree-trunk foraging habit.

It is of interest here to note that the four woodhewer genera which are somewhat intermediate between the Furnariidae and Dendrocolaptidae in many anatomical characters, *Dendrocincla*, *Sittasomus*, *Deconychura*, and *Glyphorhynchus*, show the sternal pattern of the ovenbirds with no tendency towards closure of the posterior border. *Dendrocincla* forages in a variety of postures (including creeping), while *Sittasomus*, *Deconychura*, and *Glyphorhynchus* creep up tree trunks like other woodhewers. I have shown elsewhere (Feduccia, 1969) that the above genera possess many primitive characters within the woodhewer assemblage, and it is possible that some may represent separate ovenbird offshoots which have reached the dendrocolaptid "grade" of anatomical organization. *Dendrocincla* even possesses the hemoglobin characteristic of the family Furnariidae. Thus, if sternal ossification is occurring with tree-trunk foraging, the lack of sternal closure in the above genera would not be surprising.

It should also be noted here that there are several ovenbirds which may at times forage like the woodhewers by hitching up tree trunks; however, all of these forms, which include *Margarornis*, *Premnornis*, *Premnoplex*, *Cranioleuca*, *Pseudocolaptes*, *Xenops*, *Automolus*, and *Pygarrhichas*, forage in a variety of manners, and hitch up tree trunks only as alternatives to other possible foraging postures. Oscines which creep up tree trunks show the same sternal pattern as non-creeping forms. As Heimerdinger and Ames (1967) have pointed out, "Oscines which have a specialized form of locomotion such as creeping on vertical surfaces (*Certhia*, *Sitta*), or which are partially terrestrial (*Eremophila*, *Cinclus*), have exactly the same sternal characters as the more typical oscines. It is also true, however, that many of these specialized species are migratory; the importance of certain regular, but short-time, activities during the life span may override a tendency toward adaptation for the daily type of locomotion."

THE STERNUM IN THE PICIFORMES

If it is expected that closure of sternal notches occurs with the evolution of tree-trunk foraging behavior, then one should be able to find a similar condition in other climbing birds.

In order to test the hypothesis that closure in the posterior border of the sternum is a result of selection pressures for stronger sterna associated with tree-trunk foraging, I turned to the diverse order Piciformes. Unlike the ovenbirds and woodhewers which possess diverse sternal types, making comparisons very difficult, all of the piciform birds that I examined possessed type 6 sterna (four notches). Within the order Piciformes are found both trunk-foragers and perching types. If trunk foraging is associated with sternal closure then it should be obvious in piciform birds. In order to compare various piciform birds with respect to sternal closure I have taken the ratio of depth of median notch of the sternum to the total sternal length. The means and ranges from these data are shown in Figure 2. Small sample size for most species prohibits elaborate statistical testing, but certain trends are obvious within the diagram. The most important point is that the tree-trunk foraging piciform birds (nos. 24–60) show, in general, more sternal closure than the non-trunk foraging piciforms (nos. 1–23). However, when one views the diagram in segments one finds many interesting points. The Galbulidae (nos. 1–3) seem to form a cohesive group as do the Bucconidae (nos. 4–7). However, the Capitonidae (nos. 8–12) are tremendously variable. Why *Capito niger* (no. 8) should show great closure of the sternal border is an enigma. The species of the Indicatoridae (nos. 13–14) seem to be very homogeneous. The Ramphastidae (nos. 15–20) are of great interest, for although they form a cohesive group, they clearly show more sternal notch closure than the other perching piciform birds. The Jynginae (no. 21), and the Picumninae (nos. 22–23), as expected from the hypothesis, have relatively open sterna as compared to other members of the Picidae. The large woodpeckers, *Dryocopus pileatus* and *D. lineatus* (nos. 38–39), and *Phloeoceastes guatemalensis* and *P. rubicollis* (nos. 59–60), are towards the bottom of the woodpeckers with respect to sternal closure, but the medium-sized woodpeckers, *Piculus simplex* and *P. flavigula* (nos. 29–30), and *Meiglyptes tukki* (no. 37), show equally closed sterna.

If the trend towards closure of the posterior sternal border were truly invariable, then one might expect to see some trend in closure corresponding to the relative amount of time that the forms spend on tree trunks. Thus, the series might go from *Colaptes* to *Asyndesmus* to *Melanerpes* (see Burt, 1930; and Spring, 1965). However, no such trend appears to be evident. Therefore, I feel that the tendency towards closure (as was the case for the woodhewers) should be stated as a general trend, not as a strict anatomical law. As in the case of the woodhewers, there is a general trend towards closure of the poste-

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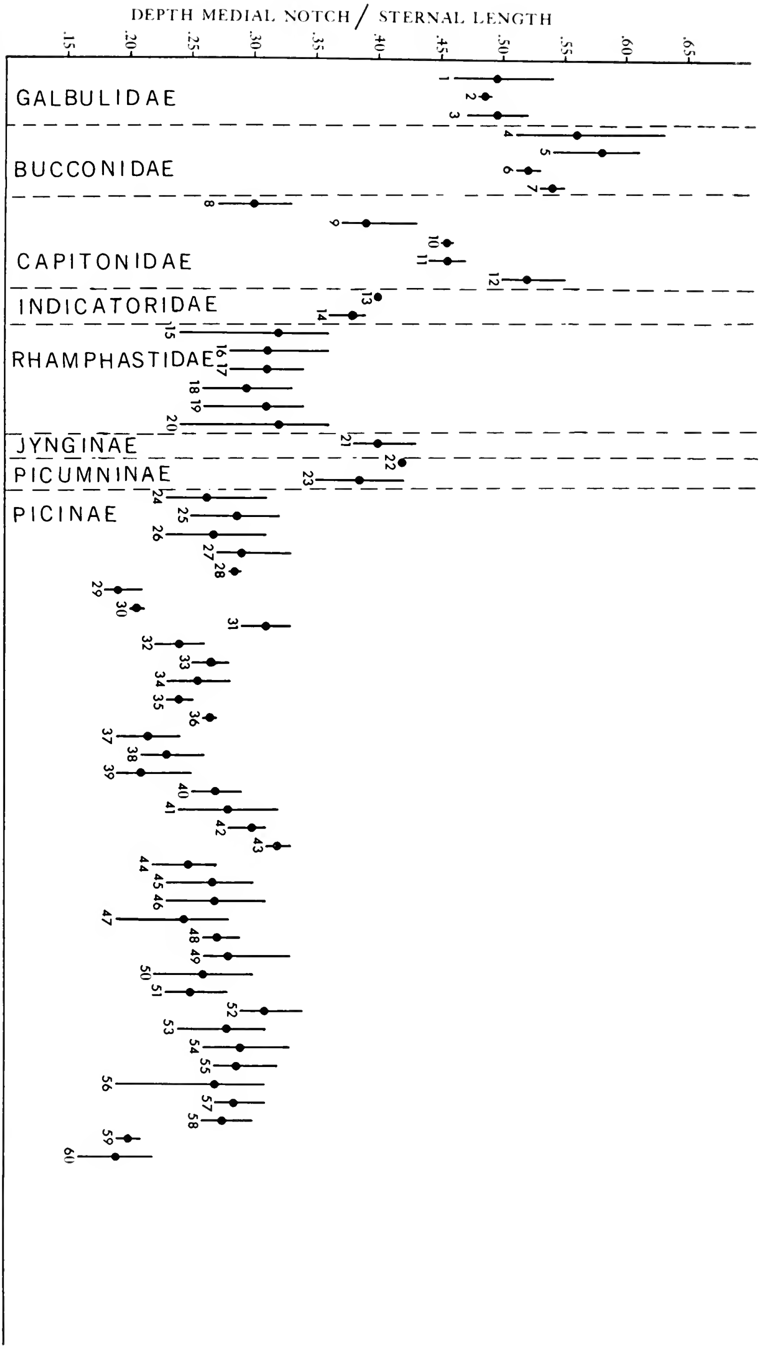
FIG. 2. Means and ranges for the ratio of depth of medial notch of sternum to total length of sternum for the following piciform birds: Family Galbulidae: no. 1, *Galbula ruficauda* (4 specimens), no. 2, *G. galbula* (2), no. 3, *G. dea* (2); Family Bucconidae: no. 4, *Malacoptila panamensis* (3), no. 5, *Notharchus macrorhynchos* (5), no. 6, *Monasa atra* (2), no. 7, *Chelidoptera tenebrosa* (3); Family Capitonidae: no. 8, *Capito niger* (2), no. 9, *Semnornis rhamphastinus* (3), no. 10, *Tricholaema lachrymosum* (2), no. 11, *T. diadematum* (2), no. 12, *Trachyphonus darnaudi* (3); Family Indicatoridae no. 13, *Indicator variegatus* (2), no. 14, *I. indicator* (3); Family Ramphastidae: no. 15, *Pteroglossus torquatus* (5), no. 16. *P. castanotis* (8), no. 17, *P. aracari* (3), no. 18, *Ramphastos swainsonii* (5), no. 19, *R. toco* (5), no. 20, R. *sulfuratus* (6); Family Picidae: Subfamily Jynginae: no. 21, *Jynx torquata* (3); Subfamily Picumninae: no. 22, *Picumnus temminckii* (2), no. 23, *P. minutissimus* (4); Subfamily Picinae: no. 24, *Colaptes cafer* (6), no. 25, *C. auratus* (11), no. 26, *C. campestris* (4), no. 27, *C. melanochloros* (3), no. 28, *C. punctigula* (2), no. 29, *Piculus simplex* (3), no. 30, *P. flavigula* (2). no. 31, *Campethera nubica* (3), no. 32. *C. abingoni* (2), no. 33, *Celeus elegans* (2), no. 34, *C. undatus* (2), no. 35, *C. flavus* (2), no. 36, *Picus viridis* (2), no. 37, *Meiglyptes tukki* (2), no. 38, *Dryocopus pileatus* (7), no. 39, *D. lineatus* (5), no. 40, *Asyndesmus lewis* (2), no. 41, *Melanerpes erythrocephalus* (8), no. 42, *M. formicivorus* (5), no. 43, *M. carolinus* (5), no. 44, *M. uropygialis* (6), no. 45, *M. aurifrons* (9), no. 46, *M. chrysogenys* (3), no. 47, *M. pucherani* (4), no. 48, *Leuconerpes candidus* (3), no. 49, *Sphyrapicus varius* (11), no. 50, *Veniliornis fumigatus* (3), no. 51, *V. spilogaster* (3), no. 52, *Dendrocopus major* (3), no. 53, *D. villosus* (18), no. 54, *D. pubescens* (11), no. 55, *D. borealis* (6), no. 56, *D. scalaris* (6), no. 57, *Picoides tridactylus* (5), no. 58, *P. arcticus* (5), no. 59, *Phloeoceastes guatemalensis* (3), no. 60, *P. rubicollis* (3). All of the above piciform birds possess type 6 sterna with the exception of *Celeus elegans*, which has the median notches open, but with one large perforation laterally on each side of the sternum. *Celeus undatus* and *C. flavus* both possess normal type 6 sterna.


DEPTH MEDIAL NOTCH / STERNAL LENGTH
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GALBULIDAE
BUCCONIDAE
CAPITONIDAE
INDICATORIDAE
RHAMPHASTIDAE
JYNGINAE
PICUMNINAE
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rior border of the sternum, but closure may only occur where it does not interfere with other sternal functions which may be necessary at sometime during the life history of the organism, but which are under opposing selection forces.

Short's (1971) paper on the evolution of terrestrial woodpeckers points to the fact that though there are as many as twelve species of terrestrial or semi-terrestrial woodpeckers, they tend to spend part of their life histories on tree trunks or vertical surfaces. These forms might therefore be under selection forces for maintaining adaptations associated with tree-trunk foraging. Even the most terrestrial form, the Andean Flicker (*Colaptes rupicola*), roosts commonly in excavated holes in vertical surfaces (Short, op. cit., Fig. 11). As Short (op. cit., p. 15) also points out, "Arboreal woodpeckers . . . may vary greatly in the use of their legs during climbing, and structural parallelism may result between terrestrial and certain arboreal woodpeckers even though their legs function differently in locomotion." "The tail too is apt to be utilized diversely in woodpeckers . . . so that clear-cut differences between ground woodpeckers and typically arboreal woodpeckers are not apparent." The foregoing might at least partially explain the lack of clear-cut differences in sternal form between partially terrestrial woodpeckers (species of *Colaptes*; nos. 24–28, and *Picus viridis*, no. 36, Fig. 2), and totally arboreal picine species.

HOOPOES AND WOODHOOPOES

In an attempt to discover other groups in which there is a tendency to ossify the posterior border of the sternum with the tree-trunk foraging habit, I examined the hoopoes (Upupidae), which do not hitch up tree trunks, and the woodhoopoes (Phoeniculidae), which forage in a variety of postures, but also by hitching up tree trunks (personal observation; and Clancy, 1964, and McLachlan and Liversidge, 1957). *Upupa epops* (Upupidae), and *Phoeniculus purpurescens* and *Rhinopomastos cyanomelas* (Phoeniculidae) possess type 3 (two notched) sterna. The ratio of depth of sternal notch to total sternal length is given in Figure 3, which graphically illustrates the more open sternum of *Upupa*, as compared with *Rhinopomastos* and *Phoeniculus*. Again, small sample size prohibits meaningful statistical testing, but at least *Upupa* is clearly significantly different from *Phoeniculus*. Furthermore, one specimen of *Phoeniculus purpurescens* possessed a type 2 sternum (with two lateral fenestrae), showing even additional closure, much in the same manner as the woodhewers. Therefore, in general, woodhoopoes appear to show the same general tendency towards closure of the posterior border of the sternum associated with tree-trunk foraging as observed in the woodhewers, and begin with the same sternal ancestry, a type 3 sternum.

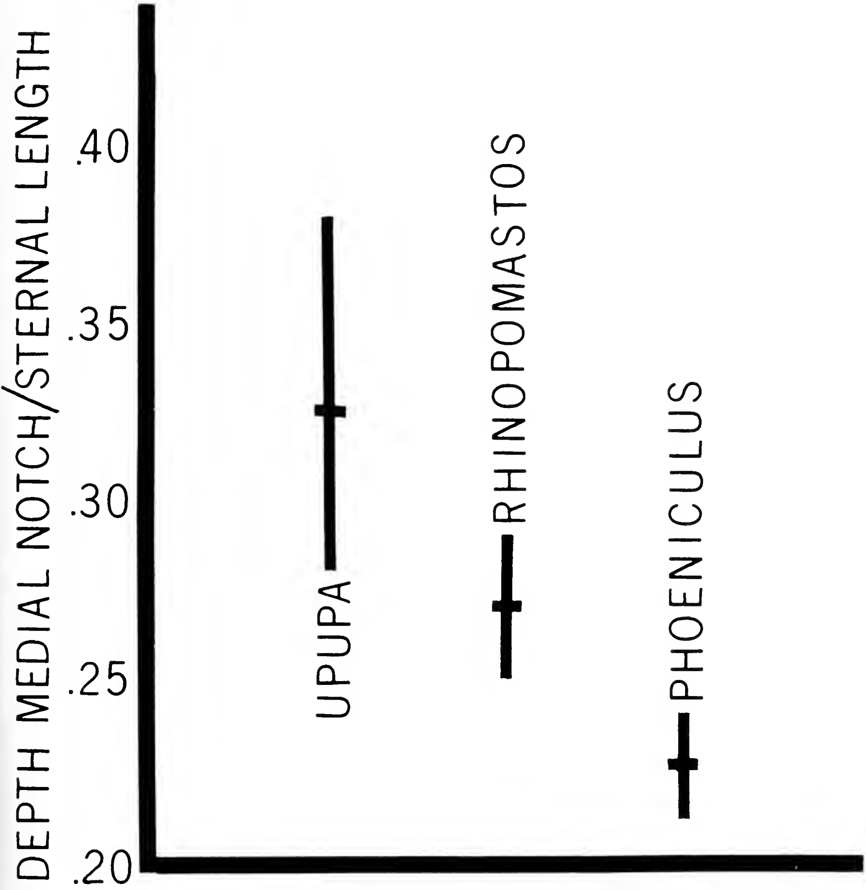

FIG. 3. Means and ranges for the ratio of depth of medial notch of sternum to total length for *Upupa epops* (n = 7), *Rhinopomastos cyanomelas* (n = 3), and *Phoeniculus purpurescens* (n = 5).

POSSIBLE FUNCTION OF THE POSTERIOR BORDER

So far I have merely established a correlation between closure of the posterior border of the sternum with the tree-trunk foraging habit, without elaborating on the possible functional reason for the closure.

The avian sternum provides attachment for two major sets of muscles. Lindsay (1885) pointed out that the outline of the posterior border of the sternum should in some way reflect the resultant of the forces of these two opposing sets of muscles. In the case of the birds under consideration in this paper, the relative powers of flight would not appear to vary greatly from one group to another. Thus, flight would not be an obvious place to look for

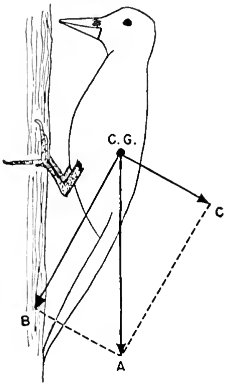

FIG. 4. Diagram (from Stolpe, 1932) to show the forces acting on the climbing bird. A downward and inward force, B, and an outward force, C, constitute the two components of the gravitational pull, A.

functional correlates to explain the form of the posterior border of the sternum. However, if one considers the posture of a tree-trunk foraging bird on the trunk (Fig. 4), with the forces acting on a climbing bird, then one should be able to postulate the manners in which the bird could counteract the gravitational forces which act to pull the bird downward. Figure 4 is taken from Stolpe (1932), and was used by Bock and Miller (1959) to explain the functioning woodpecker foot. As Bock and Miller pointed out, the gravitational force, A, is divided into two component forces, B, and C. They further point out, "Force B, which is the larger of the two components, is directed downward and inward along the axis of the tail. The tail and fore toes (two and three) act together to counterbalance force B; the tail provides the greatest support. The outward force C tends to pull the woodpecker away from the tree trunk. This force is overcome by a combined action of the fore toes and the laterally directed fourth toes, of which the latter are probably the most important." However, while the fore toes and tail are of paramount importance in counteracting the gravitational forces, certain muscles must also function in this capacity. The most obvious set of muscles which might counteract the outward component force (C) are the abdominal muscles, and indeed, it is this set of muscles which attaches to the posterior border of the sternum. The main muscles involved are the M. obliquus externus abdominis, M. rectus abdominis, and M. transversus abdominis, all of which originate along the posterior border of the sternum (see Burt, 1930). I would postulate that the outward component force C is additionally counteracted by increasing the forces exerted by the abdominal muscles, thereby necessitating an increase in the strength of the posterior border of the sternum. Although

I have not had the opportunity to examine the abdominal muscles of creeping and non-creeping piciforms, I have examined these muscles in an ovenbird and woodhewer of approximately the same size (*Autumolus ochrolaemus* and *Xiphorhynchus guttatus*). My qualitative observations clearly showed that the woodhewer possesses much more mass in all of the abdominal muscles. Quantification of these types of comparisons will be necessary to fully test this hypothesis; until then it may at least bear the name of a strong hypothesis.

Though I have attempted to outline a general functional anatomical reason for an increase in sternal ossification in the posterior border of the sternum in tree-trunk foraging birds, there may be other factors involved. Short (1971) emphasizes what he calls the attribute of "toughness" of woodpeckers. Such undefinable attributes associated with climbing and tree-trunk foraging habits probably account for the fact that (Short, op. cit., p. 21), ". . . woodpeckers are remarkably thick-skinned, tough birds that are tenacious of life . . ." The same general attributes are assignable to woodhewers as well, and may be assessed, though poorly understood, as having to do with tree-trunk foraging adaptations.

PHYLOGENETIC ALTERNATIVES

Bock (1967:67) introduced the term paradaptation to apply to "Those aspects of a feature that are dependent upon, resulting from, or under the control of chance-based evolutionary mechanisms . . ." He used as his example the evolution of perching feet in birds. Anisodactyl, syndactyl, zygodactyl, and heterodactyl feet have evolved in birds as multiple evolutionary pathways for efficient perching mechanisms. As Bock (op. cit.) pointed out, ". . . each represents a different adaptation to the selection force for a more efficient perching foot because each is an adaptive advance for perching as compared to the ancestral foot." The perching foot types are therefore "paradaptive" because of their chance-based evolution, but are also adaptive in the sense that each type has been accepted by selection as an efficient perching foot.

A modified form of Bock's concept of paradaption (see also Bock, 1969; and previous emphasis of the role of accident in evolution by Mayr, 1962) appears to me to be useful in renewed emphasis. However, I do not feel the necessity for the introduction of a new term, nor do I feel that the term "mechanism" should be used in this context, as it carries a connotation of mutationism or macroevolutionary mechanism. However, it is true that phyletic lines begin their evolution with different structural forms which when placed under similar selection forces may result in different modifications to achieve similar goals. Thus, I used the term "phylogenetic alternatives" instead of paradaptation, emphasizing differences in phylogenetic background.

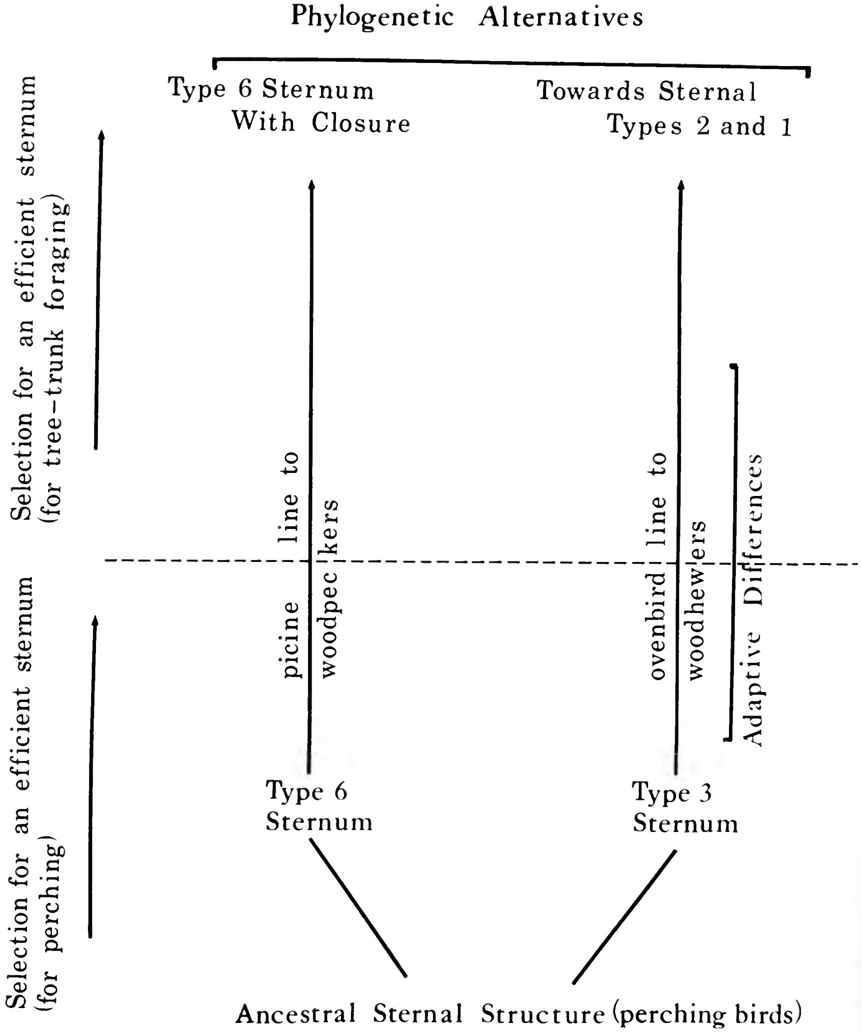

FIG. 5. Schematic diagram (following Bock, 1967) to show multiple evolutionary pathways of the sternal types of woodpeckers and woodhewers. The two ancestral sternal types (6 and 3) were first under the same selection force for a more efficient sternal type for perching, later under the same selection force for tree-trunk foraging. Vertical differences are adaptive; horizontal differences are owing to the ancestral character state.

but not as a macroevolutionary mechanism; these are simply aspects of evolutionary opportunism. In Figure 5, I have attempted to show how this concept might apply to the posterior border of the sternum, following the diagram given by Bock (1967) for the evolution or foot types in birds. In this case, there are multiple pathways of evolution. Type 6 sterna evolve in early picines and type 3 sterna in the ovenbird ancestors of woodhewers, both under similar selection forces for a more efficient sternum for perching; but "evolutionary background" provided each group with different, but perhaps equally efficient, sternal types. When tree-trunk foraging groups evolve from each evolutionary line, the selection force changes to produce an efficient sternum for tree-trunk foraging. However, with the different evolutionary backgrounds in each group, a slightly different solution to the problem is found in each case. In the woodpeckers, the solution is apparently to increase closure of the border of the sternum by ossification; in the woodhewers, the number of notches becomes reduced.

SUMMARY

The evolution of the posterior border of the sternum in unrelated groups of tree-trunk foraging birds may be characterized, in general, by a tendency to increase the ossification of the border. In woodpeckers, which possess a four-notched sternum (type 6), there is an increase in the amount of closure of the notches. In woodhewers and woodhoopoes, which possess basically a two-notched sternum (type 3), there is a tendency to reduce the notches, resulting in some species in type 2 (with lateral fenestrae), and even type 1 (with no notches) in one species. Increasing the ossification of the posterior border of the sternum in the Dendrocolaptidae, Picidae, and Phoeniculidae is probably associated with increasing the strength of the sternum for tree-trunk foraging.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bock, W. J. 1967. The use of adaptive characters in avian classification. Proc. XIV Internatl. Ornithol. Congr. 1966:61–74.

Bock, W. J. 1969. Comparative morphology in systematics, p. 411–448. *In* Systematic Biology. Natl. Acad. Sci. Publ. No. 1692.

Bock, W. J., and W. D. Miller. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Novit., No. 1931:1–44.

Burt, W. H. 1930. Adaptive modifications in the woodpeckers. Univ. California Publ. Zool., 32:455–524.

CLANCY, P. A. 1964. The birds of Natal and Zululand. Oliver and Boyd, Edinburgh and London.

FEDUCCIA, J. A. 1969. Evolutionary trends in the avian families Furnariidae and Dendrocolaptidae. Unpubl. Ph.D. Diss., Univ. Michigan.

HEIMERDINGER, M. A., AND P. L. AMES. 1967. Variation in the sternal notches of suboscine passeriform birds. Yale Univ., Peabody Mus., Postilla, 105:1–44.

LINDSAY, B. 1885. On the avian sternum. Zool. Soc. London 1885, Proc.:684–716.

MAYR, E. 1962. Accident or design, the paradox of evolution, p. 1–14. *In* The evolution of living organisms (G. W. Leeper, Ed.), Melbourne Univ. Press, Victoria.

McLACHLAN, G. R., AND R. LIVERSIDGE. 1957. Roberts Birds of South Africa. Cape & Transvaal Printers Ltd., Cape Town.

SHORT, L. L. 1971. The evolution of terrestrial woodpeckers. Amer. Mus. Novitates, no. 2467, pp. 1–23.

SPRING, L. W. 1965. Climbing and pecking adaptations in some North American woodpeckers. Condor, 67:457–488.

STOLPE, M. 1932. Physiologisch-anatomische Untersuchungen uber die hintere Extremitat der Vogel. J. Ornithol., 80:161–247.

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ANNOUNCEMENT

The Proceedings of the First Conference on the Status of the North American Osprey are expected to be available for distribution in late summer. This conference met in February 1962 at the College of William and Mary, under the chairmanship of Mitchell A. Byrd. Eighty persons attended the three-day affair. Copies of the Proceedings may be obtained by writing Dr. Mitchell A. Byrd, Department of Biology, College of William and Mary, Williamsburg, Virginia 23185. A bill will be sent at the time the order is filled, and no money need accompany the order. The price is expected to be no more than $2.

CRANIAL PNEUMATIZATION PATTERNS AND BURSA OF FABRICIUS IN NORTH AMERICAN SHOREBIRDS

Raymond McNeil and Jean Burton

A study of age criteria in some species of North American shorebirds brought us to consider two of the best known techniques of age determination in birds, the size of the bursa of Fabricius and the degrees and patterns of skull pneumatization. The only attempt, known to us, to correlate bursa of Fabricius and gonadal development with the ossification of the skull is that of Davis (1947).

The bursa of Fabricius is a lympho-epithelial organ lying dorsally above the cloaca. At least in some species it has an opening in the cloaca. It reaches its maximum size at 4–6 months and then begins involution (Davis, 1947). By cloacal examination of the bursal pouch, it is possible to distinguish juvenile from adult individuals of some taxa of birds especially Anseriformes and Galliformes (Gower, 1939; Hochbaum, 1942; Linduska, 1943; Kirkpatrick, 1944). Unfortunately, in shorebird species, the bursa of Fabricius has no cloacal opening and thus cannot be used as an age criterion of living birds.

The pneumatization of the skull has been used as a criterion for estimating the age of birds by C. L. Brehm as far back as 1822 (Niethammer, 1968), but it was not generally used until the turn of the century (Serventy et al., 1967). Miller (1946) describes the skull ossification process as follows:

> "The skull of a passerine bird when it leaves the nest is made of a single layer of bone in the area overlaying the brain; at least, the covering appears single when viewed macroscopically. Later the brain case becomes double-layered, the outer layer being separated from the inner layer by an air space across which extend numerous small columns of bone. . . . Externally the skull of an immature bird appears uniform and pinkish in live or freshly killed specimens. The skull of the adult is whitish, due to the air space, and also it is finely speckled as a result of the dense white bony columns between the layers."

Nero (1951) and Serventy et al. (1967), in their respective studies of *Passer domesticus* and *Taeniopygia castanotis*, give examples of the pattern and rate of cranial ossification, from the juvenile to the adult; through a series of stadia ending with the complete pneumatization of the cranial roof in the adult before it is one year of age. This general rule, applied to the Passerines, admits some exceptions as mentioned by White (1948), Chapin (1949), Grant (1966), McNeil and Martinez (1967), and Payne (1969). Chapin (1949) also reported that "swifts and small sandpipers retained a condition throughout life that suggested immaturity. In some other larger birds the pneumatization of the cranial vault seemed to proceed very rapidly." Other workers like Chapin (1949), Verheyen (1953), Harrison (1958, 1964) were interested in the evolutive and adaptive significance of the fully versus incompletely pneumatized skull in birds.

Although cognizant of the fact that adult shorebirds have incompletely ossified cranial roofs, we undertook the present studies to ascertain whether or not the rate of skull ossification can be used as an indication of age in living and dead birds.

MATERIAL AND METHODS

Series of shorebirds representing 21 species were collected in the Kamouraska region, Quebec, on the south shore of the St. Lawrence River in 1968 (spring, summer, and fall) and 1969 (spring), and on Magdalen Islands, Quebec, in fall 1969. A few specimens also were brought from Venezuela by the senior author in November 1968. These specimens were all prepared as study skins to examine the age characteristics, but the skull roofs were removed and kept separate for further examination of the unpneumatized areas. These skull vaults were then held against a window allowing light to illuminate the unpneumatized areas which were outlined.

The cloaca of each bird was excised and measurements (mm) were taken of the length (A) and height (B) of the fresh bursa of Fabricius; both measurements were used in the approximation of the size of the organ (AB). All birds which had a bursa of Fabricius were considered as immature. However, some birds which had a damaged cloaca were considered as immature if they bore juvenile feathers, especially among the wing coverts. In addition to the above mentioned specimens, we used measurements of the bursa taken by Miss Françoise Cadieux during another study.

RESULTS AND DISCUSSION

Bursa of Fabricius.—The bursa of Fabricius was absent in yearling specimens taken in May and June. Thus the bursa is eliminated within the first year of growth. Moreover, two specimens from Venezuela in November, a Least Sandpiper (*Erolia minutilla*) and a Lesser Yellowlegs (*Totanus flavipes*), had almost fully regressed bursae, though their basic I plumage (first winter) still retained characteristic juvenal feathers. This suggests that, at least in some individuals, the involution of the bursa of Fabricius is completed in less than six months.

The measurements of the average size of the bursa ($\overline{AB}$), as shown in Table 1, indicate that the size of this structure diminishes from July to November. The best examples are the Semipalmated Plover (*Charadrius semipalmatus*), the Ruddy Turnstone (*Arenaria interpres*), the Greater Yellowlegs (*Totanus melanoleucus*), Lesser Yellowlegs, and the Short-billed Dowitcher (*Limnodromus griseus*). The same general trend appears in most of the twelve remaining species, but less clearly because of too small sample sizes.

Cranial Ossification Patterns.—All adult as well as immature skulls were characterized by the presence of unpneumatized "windows," the size of which shows great individual variations. Two different patterns of cranial pneumati-

TABLE 1

Mean Size ($\overline{AB}$) (in mm^2) of the Bursa of Fabricius from July to November in North American Shorebirds

Species	July	August		September		October		November*
	16–31	1–15	16–31	1–15	16–30	1–15	16–31	16–30
Charadrius semipalmatus	45.2 (2)	49.0 (1)	37.5 (4)	30.1 (5)	27.6 (5)	20.1 (7)	16.6 (3)	27.5 (2)
Charadrius vociferus		86.6 (3)	76.5 (1)	80.0 (1)	88.0 (1)			
Pluvialis dominica				90.0 (1)		48.0 (2)		
Squatarola squatarola					136.0 (1)		130.7 (17)	42.0 (1)
Arenaria interpres			82.0 (4)	60.1 (6)		59.5 (2)		
Capella gallinago			111.0 (4)					
Actitis macularia		24.6 (3)						
Totanus melanoleucus			140.3 (6)	133.5 (18)			70.3 (4)	
Totanus flavipes		59.3 (3)	58.7 (17)	41.4 (18)			38.3 (3)	35.0 (2)
Calidris canutus			113.4 (4)	103.0 (3)				
Erolia melanotos			36.0 (1)				24.6 (3)	
Erolia fuscicollis							33.1 (10)	
Erolia minutilla		26.3 (28)	23.1 (24)	26.9 (8)				
Erolia alpina					30.0 (1)		44.0 (16)	
Limnodromus griseus		81.0 (1)	83.9 (20)	47.3 (4)				55.6 (5)
Ereunetes pusillus	16.0 (1)	23.5 (5)	28.7 (16)	22.6 (47)	14.9 (30)			20.9 (3)
Crocethia alba		25.0 (1)		44.5 (6)	36.1 (12)		40.6 (8)	

* Birds collected in Venezuela by the senior author in November 1968.
Note: Numbers in parentheses represent the sample size.

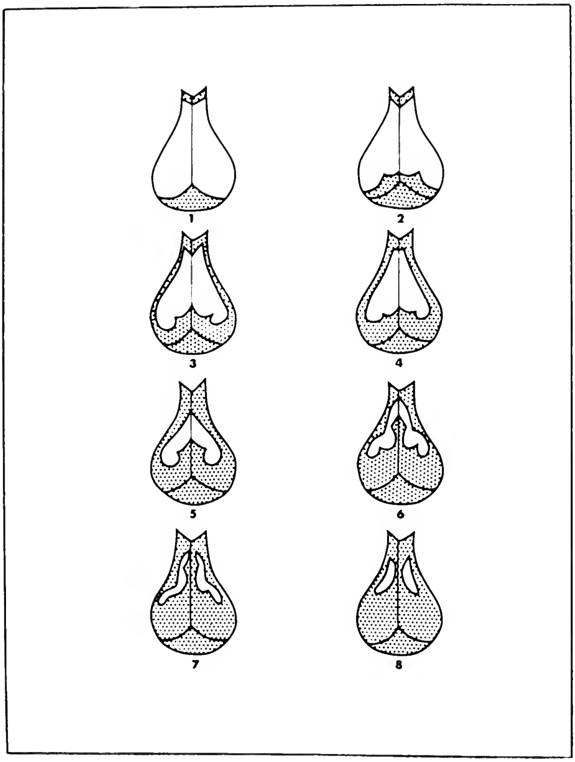

FIG. 1. Different stages of the type I of cranial pneumatization pattern in North American shorebirds. The clear areas represent the absence of pneumatization.

zation are found among the species of shorebirds belonging to the two families that were investigated (Charadriidae and Scolopacidae). The type I (Fig. 1) occurs in the majority of the species of both families (Table 2). It was divided into ten stages of degrees which do not clearly appear to be related to age but may be progressive. Four species had a different pattern that we are designating as type II (Fig. 2), in which we distinguished six consecutive stages. These species were the Common Snipe (*Capella gallinago*), Knot (*Calidris canutus*), Short-billed Dowitcher, and American Woodcock (*Philohela minor*).

Cranial pneumaticity cannot be used as an indication of the age of shorebirds. In fact, no clear correlation exists between the age of the birds and the extent to which their skulls are ossified (Tables 2 and 3); some immature (first year) birds have a skull roof as pneumatized as that of some adults.

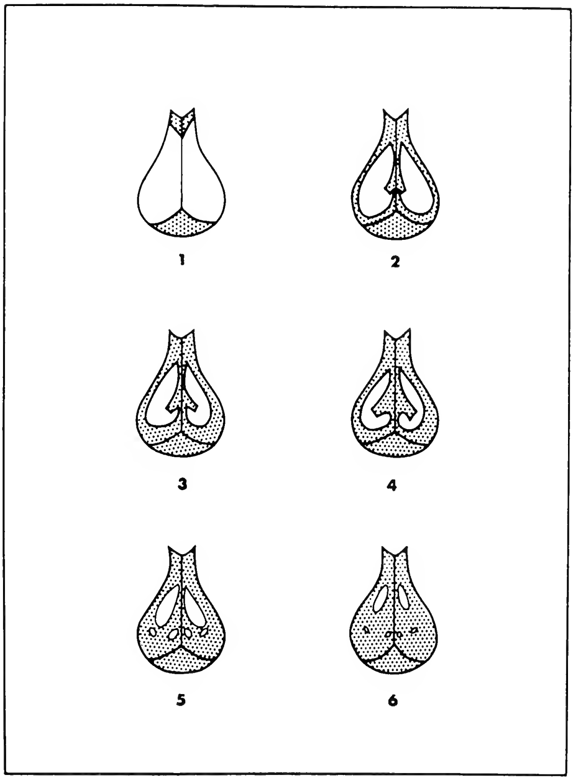

FIG. 2. Different stages of the type II of cranial pneumatization pattern in North American shorebirds. The clear areas represent the absence of pneumatization.

However, the different stages found in each type of cranial ossification are probably time progressive. Categories 7 and 8 in Table 2 are found almost exclusively in the adult age class, which suggests that there may be some age significance.

The extent of skull ossification attained in the shorebird species following the type I of cranial pneumatization (Table 2) varies between the genera and species. It seems obvious that the genera of Charadriidae attain a higher degree of cranial ossification than the genera of Scolopacidae. The stages or categories numbered 6, 7 and 8 are found almost exclusively in *Charadrius*, *Pluvialis*, *Squatarola*, and *Arenaria*, while the stages numbered 1 and 2 are found almost exclusively in the genera of Scolopacidae, especially in *Erolia*, *Ereunetes*, *Limosa*, and *Crocethia*. The two *Totanus* species seem to be intermediate between the two groups. It would be hazardous to draw conclusions about *Numenius*, *Actitis*, and *Tringa* because of the small sample sizes.

TABLE 2

VARIATION IN THE EXTENT OF SKULL OSSIFICATION IN SHOREBIRD SPECIES FOLLOWING THE TYPE I OF CRANIAL PNEUMATIZATION[a]

Species	Age Status[b]	Stages of cranial pneumatization							
		1	2	3	4	5	6	7	8
Charadrius semipalmatus	A		2.1(3)	24.4(34)	14.3(20)	24.4(34)	27.3(38)	6.4(9)	0.7(1)
	B			17.5(7)	17.5(7)	50.0(20)	15.0(6)		
Charadrius melodus	A						100.0(1)		
	B								
Charadrius vociferus	A					22.0(9)	44.0(18)	12.0(5)	22.0(9)
	B				25.0(2)	37.5(3)	37.5(3)		
Pluvialis dominica	A				100.0(1)				
	B			40.0(2)	40.0(2)	20.0(1)			
Squatarola squatarola	A			36.3(12)	48.4(16)	6.0(2)	6.0(2)	3.0(1)	
	B				44.4(8)	22.2(4)	16.6(3)	16.6(3)	
Arenaria interpres	A			20.3(13)	59.3(38)	17.7(11)	1.5(1)	1.5(1)	
	B			30.0(3)	50.0(5)	10.0(1)		10.0(1)	
Numenius phaeopus	A					100.0(2)			
	B								
Actitis macularia	A		16.6(1)	16.6(1)	33.3(2)	33.3(2)			
	B		25.0(1)	50.0(2)	25.0(1)				
Tringa solitaria	A			50.0(2)	50.0(2)				
	B								
Totanus melanoleucus	A			22.5(16)	57.7(41)	14.1(10)	4.2(3)	1.4(1)	
	B			16.0(4)	72.0(18)	12.0(3)			

TABLE 2 Continued

Species	Age Status[b]	Stages of cranial pneumatization							
		1	2	3	4	5	6	7	8
Totanus flavipes	A			61.5(24)	28.2(11)	7.7(3)	2.6(1)		
	B	3.1(1)		62.5(20)	25.0(8)	7.7(3)			
Erolia melanotos	A				100.0(1)				
	B				100.0(3)				
Erolia fuscicollis	A		4.0(4)	20.0(20)	61.0(61)	15.0(15)			
	B			11.1(1)	55.5(5)	33.3(3)			
Erolia minutilla	A	2.8(5)	14.8(26)	26.3(46)	36.6(64)	18.2(32)	0.5(1)	0.5(1)	
	B	7.0(4)	24.5(14)	24.5(14)	36.8(21)	7.0(4)			
Erolia alpina	A				100.0(2)				
	B	6.3(1)		25.0(4)	68.7(11)				
Ereunetes pusillus	A		26.6(66)	42.3(105)	29.1(72)	2.0(5)			
	B		47.3(45)	34.7(33)	17.9(17)				
Limosa haemastica	A	35.0(14)	5.0(2)	15.0(6)	32.5(13)	12.5(5)			
	B								
Crocethia alba	A			65.8(23)	17.1(6)	17.1(6)			
	B	20.0(2)	40.0(4)	10.0(1)	10.0(1)	20.0(2)			

[a] The variation is expressed in percentage (and number of examined skulls) falling in each stage of cranial pneumatization.
[b] A = Adult birds without bursa of Fabricius; B = First year birds with bursa of Fabricius.

TABLE 3

VARIATION IN THE EXTENT OF SKULL OSSIFICATION IN SHOREBIRD SPECIES FOLLOWING THE TYPE II OF CRANIAL PNEUMATIZATION[a]

Species	Age Status[b]	Stages of cranial pneumatization					
		1	2	3	4	5	6
Capella gallinago	A				33.3(1)	33.3(1)	33.3(1)
	B					100.0(4)	
Calidris canutus	A	2.3(1)	45.5(20)	25.0(11)	6.8(3)	20.5(9)	
	B	42.8(3)	28.6(2)		14.3(1)	14.3(1)	
Limnodromus griseus	A		31.8(8)	23.8(5)	28.5(6)	9.5(2)	
	B	0.7(1)	21.2(30)	29.1(41)	34.0(48)	12.1(7)	2.8(4)

[a] The variation is expressed in percentage (and number of examined skulls) falling in each stage of cranial pneumatization.
[b] A = Adult birds without bursa of Fabricius; B = First year birds with bursa of Fabricius.

A few workers have attempted to find the evolutionary and/or adaptive significance of the fully versus incompletely pneumatized skull vault in birds. Chapin (1949) mentioned that "the skull-roof of most woodpeckers is composed of single layer of bone, thicker and stiffer than that seen in the young of Passeres." He "considered this as a direct adaptation to their hammering and the use of the beak as a chisel." As far as Verheyen (1953) is concerned:

> "les os dermiques pneumatiques présentent . . . l'avantage de mieux résister aux vibrations et de mieux amortir les secousses que les lames épaisses qui manquent de souplesse. Aussi la plupart des espèces arboricoles (donc celles qui, au cours de leurs évolutions aériennes, peuvent se cogner la tête contre divers obstacles) possèdent-elles un crâne pneumatique tandis que celles qui vivent sur l'eau ou qui évitent les terrains boisés ont un dermatocrâne incomplètement pneumatisé."

On the other hand, according to Harrison (1958), the skull pneumaticity of birds is related to their mode of life, depending upon whether they are swimming or diving birds, hammering species, swift or slow fliers. Harrison (1964) believed that birds "showing diminished pneumatisation can be loosely classified as "swift fliers" and include such species as the gallinaceous birds (Galliformes) which accelerate rapidly, sandgrouse (Pteroclididae), most of the limicoline birds (Charadrii), and the swifts *Apus apus* and *A. affinis.* An exception among the Charadrii is the slow-flying Jack Snipe *Lymnocryptes minimus*, which develops complete pneumatization." The present results indicate that the Killdeer, American Woodcock, Common Snipe, Knot, and Short-billed Dowitcher are the shorebird species that show less unpneumatized skulls: some specimens of these species had almost fully ossified skulls, almost as pneumatized as that of the Jack Snipe. One fact is against Harrison's theory of swift versus slow fliers. The Common Snipe, while performing its aerial nuptial evolutions, dives to the ground from at least a hundred yards and then suddenly, before swooping down upon the ground, turns back abruptly and starts again the same aerobatics. The Killdeer, American Woodcock, Common Snipe, Knot and, even the Jack Snipe (Bent, 1927, 1929), also perform aerial evolutions at the time of breeding, although they are less spectacular. This means that these species are subjected to a heavy acceleration followed by an equal deceleration, and according to Harrison's theory, a much less fully ossified skull would be advantageous.

On the other hand, we would be tempted to make a comparison between the incompletely ossified skull of shorebirds and the ones of the woodpeckers. According to Harrison (1964), "the partial absence of skull pneumatization in woodpeckers suggests that this type of skull may be relatively heavier and therefore a more effective hammer." Shorebirds, excluding plovers and turnstones, feed by probing and making series of holes in sand and/or mud, so it may be that a heavier type of skull could possibly be of some advantage.

SUMMARY

The involution of the bursa of Fabricius begins in the autumn and is fully achieved by the end of the winter in all studied species. The presence of this organ may be used as an age criterion in shorebirds collected during fall migrations. The degree of cranial ossification does not permit distinguishing young birds from adults, since large "windows" persist generally in adult was well as in juvenile shorebirds. Two different patterns of cranial ossification are found in shorebirds; one applies to most species while the other one is found in the American Woodcock, Common Snipe, Knot, and Short-billed Dowitcher. The genera of Charadriidae attain a higher degree of cranial ossification than the genera of Scolopacidae. The authors also discuss the adaptive value of the skull pneumaticity.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bent, A. C. 1927. Life histories of North American shorebirds. U. S. Natl. Mus., Bull. 142.

Bent, A. C. 1929. Life histories of North American shorebirds. U. S. Natl. Mus., Bull. 146.

Chapin, J. P. 1949. Pneumatization of the skull in birds. Ibis, 91:691.

Davis, D. E. 1947. Size of bursa of Fabricius compared with ossification of skull and maturity of gonads. J. Wildl. Mgmt., 11:244–251.

Gower, I. O. 1939. The use of the bursa of Fabricius as an indication of age of game birds. Trans. N. Amer. Wildl. Conf., 4:426–430.

Grant, P. R. 1966. Retarded or arrested cranial development in a Mexican passerine, *Myiopagis viridicata* (Vieillot). Amer. Midl. Nat., 75:142–149.

Harrison, J. G. 1958. Skull pneumaticity in wildfowl in relation to their mode of life. The Wildfowl Trust Ninth Annual Report (1956–1957):193–196.

Harrison, J. G. 1964. Pneumatisation of bone. *In* Thomson, A. L. (Ed.), New dictionary of birds. McGraw Hill, New York, pp 649–650.

Hochbaum, H. A. 1942. Sex and age determination of waterfowl by cloacal examination. Trans. N. Amer. Wildl. Conf., 7:299–307.

Kirkpatrick, C. W. 1944. The bursa of Fabricius in Ring-necked Pheasants. J. Wildl. Mgmt., 8:118–129.

Linduska, J. P. 1943. A gross study of the bursa of Fabricius and cock spurs as age indicators in the Ring-necked Pheasant. Auk, 60:426–437.

McNeil, R., and A. Martinez. 1967. Retarded or arrested cranial development in *Myiornis ecaudatus.* Wilson Bull., 79:343–344.

Miller, A. H. 1946. A method of determining the age of live passerine birds. Bird-Banding, 17:33–35.

Nero, R. W. 1951. Pattern and rate of cranial "ossification" in the House Sparrow. Wilson Bull., 63:84–88.

Niethammer, G. 1968. Pneumatization of the cranium as a criterion of age. Ibis, 110: 106.

PAYNE, R. B. 1969. Unpneumatized skull condition in adult Scaly-fronted Weavers, *Sporopipes frontalis.* Auk, 86:570.

SERVENTY, D. L., C. A. NICHOLLS, AND D. S. FARNER. 1967. Pneumatization of the cranium of the Zebra Finch, *Taeniopygia castanotis.* Ibis, 109:570–578.

VERHEYEN, R. 1953. Contribution à l'étude de la structure pneumatique du crâne chez les oiseaux. Bull. Inst. Roy. Sci. Nat. Belg., 29:1–24.

WHITE, C. M. N. 1948. Skull ossification in certain Passeriformes. Ibis, 90:329.

DÉPARTEMENT DES SCIENCES BIOLOGIQUES, UNIVERSITÉ DE MONTRÉAL, C.P. 6128, MONTRÉAL 101, QUÉBEC, CANADA. 12 OCTOBER 1971.

REQUEST FOR INFORMATION: SANDERLING

For the past two years, the Long Point Bird Observatory has undertaken a study on the relationship between fat deposition and fall migration in the Sanderling. In conjunction with this study, a large number of birds have been color-marked and sightings of these marked birds away from Long Point have indicated that most of the birds fly directly from the study area to the East Coast.

During 1972, the Observatory hopes to individually color-mark and color-code several hundred Sanderling in order to further investigate this phenomenon.

Birds will be feather-dyed on the breast and abdomen with one of four colors: red, yellow, green, or white (no color); according to the percentage of the bird's total body weight attributable to fat.

The birds will be wing-tagged on *each* wing with semi-permanent wing tags of the following colors: black, blue, brown, green, red, orange, yellow, and white. The wing-tagging will individually identify each bird.

Birds banded on the right leg will be adults and those banded on the left leg will be immatures.

The Observatory would be pleased if anyone sighting these birds would report the following information to us: Date of sighting; Location (including nearest city or town); Color of feather-dye on the breast and abdomen; Color of the wing tag on the right wing; Color of the wing tag on the left wing; Leg on which the bird is banded.

Co-operators will receive a short note explaining the project's application to the preservation of the Long Point peninsula in a natural state and the date on which the bird was last seen on Long Point. Reports of marked birds should be sent to: Long Point Bird Observatory, Long Point, Ontario, CANADA.

GENERAL NOTES

Spectacular hawk flight at Cape May Point, New Jersey on 16 October 1970.—After the passage of a moderate cold front through Cape May on 4, 5, and 6 October, 1970; the center of high pressure responsible for it lingered off the coast till 15 October. This caused for nine days a flow of air from a generally southern and eastern direction whose western boundary extended along a stationary front from the Gulf near New Orleans in a northeastern direction west of the Alleghenies and along the St. Lawrence to its Gulf. It is possible that these continuous southerly winds acted as a temporary brake on the fall bird migration. A high pressure center moving south from Canada centered about Kansas on 14 October. Its northwestern winds extended to the Alleghenies on a front that reached from the St. Lawrence valley almost to the Gulf of Mexico. As it moved eastward this wide swath of strong northwestern wind swept large numbers of migrating birds toward the coast. About 15:00 on 15 October, the arrival of this front in the Cape May area was heralded by thunderstorms and heavy rain which continued throughout the night until about 09:00 the next morning, tapering off in intermittent showers about 11:00. The northwest wind, which registered 25 to 30 miles per hour with occasional gusts up to 50 on a local wind gauge, continued throughout the day.

About 08:30 I was alerted by a neighbor, J. d'Arcy Northwood, to the fact that despite the driving rain many hawks were on the wing. So I made my way about a quarter-mile to the Cape May Point State Park, where I met Alfred Nicholson at 09:00. We took up a station about 100 yards east of the lighthouse, which gave us an unobstructed view to the north and east over the marshes, to the south over the beach and the ocean, and an open area to the west for 100 yards with low trees and small buildings in the background. Flying in a westerly direction as they came down the coast in a wide swath, the hawks veered toward the north as they approached the tip of the Cape May peninsula.

Our first problem was to come up with a means of approximating the number of Sparrow Hawks (*Falco sparverius*) rapidly passing by. We finally decided that using the lighthouse as a reference point, as though it were 12 on a watch lying horizontally in front of us, we would together scan the area using our binoculars in a clockwise direction from 12 through 1, 2 and 3 back to 12, the lighthouse. After several trials we arrived at an estimate of 100 birds seen in one sweep around. We then calculated that it took about one minute for the 100 in sight at a given moment to be replaced by a succeeding 100. We checked this method of counting several times in the course of the morning and arrived at approximately the same figures. The flight continued with undiminished intensity for three hours giving us about 6000 Sparrow Hawks per hour until noon. Then the numbers dropped to about 65 per minute making it about 4000 in the hour from 12:00 to 13:00. Numbers continued to drop as we recorded 2000 hawks from 13:00 to 14:00, 700 from 14:00 to 15:00, 100 from 15:00 to 16:00, and 75 from 16:00 to 17:00. The total for the day was about 25,000 Sparrow Hawks.

A second problem was to assure ourselves that birds were not circling after they left the Point and passing us a second time. To check on this Alfred Nicholson went about noon to the Higbee Beach area two miles north of Cape May Point on the Delaware Bay. He found that the flight continued up the bay shore with all birds flying northward although in lesser numbers than at the Point. An hour or so later to check the intervening area I went north on the Bay Shore Road for about two miles. This road parallels the bay shore about a mile inland. Quite a few birds were seen to the west of the road and only 10 on its east side. All were flying toward the north. This made it evident that the flight was continuous with no repetitions.

So engrossed were we with the numbers of Sparrow Hawks that the recording of only three Pigeon Hawks (*F. columbarius*) suggests that some of this species were overlooked. Other hawks recorded were: Sharp-shinned (*Accipiter striatus*) 613, Cooper's (*A. cooperii*) 6, Red-tailed (*Buteo jamaicensis*) 7, Red-shouldered (*B. lineatus*) 4, Marsh (*Circus cyaneus*) 82, Osprey (*Pandion haliaetus*) 14, and Peregrine (*F. peregrinus*) 4. Our total for the day was approximately 25,600. This estimate is conservative particularly in view of the fact that birds flying before 09:00 are not included.

We also noted four Turkey Vultures (*Cathartes aura*), 15 flocks of Canada Geese (*Branta canadensis*) with 50 to 250 in each flock, several flocks of Robins (*Turdus migratorius*), one of about a thousand birds in such a compact mass that it seemed to bounce along in a gusty wind like a ball, a flock of 13 Great Blue Herons (*Ardea herodius*), and overwhelming numbers of small passerines mostly sparrows and warblers.—ERNEST A. CHOATE, *Cape May Point, New Jersey 08212, 20 December 1971.*

Osprey carrying a mammal.—During our investigation of the Peace River near its confluence with Branch Creek in Hardee County, Florida, on 6 January 1972 at 14:00, we were surprised to observe an Osprey (*Pandion haliaetus*) unmistakenly carrying a mammal in its talons. The mammal was approximately the size of a squirrel or small rabbit. The bird flew over at a height of 30 feet about 75–100 feet downstream from our position. It paralleled the river for a short distance before disappearing into the bordering woods.

Ospreys are known to be almost exclusively piscivorous, but occasionally are reported to take crustaceans, amphibians, and birds (Brown and Amadon, Eagles, hawks and falcons of the World, Vol. 1, p. 198, 1968). Bent (Life histories of North American birds of prey, U.S. Natl. Mus. Bull., 167:368–369, 1938) mentions that Ospreys have been known to take beetles and reptiles on rare occasions. Sindelar and Schluter (Wilson Bull., 80:103, 1968) reported an Osprey carrying what was believed to be a Cardinal (*Richmondena cardinalis*).

We assume this occurrence occurred as a direct result of a large phosphate slime spill entering the Peace River from a detention pond that burst on 3 December 1971. Over 90 per cent (Florida Game and Fresh Water Fish Commission sample estimate) of the resident fish were killed by the choking slime. The spill may have forced the Osprey to turn to other prey items for sustenance—in this case the mammal.—WILLIAM W. TAIT, H. MALCOLM JOHNSON, AND WILLIAM D. COURSER, *Southwest Florida Water Management District, Post Office Box 457, Brooksville, Florida 33512, 28 January 1972.*

The migration of the Buff-breasted Sandpiper through Surinam.—The migration of the Buff-breasted Sandpiper (*Tryngites subruficollis*) through continental South America, to and from its winterquarters in Paraguay, Uruguay, and Argentina is but poorly known. According to my cooperator Mr. Th. Renssen, who lived for some time at the sugar estate Marienburg (Commewijne Dist.), Surinam and whom I thank for sending me the specimens mentioned below, it is a regular but not numerous migrant both in the northern fall and spring. It favors open ground with a very low vegetation but especially recently harvested and burnt over sugar cane fields. This same habitat is frequented by the American Golden Plover (*Pluvialis dominica*) and the Upland Plover (*Bartramia longicauda*) and the Buff-breasted Sandpiper is often in company with these two species. The earliest date during the fall migration is 15 August 1969 (sight) and birds were collected (all in the Leiden Museum) on 20 September 1966 (male, weight

50.5 g), 17 October 1963 (male, 43 g) the latest record being 13 November 1968 (Male, 60.5 g). In the northern spring there is a sight record on 15 March 1969, the latest records being two birds collected on 12 May (female, 53 g) and 13 May 1967 (female, 69 g very fat). It is clear from these records that both fall and spring migration is extended over long periods and that the birds seem to be in no hurry.

The Buff-breasted Sandpiper is not yet known from neighboring French Guiana (Berlepsch, Nov. Zool., 15:251, 1909) and there is only a single sight record from Guyana on 20 April 1965 (Snyder, The birds of Guyana, 1966, p. 96).—F. HAVERSCHMIDT, *16 Wolfskuilstraat, Ommen, Holland, 7 February 1972.*

Congenital foot abnormality in the Ring-billed Gull.—During ecological and behavioral studies of Ring-billed Gulls (*Larus delawarensis*) on Granite Island, Ontario (48° 43′N, 88° 27′W), we leg-banded 359 newly-hatched chicks. On 10 June 1971 we found a one-day-old Ringbill chick with a foot abnormality known as polydactyly (Fig. 1). An X-ray photograph (Fig. 2) indicates the extra foot elements on each leg originated distally from the median anterior portion of the tibiotarsus. In that the phalangeal portion of the avian foot normally develops from the distal aspect of the tarsometatarsus, it is conceivable that, with secondary induction, phalangeal elements may arise from the metatarsal elements of the tibiotarsus. Although the abnormality reported here is not bilaterally symmetrical, the middle toe is more fully developed on both sides than the inner or outer toes. No hallux is apparent on either extra foot. The bird did not seem to be handicapped by the abnormality at the time of capture.

Relative to the amount of past and current research using larids, the paucity of reports of congenital abnormalities is somewhat surprising (see Austin, Auk, 86:352, 1969 and Smith and Diem, Auk, 88:435, 1971). It may be that non-passerines are not able to adapt their behavior to abnormalities as well as passerines and thus are eliminated rapidly. This was noted by Pomeroy (Brit. Birds, 55:49–72, 1962) referring to bill abnormalities.

Bellairs (Skeleton. *In* A new dictionary of birds, A. L. Thomson, Ed. Nelson & Sons, London, 1964) stated that inherited skeletal abnormalities of many types occur in birds. However, only the "fowl" have been studied extensively, presumably because of their economic importance. Napier (Wildfowl Trust Ann. Rept., 14:170–171, 1963) discussed foot malformations in Mallards (*Anas platyrhynchos*) and noted polydactyly can occur from genetically determined increases in mesenchymal plates which later give rise to the foot. Little information is available on effects of secondary inducers which may affect early embryonic development in wild birds. Kear (Wildfowl Trust Ann. Rept., 15:99, 1964) summarized results of studies of congenital malformations in wildfowl bred at Slimbridge, England. She reported an incidence (0.56 per cent) of abnormalities in 1961 which did not occur in the subsequent two seasons and suggested the effects of agricultural chemicals might be investigated.

We do not infer the malformation reported here is necessarily purely genetic in origin. Recently Hays and Risebrough (Auk, 89:19–35, 1972) recorded incidences of 0.1 per cent abnormalities in 1969 and 1.3 per cent in 1970 from a sample of over 4,000 young Common Terns (*Sterna hirundo*) and more than 1,600 young Roseate Terns (*S. dougallii*) at Great Gull Island, New York. The abnormalities reported by Hays and Risebrough (ibid.) resemble those produced experimentally in domestic chickens by the chlorinated dibenzo-p-dioxins and some polychlorinated biphenyls.

In view of a possible important relationship between chemical residues in birds, and congenital abnormalities we ask for increased monitoring and communication of inci-

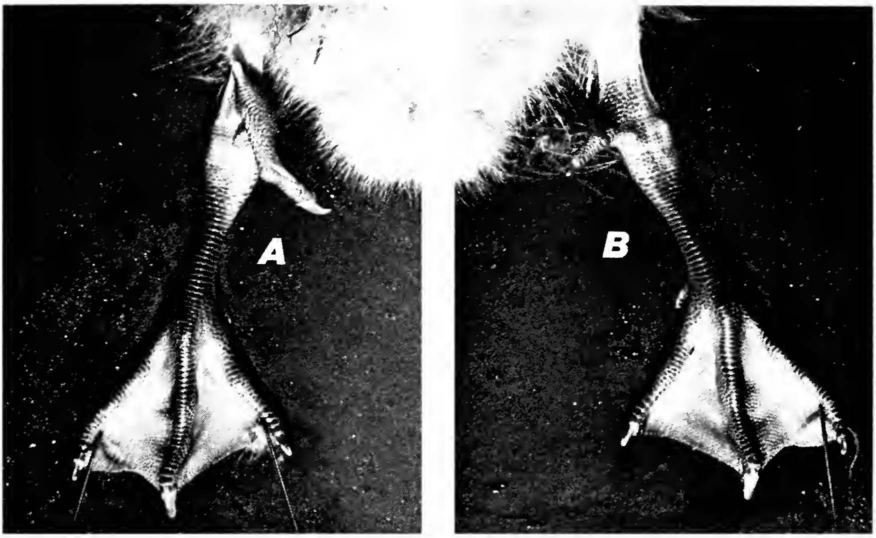

FIG. 1. Extra digits on right (A) and left (B) of one-day-old Ring-billed Gull.

FIG. 2. X-ray showing polydactyly on both feet of one-day-old Ring-billed Gull.

dences of these phenomena.—John P. Ryder and David J. Chamberlain, *Department of Biology, Lakehead University, Thunder Bay "P," Ontario, 4 October 1971.*

Swallow-like behavior in the Rusty-margined Flycatcher, *Myiozetetes cayanensis*, in Colombia.—On 20 November 1970, while collecting birds near Mitú, Vaupes, Colombia, I noticed a curious swallow-like behavior in a pair of Rusty-margined Flycatchers (*Myiozetetes cayanensis*). During two rainstorms, the flycatchers flew low over the surface of the water (a river), in company with more than a dozen swallows engaged in the same type of behavior. Such behavior is of course typical of feeding swallows, but I find no published description of tyrannids behaving in this manner.

The flycatchers flew like this throughout both rainstorms, each of which lasted approximately fifteen minutes. They sustained glides for two or three seconds, then regained their speed with strong and rapid wing beats before gliding again. At least once every five minutes they rested for about a minute on a branch at the edge of the river, but did not preen while perched at this time. At the termination of each rainstorm, they resumed feeding in a fashion typical of this species.

The pair did not appear to exhibit extraordinary powers of flight, as flycatchers are capable of gliding up to several seconds during routine movements to new perches. Nor did they appear to endure exceptionally long periods of flight.

The purpose of this behavior was not clear, and it could possibly represent bathing. I could not ascertain if the flycatchers obtained food while flying in this fashion, but this possibility cannot be ruled out, as the family exhibits considerable versatility with regard to feeding behavior. The Great Kiskadee (*Pitangus sulphuratus*) is reported to take small fish by "diving just like a kingfisher" (Haverschmidt, Birds of Surinam, 1968); *Myiozetetes similis*, in Central America, captures aquatic animals by wading out into shallow water, and picks up food by flying down to the surface of the water (Skutch, Pacific Coast Avifauna, 34:428, 1960).

I was unable to remain in the Mitú vicinity for more than one day, so I could not determine if swallow-like behavior was typical of this pair of Rusty-margined Flycatchers. Professor Jose-Ignacio Borrero, at the Universidad del Valle in Cali, had not observed comparable behavior in this or any other flycatcher during his extensive studies of Colombian birds.

One of the specimens is now in the Zoological Collections at Texas Tech University. The study that made this observation possible was supported in part by the International Center for Medical Research and Training, Cali, Colombia.—Michael Kent Rylander, *Department of Biology, Texas Tech University, Lubbock, Texas 79409, 12 February 1972.*

The recent history of Bachman's Warbler.—The recent history of Bachman's Warbler (*Vermivora bachmanii*) can best be understood against a background of its earlier history (1880–1910). For this purpose, it should suffice to mention the records of only a few observers in Florida—that is, south of the species' known breeding range, but on its chief migration route. In the spring migration, Brewster and Chapman (Brewster, 1891) encountered large, but unspecified, numbers in March, 1890. Of these, 46 specimens were collected! In the same general area, Arthur T. Wayne (1893) collected 50 specimens in 1892 and 1893, but also made no reference to the *total* number seen. Farther north, he collected eight specimens on the Wacissa River in 1894 (Wayne, 1895).

In the fall migration, the best documented records were made at Key West, where J. W. Atkins (Scott, 1887, 1888, 1890*a*) encountered the species in July and August, 1887 to 1889, collecting at least 58 specimens and seeing a total of perhaps 150 to 200! He mentioned a peak of "25 or 30" on 8 August 1889. Oddly, there seems to be no mention of the bird's occurrence there in spring, although two collected on the Dry Tortugas in 1890 were about 65 miles farther west (Scott, 1890*b*).

Although the numbers seen on the species' breeding grounds during these early years were hardly comparable, it seems likely that the chief migration pathway was relatively narrow, thus concentrating the birds much more, and that Florida received more ornithological attention than other states in those days. Even so, Embody (1907) found at least 22 singing males in Kentucky in 1906, and collected five of them.

During the present century, numbers apparently dwindled steadily. By the time Howell's "Birds of Alabama" appeared (1928) the species was considered "one of the rarest and least known of the warblers." He cited only nine records at widely separated localities, plus one nest in Bear Swamp. Other states experiencing declines in the number of records during this period (1910–1930) were Louisiana, Georgia, and South Carolina, and it seems obvious that there was indeed a sharp decrease in its total population.

During the time I studied birds in north Alabama (1930's and early 1940's) the species still persisted in small numbers where the habitat was suitable. It may be pertinent to itemize these records here, though some have been published before (Wilson Bull., 50: 36–41, 1938).

1. Irondale, a presumed migrant seen and heard singing on 9 and 13 April, 1936 (with Harry Wheeler on the 13th).
2. Moody Swamp, Tuscaloosa, 9 April 1937, a singing male; 1 May 1937, pair and nest containing three young "scarcely a week old"; with Harry Wheeler. None could be found there on 29 May, when my journal indicated that "a lot of timber had been cut."
3. Bear Swamp (Autauga Co.), 8 May 1937, singing male; with Harry Wheeler, et al. None found on return trip, 1–5 June.
4. Moody Swamp, 25 March 1939, two singing males.
5. Moody Swamp, 27 March 1939, two singing males and one female.
6. Moody Swamp, 8 April 1939, "several"; one male displaying on or about this date, but female not seen. (Trips to swamp interrupted by illness, *c.* April 14–20).
7. Moody Swamp, 22 April 1939, "one" (sex?).

Thus there were no records after 22 April 1939, in Moody Swamp, or 1 May 1937, in that swamp, or 8 May 1937, in Bear Swamp. Early nesting in this species is presumably followed by early diminution of song, early molt, and early fall migration.

By 1950 Bachman's Warbler had become truly rare, as a search for *published* records since that time reveals. Most of these records appeared in various issues of *Audubon Field Notes*, and most records involved a single male. The breakdown of numbers of individuals by years follows: 1950, 2; 1951, 3; 1952, 3; 1953, 0; 1954, 3; 1955, 2; 1956 and '57, 0; 1958, 3; 1959, 3; 1960, 6; 1961, 2; 1962, 1; 1963, 1; 1964 and 65, 0; 1966, 1; no record since 1966. It is interesting to note that nearly all of these records were made within, or at least not south of, the bird's geographic breeding limits and involved singing males. It is under just such conditions that discovery would be enhanced. In other words, the *hundreds* formerly seen on migration in Florida stand in striking contrast to the *two* reported there since 1949.

It is not necessary to argue for the validity of all of the 30 sight records (no specimens, one photograph) over the past two decades, or to hold that all unpublished records should be summarily dismissed. The point is simply that the number of records—published or unpublished—is roughly proportional to the total population of the species, thus the picture is a bleak one by any standard. With the full realization of the species' previous ups and downs, and the consequent risk of being wrong, I nevertheless believe Bachman's Warbler to be on the verge of extinction.

At least one experienced ornithologist around 1960 indicated to me a belief that the bird was probably being overlooked among the hordes of other small, migrating land birds. However, note that Brewster and Chapman made *direct comparisons* of its degree of abundance with that of other species. Although they ranked it less common than the Parula, Myrtle, Black-and-white, and Yellow-throated Warblers, the Blue-gray Gnatcatcher, and the Ruby-crowned Kinglet, it *outnumbered* such relatively common species as the Orange-crowned Warbler, and the Red-eyed, Solitary, and Yellow-throated Vireos. Thus, they specified, it ranked seventh in abundance among small woodland transients along the lower Suwannee River in March.

My recent attempts to find Bachman's Warbler in two swamps where it formerly nested have proven futile in each case. I looked for it in early April of 1964 and 1966 in Moody Swamp, near Tuscaloosa, Alabama, where it was last known to nest, and Dan Holliman wrote me that he had spent a week in this swamp without success a few years earlier. In Bear Swamp, northwest of Montgomery, which is the site of the *other* Alabama nest, four of us failed to find it in early April, 1970 and 1972. In other recent years I have searched unsuccessfully in two other swamps slightly south of its known breeding range.

If Bachman's Warbler is, indeed, on the verge of extinction, what causes may be assigned to its sharp decrease? The answers are not easy to find. Although some have maintained that the draining of swamps is to blame—and it may be in some cases—the two swamps I revisited in the last ten years appeared much the same as they did when the bird was there 30 years ago. If they have somehow been made less appealing to the bird, the difference is too subtle for me to see. Thinking that there may have been widespread habitat destruction on its wintering grounds (Cuba and the Isle of Pines), I contacted Senor Orlando Garrido about the bird's status in Cuba. He concurred that it was becoming very rare, the last specimens having been taken in 1942, with sight records of three females as recently as 1963 and '64. However, he emphasized that there had been no important habitat destruction. In the case of the Isle of Pines, Dr. Albert Schwartz made the same point.

The possibility of over-collecting in the early years has also been mentioned. Some fragmentary data, along with a bit of reasoning, should exonerate these collectors. The largest number collected in one day by Brewster and Chapman on the Suwannee River in 1893 was 10 on 23 March on which date they saw "upwards of 30"; in other words, less than one-third of the number seen along one small part of the river on a single day were actually collected. Their records, however, indicated that the bird occurred at all points along the river except near the Gulf over a period of at least two weeks. How many additional thousands may have been in other parts of its migration route during that period, if not still on its wintering grounds or already on its breeding grounds? How long should it take such a population, for that matter, to compensate for the entire number of merely 46 specimens these observers collected that year? Data given by Atkins at Key West in 1888 are similar in that few were collected on the days when the largest numbers were estimated: July 26, 4 out of "2 dozen"; August 6, 5 out of "2 dozen"; August 8, 5 out of 17. In summary, only 14 out of about 40 were collected. Key West, like the lower Suwannee River, evidently was only a minute part of the bird's total migration route. Furthermore, I do not know of a single specimen collected in the United

States since 1940, when I had the impression that the bird was in no danger of extinction. Only three specimens have been collected in Cuba, all in 1942 (Orlando Y. Garrido, pers. comm.).

Taking a parallel case, Swainson's Warbler is also a swamp-inhabiting bird, and its population today may be less than that of Bachman's Warbler during the 1880's and 1890's. Yet I venture to state that if all licensed collectors living today set out to collect every Swainson's Warbler they saw, they would scarcely make a dent in the total population.

Thus, despite the fact that man has played the major role in the decline of so many organisms, I doubt that he is guilty in this instance. For some reason, Bachman's Warbler seems to be poorly equipped for survival even under the conditions it demands and is not sufficiently adaptable to survive under different conditions. In the long process of the evolution, flourishing, and eventual extinction of species, perhaps this is one whose time has come. In this pessimistic outlook, however, I sincerely hope that I may be proven wrong.

LITERATURE CITED

Brewster, W. 1891. Notes on Bachman's Warbler (*Helminthophila bachmani*). Auk, 8:149–157.

Embody, G. C. 1907. Bachman's Warbler breeding in Logan County, Kentucky. Auk, 24:41–42.

Scott, W. E. D. 1887. Another Bachman's Warbler in Florida. Auk, 4:348.

Scott, W. E. D. 1888. Bachman's Warbler (*Helminthophila bachmani*) at Key West, Florida, in July and August. Auk, 5:428–430.

Scott, W. E. D. 1890*a*. A summary of observations on the birds of the Gulf coast of Florida. Auk, 7:14–22; 114–120.

Scott, W. E. D. 1890*b*. On birds observed at the Dry Tortugas, Florida, during parts of March and April, 1890. Auk, 7:301–314.

Wayne, A. T. 1893. Additional notes on the birds of the Suwannee River. Auk, 10: 336–338.

Wayne, A. T. 1895. Notes on the birds of the Wacissa and Aucilla River regions of Florida. Auk, 12:362–367.

Henry M. Stevenson, *Department of Biological Science, Florida State University, Tallahassee, Florida 32306, 1 January 1972.*

Winter habitat of Kirtland's Warbler.—The alarming decline of Kirtland's Warblers (*Dendroica kirtlandii*) on the nesting ground in northern Lower Michigan (Mayfield, Auk, 89:263–268, 1972) has stimulated interest in its survival problems on the wintering ground in the Bahama Islands. As an aid to those who may be looking for the bird in the Bahamas, I am bringing together what we know about the winter habitat.

Observers have found Kirtland's Warbler on several of the major islands of the Bahamas from the northernmost to the southernmost, but no one has seen it in winter on the nearby mainland of Florida nor on the nearby islands of Cuba and Hispaniola. The greatest numbers of reports have come from those islands visited by the greatest numbers of bird students. On New Providence near Nassau collectors took 45 specimens between 1884 and 1915; and on Grand Bahama visiting groups of the Florida Audubon Society and local residents have found it every year from 1959 through the 1960s.

Yet the bird has proved difficult to find by those seeking it. James Bond spent about 100 days in these islands, mainly in the 1930s, and saw the Kirtland's Warbler only once. Josselyn Van Tyne and I spent 59 man-days on New Providence and Eleuthera searching for it in January and February of 1949, and I have made a number of brief trips to Great Abaco, Grand Bahama, and Inagua since that time without ever finding the bird. John Emlen spent about 500 hours systematically combing measured tracts on Grand Bahama and Andros, with brief visits to other islands from 1968 to 1971, without seeing it. His time in the field exceeded 200 days. Others have had similar experiences for shorter periods.

Unless the birds are concentrated in some locality or in some unusual habitat not yet discovered, the prospect of finding them is discouraging indeed. The 400 Kirtland's Warblers in existence in 1972 are to be sought on 4,466 square miles of the Bahamas distributed among 15 islands larger than 10 square miles each, 700 smaller cays, and 2,400 "rocks."

The person with most experience with Kirtland's Warbler on its wintering ground was C. J. Maynard, who collected 38 specimens between 1884 and 1915 on New Providence and Eleuthera. Writing in 1896 about his experience in 1884 when he collected 26 specimens, he described the behavior and habitat of these birds as follows: ". . . shy birds of solitary habits, for never in any case did I find two together. They inhabit the low scrub, preferring that which is only three or four feet high, but retire at night to roost in the higher, more dense shrubbery near the spots which they frequent during the day. Those taken were, with one or two exceptions, found in an exceedingly limited area, within a mile or two of the city [Nassau], and always in old fields grown up to low shrubbery . . . the only note that they uttered was a harsh chirp, with which they greeted me when alarmed at my approach. When one was not secured at first sight, it generally retreated into the bushes and silently disappeared. The thick and tangled character of the scrub rendered any quiet or swift pursuit impossible, thus a retreating bird was never seen again that day, and a number escaped this way . . . twice at least as I was making my way through the thickets in search of the Greater Yellow-throat . . . birds appeared from out of the thicket within a yard of my path, remained a few seconds then darted off into the scrub." (Birds of eastern North America, rev. ed.:594).

C. B. Cory, who collected the first winter specimen (on Andros) on 9 January 1879, said it behaved like a Myrtle Warbler (*Dendroica coronata*) and seemed to prefer thick brush (Bull. Nuttall Ornithol. Club, 4:118, 1879). The last winter specimen also was taken in brush, on Watling Island (San Salvador) on 27 December 1965, ". . . at the edge of an extensive area of scrub forest or low coppice with canopy about 8 to 10 feet above the ground, i.e., composed of what could be called small trees . . . Palms were scarce there." (Dennis Paulson, in litt., 22 October 1966).

All modern observers mention the presence of scrub: on Inagua between 1935 and 1940 "in scrub near the sea" (James Bond, in litt., 22 March 1946); on Eleuthera in "scrub growth" (Margaret Hundley, Auk, 84:426, 1967); on Paradise Island, called Hog Island before 1962, across the harbor from Nassau "in low broad-leafed scrub . . . along a path through a plantation of Australian pine, *Casuarina equisetifolia*" (David Challinor, Jr., Wilson Bull., 74:290, 1962), and in "woods . . . fairly open, consisting of tall pines [*Casuarina*?] with a considerable (but not dense) undergrowth of palmettos and unidentified broad-leaved shrubs rather than in the pines." (George Wallace, Jack-Pine Warbler, 46:7, 1968).

The first of the modern series of records on Grand Bahama came in November, 1959, "in scrub and *Casuarina* growth near West End airport (Dorothy Blanchard, Jack-Pine

Warbler, 43:39–42, 1956). Charles F. Walker saw the bird at West End on 28 December 1969. He detected it first on the lawn of the hotel, watched it pursue a moth to the concrete floor of the porch, fly to the top of a small shrub in the lawn, and finally vanish at low level in a dense row of broad-leaved shrubs. Although he searched the area carefully for the next several days, he did not find the bird again (30 December 1971). However, the "usual place" for finding the Kirtland's Warbler on Grand Bahama has been an open stand of large ". . . Caribbean pine (*Pinus caribeae*) with an understory of poisonwood (*Metopium toxiferum*) and palmetto (*Serenoa repens*)." (Hundley, op. cit.). Here the Kirtland's Warblers gleaned food from the trunks and branches like Black-and-white Warblers (*Mniotilta varia*). In April, 1969, Paul Fluck mist-netted and banded a Kirtland's Warbler "in fairly open, young Caribbean pine about 25 feet high, with a shrubby understory" (John T. Emlen, in litt., 14 December 1971).

From all of these reports, old and modern, I conclude that the Kirtland's Warbler usually inhabits low broad-leaved scrub in the Bahamas. Areas that have been cleared and then allowed to grow back but have not yet reached their maximum height and density may hold particular promise. I think it is significant that no one has reported them in the high scrub or coppice, trees 15 feet or more in height, that abounds in these islands. The presence of pines where the warblers have occurred repeatedly on Grand Bahama I think may be incidental or of secondary importance. By shading and by encouraging ground fires the pine may hold back the brushy understory to the desired state of sparseness and low height. All of the large pines I have examined show fire scars at the base. Only the northernmost islands of the Bahamas have pines, and even on these the Kirtland's Warbler has occurred frequently on portions that have no pines. The several mentions of Australian pine I think is a consequence of the widespread planting of this exotic in resort areas visited by tourists; that is, the tree happens to be where the visitors are.

Unfortunately for the searcher, low broad-leaved scrub is abundant on all the islands of the Bahamas.—Harold F. Mayfield, *9235 River Road, Waterville, Ohio 43566, 14 January 1972.*

Stability of a population of male Red-winged Blackbirds.—An important aspect in the survival of a species is its ability to recover rapidly from a low population resulting from some catastrophe. The history of a population of Red-winged Blackbirds (*Agelaius phoeniceus*) for 8 years illustrates a method of rapid increase after a decline occasioned by a series of drought years. During the drought the number of nesting females declined drastically but the number of males holding territories remained essentially constant. This arrangement permitted rapid increase once conditions became more favorable because the males were ready each year on their territories for the available females.

The Redwings of Millbrook Marsh near State College, Pennsylvania were studied by several persons beginning in 1960. The details of the vegetation changes resulting from a drought are recorded by Brenner (Amer. Midl. Naturalist, 76:201–210, 1966). His data show that monthly precipitation in 1960, 1962, and 1963 was about 20 per cent below normal. During these years a rainfall deficit of 26 inches occurred, mostly during the growing season. During this drought the marsh changed from vegetation, measured in biomass, composed of cattails (48.3 per cent) and sedges (39.3 per cent) to few cattails (4.6 per cent) and many sedges (89.5 per cent). For five years the territories of the breeding males were mapped in considerable detail (Brenner, op. cit.). For 1965–67 Peek mapped the territories. In these latter years, due to some changes in drainage of the stream, an adjacent area became available for Redwings and the total population of the marsh increased. However, the figures cited here refer only to the area inhabited originally in 1960.

The number of territorial males beginning in 1960 are: 21, 17, 19, 17, 18, 21, 20, and 19. Data for the number of females for all years except 1965 are: 42, 35, 19, 7, 17, ?, 28, and 30. It will be noted that although the number of males remained stable the number of females dropped as low as seven at the time of maximum drought and then returned to a normal level. Thus, while the total population changed rather drastically and the production of young decreased during the drought, nevertheless, the number of males remained constant. These males were ready for maximum breeding as soon as the drought ended and the marsh again became suitable for nesting. It would appear that the system of stability of males allows a population to recover rapidly from a low level.

Brown (Wilson Bull., 81:293–329, 1969) commented on the report by Brenner (op. cit.) from a somewhat different viewpoint. He noted that the territorial behavior stabilized the male population and buffered the breeding density.—David E. Davis, *North Carolina State University, Raleigh, North Carolina 27607* and Frank Peek, *University of Minnesota, St. Paul, Minnesota, 10 January 1972.*

NEW LIFE MEMBER

Dr. M. Philip Kahl of Naples, Florida is a new Life Member of the Wilson Ornithological Society. Dr. Kahl, who holds degrees from Butler University and the University of Georgia, is currently engaged in research on the flamingos of the world under grants from the National Geographical Society, the New York Zoological Society, and the International Council for Bird Protection. He is a recognized authority on the large wading birds and has published some 18 papers as a result of his studies. His interests extend to wildlife photography, and persons who attended the banquet at the Williamsburg Annual Meeting will remember his excellent film on the storks of the world that was shown on that program, although Dr. Kahl was not present. Dr. Kahl is married and has one son, and is a member of the AOU, the BOU, and the Deutsch Ornithologen-Gesellschaft.

ORNITHOLOGICAL NEWS

The full account of the 1972 Annual Meeting appears elsewhere in this issue but it is appropriate that we offer further congratulations here to Frances James for winning the Edwards prize for the best paper published in *The Bulletin* in 1971, and to Anthony Erskine as runner up for this prize, as well as to W. John Richardson for winning the Alexander Wilson Prize for the best paper presented by a student or non-professional at an Annual Meeting.

It has been called to the Editor's attention that many people are unfamiliar with the Edwards prize. Through the generosity of Ernest P. Edwards, the Society is in the position to award a prize of $150 to the author of the best paper appearing in *The Bulletin* in a given year, and a prize of $50 for the second best paper. The papers are judged by a committee of three on the basis of both the caliber of the work presented and the quality of the presentation.

The Council of Biological Editors has recently published the third edition of the "CBE Style Manual", available from the American Institute for Biological Sciences, 3900 Wisconsin Avenue NW, Washington, D.C. This style manual is the ultimate authority in matters of style for *The Wilson Bulletin.* Much of the book is devoted to "helpful hints" in the preparation of MSS for publication, and prospective authors of papers to be submitted to *The Bulletin* will find that consultation of the Manual will make life smoother for both them and the editor during the process of conversion of a MS to a published paper.

FROM THE A.O.U.

At the annual meeting of the A.O.U. at Grand Forks, North Dakota on 14 August the following officers were elected.

President: Joseph J. Hickey   Secretary: Richard C. Banks
First Vice-President: George A. Bartholemew, Jr.   Treasurer: Burt L. Monroe, Jr.
Second Vice-President: H. B. Tordoff   Editor: Oliver L. Austin, Jr.

The Brewster Medal was awarded to Barbara and David Snow for their studies on Neotropical birds. The newly established Elliott Coues Awards went to Alexander Wetmore and Niko Tinbergen.

Robert S. Arbib, Jr. has been awarded the John Burroughs Medal for excellence in nature writing for his recent book, "The Lord's Woods".

We report with regret the death on 26 May 1972 of Arlie William Schorger, Professor Emeritus of Wildlife Ecology at the University of Wisconsin, and a former Elective Member of the Council of the Wilson Ornithological Society, in his 87th year.

The Membership List of the Society is included as a separate supplement to this issue. Members should report any errors of omission or commission directly to the Treasurer. Extra copies may be purchased from the Treasurer.

ORNITHOLOGICAL LITERATURE

Ecological Isolation in Birds. By David Lack Harvard Univ. Press, Cambridge, Massachusetts, 1971: 5¼ × 8½ in., xi + 404 pp., 34 tables, 58 text figs. by R. Gillmor. $12.00.

In the last six years David Lack has written three new books, each involving extensive and intensive reviews of available literature on the ecological relations of birds. The first, "Population Studies of Birds" (reviewed in the Wilson Bulletin, 79:469–471, 1967), dealt with the regulation of population size in birds. The second, "Ecological Adaptations for Breeding in Birds" (Methuen & Co., London, 1968), focused on the evolution and adaptive characteristics of avian breeding systems. The third book, the one being reviewed here, is devoted to a synthesis of the ways in which similar species achieve ecological isolation.

The basic theme of the book is that ecologically similar, usually closely related species of birds differ from one another in (1) geographical range, (2) habitat occupied, or if they coexist within the same habitat, in (3) foods eaten. Such segregation is considered primarily an evolutionary result of competitive exclusion. Over the past three decades, Lack has contributed significantly to the development of current evolutionary and ecological theory, with particular reference to the role of competition. In this book he brings his extensive knowledge and experience to bear on a detailed review of available information on ecological isolating mechanisms in birds.

For his analysis Lack presents a comprehensive survey of those bird groups for which there is reasonably good ecological information. Specifically, he summarizes and discusses the ecological relations of the following groups: the European tits; the tits (*Parus*) of Asia, Africa, and America; the nuthatches (world-wide); the European fringillids; the European trans-Saharan migrant passerines; other European birds; North American passerines, hawks, sandpipers, and auklets; African avifaunas, turacos, brood parasites, and vultures; tropical fruit-eaters, honey-eaters, and seabirds; the Galapagos finches and Hawaiian sicklebills; the white-eyes (Zosteropidae); and an analysis of the avifauna of a tropical archipelago, the West Indies. In addition to these detailed presentations which comprise the main chapters of the book, there is an 84-page appendix which contains tables and summaries of the geographical distribution, habitat preferences, morphological characteristics, food habits, and foraging methods of the above-mentioned groups of birds. This compendium, even without regard to the main theme of the book, provides a very valuable summary of widely scattered and not always easily accessible information. For this reason alone, the book belongs in the library of anyone seriously interested in the biology of birds.

The main point of this book is well made—closely related species of birds are ecologically isolated from one another. The mechanisms involved vary with the taxonomic group, the geographic area occupied, the habitats present, the characteristics and nature of the food supply and the numbers and kinds of sympatric species. Separation by geographic range is most frequent among wholly frugivorous congeners that feed on similar sized fruit and among land-birds of oceanic archipelagos where ecological diversity is assumed to be low. Isolation by habitat is commonest among congeneric passerines on large continental areas but is generally widespread in most taxonomic groups.

Closely related species occurring sympatrically are segregated primarily by differences in foods taken. In some groups, competitive exclusion has resulted in the evolution of different body or beak sizes; such differences are not usually found among congeners separated by range or habitat. In other groups, sympatric species have evolved distinctive foraging practices, e.g. feeding at different heights or in different parts of the habitat, presumably also a result of competitive interactions. Large overlaps in the diets of sympatric congeners are considered to occur only when the food supplies are especially abundant. As these supplies become scarce, however, the overlap is reduced as each congener takes different foods. From all examples available to him, Lack concludes that no coexisting bird species take the same major prey items on a sustained basis.

Although the book provides a comprehensive survey of ecological isolation in a wide variety of birds, some aspects of this topic are only briefly considered. Lack circumvents the problem of how much overlap in habitat or in foods taken can be tolerated before competition becomes a critical factor. This is a very important practical matter that has to be considered in each case and is subject to different opinions and interpretations. A more detailed discussion of the criteria Lack used in making his judgments of each example would have been most helpful.

In the final chapter of the book Lack touches only briefly on the relevance of ecological isolation to speciation processes, adaptive radiation, species diversity, and faunal composition. Other related topics that warrant critical analysis are not included. Examples of these are the effects of ecological isolation on the structure and dynamics of avian communities, and the genetic and ecological factors that operate(d) in the evolution of such isolating mechanisms. One wishes that Lack would make these and related topics the subject of future reviews.

Nevertheless, this book provides an extremely comprehensive and useful review of current knowledge about ecological isolation in birds. It will provide the basis for continuing critical studies on the dynamics of ecological relations among birds.

I highly recommend the book to anyone interested in birds. It is very clearly written, and the drawings and sketches by Robert Gillmor are excellent.—RICHARD T. HOLMES.

GRUNDRISS DER VOGELZUGSKUNDE. 2nd Edition. By Ernst Schüz. Verlag P. Parey, Berlin—Hamburg, 1971: 7 × 9¾ in., xi + 402 pp., 142 figs. DM 88.00.

Professor Schüz, director emeritus of the State Museum of Natural History at Stuttgart and former director of the bird banding stations at Rossitten and Radolfzell, presents a completely revised edition of his comprehensive textbook on bird migration. In addition to his elaborate descriptions of the migration patterns of European species, he discusses the migrations of many species from Asia, Australia, New Zealand, Antarctica, the Americas, and Africa.

Twenty years of extensive research have passed since the first publication of this unique text. New and sophisticated information on the phenomenon and the mechanisms of bird migration has been accumulated. Schüz has delegated special topics to several young research ornithologists, H. Oelke (research methods), P. Berthold (physiology), and E. Gwinner (orientation).

In his introductory chapter, Schüz stresses the adaptive significance of bird migration, an important means for the survival of the migratory species and largely the result of their evolutionary history. Apart from a limited glossary, definitions are given throughout the book. Migration is defined as a periodic and oriented wandering. Application of this definition poses certain difficulties as there are numerous forms of transgressions from strictly resident to migratory species. The introduction lists the important institutes and stations throughout the world that devote their entire work to the investigation of bird migration. Historical sketches illuminate the origins and developments of the German bird banding stations at Heligoland, Rossitten (now Radolfzell), and Hiddensee. The introduction of the term "Vogelwarte" (bird banding station) dates back to 1883 when H. Gätke first used it for the famous Heligoland station.

The brief descriptions of research methods pertain to the qualitative and quantitative aspects of bird-watching, recording of flight calls, banding procedures, the Louisiana "moon-watching," photography, radio and radar telemetry.

The following chapters can be considered the core and masterpiece of the Schüz text. They contain substantial descriptions of different patterns of migration exemplified by migrant species from all over the world. Included are topics on specialized migrations such as the concentrated "flyway" movements in coastal ranges, the modifying effects of off-shore islands and lighthouses on the flight pattern, migrations across mountain passes, along river systems, and the importance of oases in desert habitats. The detailed description of the migration patterns of a variety of 15 species is very informative. Among these, the White Stork has been Schüz's favorite subject through many years of pioneering research which contributed much to our understanding of bird migration. Particular aspects of migration, such as aerial, terrestrial, and aquatic locomotion, diurnal and nocturnal flights, social contacts of migrants, their flight altitude, speed, and overall efficiencies during narrow and broad front migration, are given an excellent treatment. Schüz also discusses dismigration (in contrast to site tenacity), range expansion, emigration, nomadism, and other forms of environmentally induced migratory movements.

The terminology on the categories of migration directions leaves something to be desired. It might have been better to have defined the "primary direction" not as the "obviously inborn migration direction" but rather as the species- or population-specific migratory direction in the absence of disturbing environmental factors. The "secondary direction" is characterized as the deviation resulting from the influence of landmarks; however, one should not exclude the modifying effects of various astronomical, meteorological, electrical, and magnetic forces. In Europe, most of the fall migrations are directed toward the southwest; they are eight times more common than southeast flights, and south migrations are exceptional.

Berthold's introduction to the physiology of bird migration consists of chapters on methods, registration of migratory restlessness, determination of migratory disposition (fat deposition and energetics). He describes also exogenous and endogenous release and guidance systems of migration stimulated by climate, food, light, and endocrinological processes.

Gwinner informs the reader about the study of migration orientation, compass and goal-directed flights, time-evaluation and calculation of the solar movement with the aid of an "internal clock." His description of stellar orientation is historically and factually misleading. Gustav Kramer (1949), contrary to Gwinner's statements, never claimed to have worked with Blackcaps that had shown preferred directions frequently matching the autumnal migration direction of the species. Apart from his Red-backed Shrikes, Kramer had observed a single female Blackcap in ten nightly sessions to show a NE-preference. As Kramer explained, the bird's only determinable optical response was toward the reflected harbor lights of Wilhelmshaven in the northeast. Kramer had not thought of star orientation but considered effects of shortwave radiation as a guidance system for nocturnally migrating birds. After our first studies of the nocturnal migratory flights of sylviid warblers (Sauer and Sauer, 1955), in which the shooting-star response of our birds led us to the concept of star orientation, Kramer visited us in our laboratory at Freiburg. He thought our experimental cage a horrible stovepipe device into which he would never dare to place a bird. He proposed to lend us two metallic nets with two different, physically selected mesh sizes of mathematical accuracy that we ought to put over our stovepipe cage in order to filter out undesired radiation and to check the response of the migrants with regard to the two sharply defined wavelengths. Our answer that we first want to test the birds' response to the planetarium sky in the mariners' school at Bremen was met by Kramer with utter disbelief. Later he visited us in the planetarium during an experimental session. Kramer watched for some time in complete silence. Finally he signalled to leave, and quietly we stepped out of the planetarium leaving the active warbler behind. Under the impact of what he had seen, with both his hands in the pockets of his pants, Gustav Kramer stood speechless for quite a time until he said: "Im Geist hab ich's begriffen, im Gemüt bin ich erschüttert." This was the historical moment when Gustav Kramer, deeply moved by his emotions, realized the existence of avian stellar orientation. Never again were the metal nets mentioned in our talks. Gwinner's misquote might have been extracted from American ornithological literature in which it has appeared repeatedly, possibly as the result of faulty translation and subsequent compilation.

Gwinner further refers to directional finding without visual clues. His example of orientation (not necessarily in the primary direction!) under overcast skies must be supplemented in so far as one can not rule out a secondary orientation by landmarks both during the day and at night. The magnetic field of the earth and prevailing winds are mentioned as further orienting factors. He also discusses briefly the hypotheses on bird navigation, the mechanisms of goal-directed or bicoordinate flights. A more thorough treatment of the relevant literature would have brought more enlightenment.

Schüz concludes the discussions with some illuminating remarks on the origin and significance of bird migration. Though a translation of this remarkable text into English appears very desirable, it must be appreciated that the well-illustrated book is clearly written in generally understandable terms. Readers with some basic knowledge of German and a professional or amateur interest in ornithology should be able to dig through it. Students of bird migration should not bypass this book.—E. G. FRANZ SAUER.

NATURAL HISTORY OF THE SWAINSON'S WARBLER. By Brooke Meanley. North American Fauna, No. 69. Bureau of Sports Fisheries and Wildlife, U. S. Department of the Interior, Washington, D. C. 1971: 6 × 9¼ in., vi + 90 pp., frontispiece, 26 figs. $0.50. Distributed by Superintendent of Documents, U. S. Government Printing Office, Washington.

Swainson's Warbler (*Limnothlypis swainsonii*) has long needed monographic treatment; Brooke Meanley has supplied an excellent one. He has assembled and digested all available literature on the species, he has studied the birds in all their major known breeding habitats, and his approach is carefully ecological. Photographs are numerous and good, and his bibliography is comprehensive.

Of the North American wood warblers, Swainson's comes closest to having a split personality. For many years after its original discovery in South Carolina the species was quite comfortably assigned, and in literature restricted, to the southeastern Atlantic Coastal Plain, and to the lowland swamps adjacent to southern rivers. By common observation and experience, its breeding habitat was placed in canebreaks and such other dense vegetation as could tolerate warm, moist situations. Those who sought the bird on its nesting grounds turned to such situations; if they knew where to look they found the birds, and Swainson's got categorized as definitely as has Kirtland's in a jack pine situation.

Then data of an unsettling nature began to appear. On 14 June 1924, Bibbee collected a male in breeding condition in Monongalia County, West Virginia, only a few miles from the Pennsylvania state line. His record was not published for some years, and when it did appear it was dismissed; the specimen was too obviously an accidental. A short while later when Jones observed the birds, and found and collected a nest in southwestern Virginia, he, quite frankly, was not believed, and no national ornithological journal would publish his data. Presently Wetmore (who had questioned Jones' record) collected a specimen in southern West Virginia, and birds were found in the North Carolina Piedmont.

It remained for Legg, working in hilly Nicholas County, West Virgina, in the Allegheny Plateau to report the species as a locally common breeder in tangles of rhododendron, hemlock, mountain laurel, and American holly, at elevations around 1,600 feet. This was a country of far call from southern coastal canebreaks, and it became imperative that the range of Swainson's be reexamined.

The remote village of Mt. Lookout, Nicholas County, W. Va., became a mecca for those in search of Swainson's, and to the area came Sutton, Lunk, Brooks, and many others. All found the birds, sometimes in numbers, and nesting data began to accumulate.

To Meanley and others it seemed logical that these birds of the Allegheny Plateau were racially distinct from those on the distant coastal plains and riverine swamps. A separate race was proposed, but this was not acceptable to the A.O.U.'s Check-list committee, so *Limnothlypis swainsonii* remains monotypic.

Thanks to the thorough work of Meanley and others, we now know a great deal more about these birds, and we can even postulate a movement route which allows the birds to pass from coastal areas to southern Appalachians with no conspicuous gaps in its nesting range. The Savannah River in its course from mountain to ocean is certainly one such possible route; there may be others.

Although this bird is frequently considered elusive and difficult to observe, Meanley correctly points out that while it chooses dark tangles it is often quite tame when found, and will often allow close observation. In deciduous tangles just outside the limits of Charleston, West Virginia, DeGarmo, Simms, and many others have studied the species in one of its habitats of greatest abundance, and Gunn chose this area to record a series of songs which he includes in one of his LP records.

After careful study of Swainson's in all its known major breeding places, Meanley concludes, and this reviewer certainly concurs: "It is possible that the Swainson's Warbler can adapt to so-called marginal Coastal Plain habitats better than is suspected. Some occur there, but these usually are bachelor males. But if the Swainson's Warbler ever has to make a last stand it may well be in the Southern Appalachians, where many of them occur in national forests and national parks or in areas unsuitable for agricultural production."—MAURICE BROOKS.

THE TRADE WIND ZONE OCEANOGRAPHY PILOT STUDY. PART VII: OBSERVATIONS OF SEA BIRDS, MARCH 1964 TO JUNE 1965. By Warren B. King. U. S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 586. June, 1970. 8 × 10¼ in., vi + 136 pp., 36 maps and figures, 11 tables, 2 appendix tables. No price given.

This is perhaps the most systematic seabird survey ever planned. Reported here are the results of a series of cruises devoted solely to seabird ornithology, or what I would call "pelagic ornithology." This science has two main directions—one, the analysis of species variety and distribution of seabirds, and the other, the contribution to comprehensive marine biology through knowledge of the birds' niches in the pelagic community, especially in relation to food supply. The present report is a milestone in the study of species composition and distribution, owing to its multiple analyses.

As King writes, "Sea birds were observed by scientists of the Smithsonian Institution's Pacific Ocean Biological Survey Program on a systematic basis in the central Pacific Ocean for 15 months as a part of the Trade Wind Zone Oceanography Program of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. In 3561 hours of observation, 13,080 sightings were made of 65,707 birds along the replicate cruise track covering 34,384 nautical miles." During 17 cruises, each averaging 232.9 hours and 2258 miles of observation (averages calculated by reviewer), 51 species and subspecies were identified. These cruises covered about 50,000 square miles of the sea east of Hawaii.

Data were recorded on sea surface temperature and salinity, temperature at 10 meter depth, wind speed and direction, barometric pressure, weather, state of sea, swell direction and period, visibility, wet and dry bulb air temperatures, type of clouds and their amount of cover. A 25 minute surface plankton haul was made every evening, but the correlations with bird abundance are not discussed. Automatic Data Processing (ADP) as described by King et al. (1967) was used for storage and analysis of data.

The avifauna of the study area consisted of 12 families with 49 species and identifiable subspecies of 2 more species. The number of species per day ranged from 2 to 15 and the number of species per month ranged from 17 (July) to 32 (April). These numbers increased during the spring and fall migration periods. Seabird numbers were usually highest within 50 miles of Oahu though many were seen as far as 700 miles from land.

Some interesting records may be cited. A banded *Diomedea nigripes* followed the ship for 18 hours, 180 miles. This and the less abundant *D. immutabilis* showed similar ranges with midwinter expansion and spring contraction correlated with breeding. A southern species, *D. melanophris*, was recorded on January 23, 1965 for the first time in the north Pacific. Analysis of monthly distribution of *Pterodroma externa externa* and *P. e. cervicalis* is a valuable contribution to the knowledge of their pelagic range; I would add to this one example of the latter race found in Japan (Kuroda, Misc. Rep. Yamashina Inst. No. 18:222, 1962). Twelve species and subspecies in the difficult group of *Pterodroma* were identified (with some inevitable confusion) and their status clarified. Another important contribution is a detailed analysis of the seasonal ranges of the light and the southern dark phases of *Puffinus pacificus*, which were abundant at water temperatures of 25°C and 27°C respectively. In storm-petrels, *Oceanodroma leucorhoa*, besides winter stragglers of *O. furcata*, was the only species that occurred in abundance, although some *O. castro* may have been missed, as the author mentions. Monthly distributional maps of other species, especially the most abundant *Sterna fuscata* are also valuable.

The species accounts are followed by summaries and discussions of the following items: monthly summary, islands of origin of seabirds recorded in the study area and modes of utilization of the area, distance from land, analysis of density, direction of birds' movements, daily cycles of activity (shown by graphs), environmental influences (winds, temperature, and salinity) on each species, and flock analysis. Of 893 flocks recorded, Sooty Terns were present in 76 per cent of the flocks and the next most common, Wedge-tailed Shearwaters, were present in 39 per cent. Finally, there are given 28 pages of Appendix Tables of daily complete data adapted for ADP coding system.

The foregoing is only a bare summary of the contents of this important paper in which Dr. King has raised pelagic ornithology to a more comprehensive and analytical level than ever before. Much, however, remains to be studied, particularly in the marine biological aspect of seabirds (see Bourne, Proc. XIII Internatl. Ornithol. Congr.:831, 1963) and correlation of the birds with food supply in the marine community (Shuntov, Zool. Journ., 43:590, 1964; 44:441, 1965). In closing, I take pleasure in extending my congratulations to the author.—NAGAHISA KURODA.

A NATURALIST IN COSTA RICA. By Alexander F. Skutch. Univ. of Florida Press, Gainesville, 1971: 6½ × 9½ in., x + 378 pp., 2 endpaper maps, 68 photos, 8 drawings. $12.50.

A good deal of what is known of the lives of tropical American birds, especially during the vital reproductive period, we owe to the selfless dedication of Alexander F. Skutch. Here he tells us something of his life and times, his experiences as a struggling naturalist, his thoughts and aspirations during a residence of thirty-five years in Costa Rica, mostly at 2,200–2,500 feet above sea level in the General Valley. The book is divided into two parts: "A Naturalist's Wanderings" recounts his early years in Costa Rica, "A Naturalist's Homestead" describes the site and home selected and built. Both parts contain natural history observations and philosophical comments, including views on the state of man, but the major preoccupation is with birds. The bulk of the book consists of items that, in the case of birds and undoubtedly of other groups, too, the author has published at least once before, though only one such instance is acknowledged by him. These range from closely paraphrased condensations and excerpts to lengthy, virtually word for word, repetitions. Skutch's writing should appeal to devotees of his choice of words and humorless style.

The author's motivation in seeking out a wild place in which to live was the desire to "penetrate, as far as possible, to the secret springs of this multiplex phenomenon called life, to understand its significance in the whole vast drama of cosmic evolution. Here I hoped to have leisure to mature my thoughts on these baffling problems" (p. 140). His outlook on nature no doubt helped him decide where to settle (p. 191): "And as the physician gauges his patient's health by examining his tongue, so earth's liquid tongues reveal her condition: if only they are pure and transparent, she is in a sound and flourishing state; if they are opaque with silt and debris, she is sick and wasting away." Thus, "the Peña Blanca River that formed my eastern boundary ran clear and pure." Later (p. 203), we learn that the Peña Blanca River becomes "swollen and turbid from the afternoon downpours."

Page 173 offers two examples of the author's esthetics. "People who regard each other's taste in painting, sculpture, or music as barbarous may delight in the same flowers. This fact might make us question some of the newest theories about art." "This golden display is provided by a slender, woody vine of the dillenia family, for which I know no name more poetic than its scientific designation, *Davilla kunthii*." The latter sort of private enthusiasm colors his reaction to the vocalizations of birds.

As a lover of nature the author has strong views about snakes. A long black snake gliding to a rock almost beneath two young hummingbirds in a nest above a forest stream elicited these remarks (p. 124): "A snake intent upon ravin appears to become insensible to everthing else, at times even to mortal wounds. This one was no exception; it delayed immobile while I approached and delivered the stroke that sent it writhing madly into the water, where the current bore it slowly downstream to die."

In fact, the author wishes for a world in which life has evolved free of "that most hideous blot on the fair face of nature, predation, the killing and devouring of one creature by another" (p. 231). "If predation had never arisen, predators would not be necessary to prevent overpopulation. Predation, including its subtle form, parasitism, is a tragic miscarriage of evolution. It is responsible for some of the worst passions that afflict that long-time predator, man, and through them for a large share of the evils from which we suffer" (p. 232). When it comes to the population control of man, he sees a moral problem (pp. 340–341): "Are our only alternatives a hideously overpopulated world, afflicted with famine, crime, ugliness, and disease, and a 'contraceptive society,' in which men, women, and children wallow, like pigs in mire, in sex divorced from its natural function of reproduction, which gives it dignity and makes it sacred"?

Skutch's observations on the forested part of his property, now an isolated remnant subject to trespass, could only have resulted from a long-term stay (p. 338): "It is widely held that mature tropical forest is a stable vegetable formation that remains essentially unchanged from century to century. Yet in this forest, which appeared mature when I first saw it, the largest trees have been dying faster than they are being replaced by younger trees. . . . The explanation of this puzzling phenomenon may be that this forest has not yet reached its climax but represents an advanced successional stage on lands cleared by the Indians and abandoned by them centuries ago. Or could it be that climatic changes, resulting from the destruction of the surrounding woodland, cause the large, old trees to die prematurely? The smoke-laden atmosphere of the latter part of the dry season must have some effect. Even the destruction of so many [palmito] palms must alter the dynamics of the forest."

There are two very useful appendices. The first, an annotated list of the status of the species of birds identified by the author on the 100 hectares of his property between 1941 and 1970, to which have been added other species observed by him elsewhere in the General Valley since 1935, is especially valuable. The second is a chronological list of the author's books and articles since 1926.—P. SLUD.

THE HUNGRY BIRD BOOK. By Robert Arbib and Tony Soper. Taplinger Publishing Company, New York, 1971: 5¾ × 8¾ in., x + 118 pp., many drawings by Robert Gillmor. $4.95.

Robert Arbib collaborated with Tony Soper to Americanize "The Bird Table Book," a popular British book. Many comparisons are used throughout referring to English gardens and attendant bird life, but "The Hungry Bird Book" most generally delineates the variety of birds, specific habitats and foods in the area of North America covered by Peterson's eastern field guide referring to that book by page number for each species named. Only those species likely to frequent feeders and dooryards are included, a total of 99.

Suggestions for planting to attract birds, instructions and dimensions for nest boxes, supplementary food mixes, water and feeding arrangements, even an appendix on first aid make this a "not too technical" comprehensive coverage for use by such as scout troops, garden clubs, interested homeowners, and the like. Pen and ink illustrations by Robert Gillmor, both practical diagrams and captivating birds in action, add entertainment to the attendant information. Lists of sources for supplies, book references and extensive bibliography broaden the use of the book for the would-be enthusiast.

This book would seem to be helpful in answering many of the queries that come to persons reputed to have knowledge of birds.—NANCY ELLISON.

OWLS. THEIR NATURAL AND UNNATURAL HISTORY. By John Sparks and Tony Soper. Taplinger Publishing Co., New York, 1970: 6 × 8½ in., 206 pp., col. frontispiece, 17 bl. and wh. pls., many pencil drawings. $5.95.

This book is not a "scientific" product. It is disappointing when judged by such criteria as use of the relevant literature, evenness of coverage, accuracy, and absence of teleology and anthropomorphism. It is successful insofar as it provides some general knowledge of owls for laymen. The most pleasing features are the drawings and photographs by Robert Gillmor, which add immensely to the attractiveness of the book.

Throughout the book, the authors tend to digress from whatever is under discussion. This first is overdone to an irritating and distracting degree in Chapter 3, "Numbers of Owls", giving the impression that Sparks and Soper were becoming hard-pressed to produce a whole book on owls. This chapter is a generalized, rambling discourse on predator-prey interactions, including cyclic population fluctuations and the concept of food chains. Chapter 4, "Owls and Man", is subject to the same criticism. Six pages are devoted to rehashing the problem of DDT and other toxic substances introduced by man into the environment. Owls are hardly mentioned.

Errors and poor phraseology are not infrequent. For example, in Chapter 5 we are told that competition from bats and nightjars may have prevented owls from evolving insect-chasing techniques (p. 146), and that a bountiful food supply stimulated active speciation in rodents (p. 138).

Chapter 6, the final chapter, "Owls—Their Unnatural History", is an attempt to gather together references to owls and folklore about them from a variety of sources including the Bible, Shakespeare, Chaucer, the Greeks, "Red Indians", and others. Some of the information presented is thought-provoking, e.g. "Hooting nearby could mean loss of virginity to a Welsh girl." Three short appendices conclude the book.

In summary, "Owls" is a sometimes entertaining but superficial book. Readers should keep in mind that very little of the literature available on owls was utilized, and that as a result coverage is uneven and incomplete, and that inaccuracies are not rare.—J. DAVID LIGON.

GALAPAGOS ISLANDS. MUSEUM PICTORIAL NO. 19. By Alfred M. Bailey. Denver Museum of Natural History, 1970: 6 × 9 in., paper covered, 85 pp., many photos. $1.50.

Museums commonly dispatch expeditions but rarely report on them to the public. Here is an account of the Denver Museum's field trip to the Galapagos Islands in July and August 1960. The narrative is augmented by a comparison of the experiences of other field workers who have been there. The very nature of the place makes for interesting reading, and the report is larded with observations upon the plants and animals. Although the purpose of the expedition was to collect material for a habitat group, several scientific accomplishments were made. To quote from the Foreword, "The first eggs of the Galapagos Penguin and dusky gull to be reported were discovered, photographs were made of nesting dark-rumped petrels in the highlands of Santa Cruz, and information was secured covering the nesting cycle of the Galapagos albatrosses." The booklet is illustrated with a map and excellent monochrome photographs by Bailey, Robert R. Wright, and Jack A. Murphy. A bibliography is included.—PETER STETTENHEIM.

PUBLICATION NOTES AND NOTICES

FIELD WORK OF A MUSEUM NATURALIST. MUSEUM PICTORIAL NO. 22. By Alfred M. Bailey. Denver Museum of Natural History, 1971: 6 × 9 in., paper covered, 192 pp., many photos. $2.50.

This is an account of the author's field work in southeastern Alaska from 1919 to 1921 for the U.S. Biological Survey, and in Arctic Alaska from 1921 to 1922 for the Denver Museum of Natural History. Although it is intended primarily as a popular account, there is much information of value about conditions in Alaska as they were 50 years ago. The booklet is abundantly illustrated with photographs of the natives, the wildlife, and the scenery.—G.A.H.

BIRDS OF THE BUFFALO CREEK REGION, ARMSTRONG AND BUTLER COUNTIES, PENNSYLVANIA. By W. E. Clyde Todd. Edited, with an introduction, by Mary Heimerdinger Clench. Audubon Society of Western Pennsylvania, 1972: 6 × 9 in., paper covered, 21 pp, 6 photos, 4 line drawings by G. M. Sutton, one map. $2.50 (Obtainable from Mrs. R. C. Abbott, 8468 Peebles School Road, Pittsburgh, Pennsylvania 15237).

As a young boy the late W. E. Clyde Todd studied the birds on his grandfathers' farms and in their vicinity during the years 1889 to 1897, and in 1898 he prepared this account of his observations, but never published it. In 1942 Mr. Todd had given the Audubon Society of Western Pennsylvania some of the original farm property, which has been set aside as a sanctuary. On the occasion of the thirtieth anniversary of the Todd Sanctuary the Society has published this MS, with a biographical introduction, as well as annotations about the present birdlife of the area by Mary H. Clench. The account gives a valuable summary of the status of the birdlife of the region as it was 70–80 years ago.—G.A.H.

BIRD CENSUS SURVEYS OF THE HOOPES RESERVOIR AREA, NEW CASTLE COUNTY, DELAWARE. By Lloyd L. Falk. Monograph No. 1, Delmarva Ornithological Society, 1971: 5½ × 8½ in., paper covered, 87 pp. $1.75 (Obtainable from the Delmarva Ornithological Society, c/o Philip K. Klabunde, 2715 Bardell Drive, Wilmington, Delaware 19808).

This is a detailed summary of 158 bird census surveys conducted during 1943, 1944, and 1945, compared with 52 surveys made in 1964. The two surveys show very graphically the changes in birdlife over the 20-year period.—G.A.H.

THE DELMARVA ORNITHOLOGIST. The Delmarva Ornithological Society, Wilmington, Delaware. Vol. 7, No. 1, January 1972.

A new regional publication intended to appear semiannually succeeding a mimeographed publication which appeared at irregular intervals. Obtainable from the Editor, Mrs. Francis H. Beach, P.O. Box 37, Northbrook, Pa. 19361. Single copies $1.00 each.—G.A.H.

PROCEEDINGS OF THE FIFTY-THIRD ANNUAL MEETING

JAMES TATE, JR., SECRETARY

At the invitation of the Delaware Valley Ornithological Club, the New Jersey Audubon Society, and the Academy of Natural Sciences of Philadelphia, the Fifty-third Annual Meeting of the Wilson Ornithological Society was held at Cape May, New Jersey, from Thursday 15 June, through Sunday, 18 June 1972.

Early arrivals at Cape May were invited to a reception at the Wetlands Institute on the causeway between Stone Harbor and the mainland on Thursday afternoon. The Institute is about two miles from the Stone Harbor heronry, which many participants visited on their return to Cape May. Thursday evening in the Convention Hall, William E. Parker showed motion pictures which included birds photographed at the New Jersey shore and at recent Wilson meetings.

On Friday evening Merrill Cottrell presented a well recieved slide show, "New Jersey's Natural Assets." An impromptu showing of a new film "Everybody's Eagle" was presented by its producer George Allez later Friday evening.

The annual banquet was held on Saturday evening at the Colonial Hotel. Following the President's Address, the group adjourned to the Convention Hall for a premier showing of a new Audubon Wildlife Film, "Serengeti Safari" by Donald S. Heintzelman.

Throughout the meeting, paintings of North American waterfowl by William Zimmerman were on display in the Colonial Hotel.

Ornithologists visiting the Cape May peninsula were attracted to the famous breeding colony of herons and Glossy Ibis at Stone Harbor, and the beach and salt meadowland nesting colonies of gulls, plovers, terns, and skimmers. Early morning trips were held Friday and Saturday to Cape May Point. Also scheduled during the meeting for those not attending the paper sessions was a beach walk, a plant walk, and a walking tour of historic Cape May. The Sunday boat trip was washed out by the advance rains of Hurricane Agnes, but trips to the Brigantine National Wildlife Refuge and to the Osprey colonies were held.

The recipients of the Wilson Society prizes were announced at the annual banquet by First Vice-President Parkes as follows:

Louis Agassiz Fuertes Award: Donald E. Kroodsma, Oregon State University—Demes, dialects, and dispersal in the Bewick's Wren.

Margaret M. Nice Award: Mrs. Rebecca L. Radcliffe, Bloomfield Hills, Michigan—Forty-year comparison study of nesting and migratory birds of Cranbrook Campus, Oakland County, Michigan.

Ernest P. Edwards Prize: First Prize, Mrs. Frances C. James, Fayetteville, Arkansas—Ordinations of habitat relationships among breeding birds.

Second Prize, Anthony J. Erskine, Ottawa, Ontario—Some new perspectives on the breeding ecology of Common Grackles.

Alexander Wilson Prize: W. Jon Richardson, Cornell University—Spring migration over Puerto Rico: A radar study.

FIRST BUSINESS MEETING

The first business meeting was called to order by President Hofslund at 09:30. The minutes of the business meetings held at Dauphin Island, Alabama, were approved by the membership as published in The Wilson Bulletin (83:331–339, 1971). The President appointed the following temporary committees:

Resolutions: Ernest P. Edwards, Chairman;

Alexander Wilson Prize: Douglas James, Chairman; Kenneth C. Parkes, Robert D. Burns.

Auditing: C. Chandler Ross.

The names of the Nominating Committee members were announced as follows: Walter J. Breckenridge, Chairman; John T. Emlen, Jr., O. S. Pettingill, Jr.

The Secretary reported on highlights of the Council meeting of the previous evening. Reports of officers of the society which were presented at the Council meeting were summarized, and are reproduced here:

Report of the Treasurer—1971

The Internal Revenue Service made an audit of the tax return for the year 1969 and after reviewing our activities and examining the financial records, found we were in compliance and continued our Federal tax-exempt status and accepted on March 24, 1972 the return as filed.

As the Society is exempt under 501(c)(3) and qualified favorably under Section 509(a) as "not a private foundation," the filing of tax returns on the new Form 990 requires reporting in a manner that tests financial compliance each year and to some extent for compliance with activities for which exemption was granted. In consequence, any new activities contemplated need to be carefully evaluated for tax consequences and the choice of words should be carefully weighed.

The value of Life Membership was dramatized this year in several resignations which emphasized financial inability to continue many modest activities such as continuing W.O.S. membership. This appeared to indicate fewer gifts probable, especially to the Library, and offers to sell Wilson Bulletins were not uncommon.

FINANCIAL STATEMENTS

GENERAL FUND

Balance as shown by last report 31 December 1970			$9,811.26
RECEIPTS			
Membership Dues			
Active for 1971	$ 5,965.00		
Active for 1972	6,498.50		
Total Active		$12,463.50	
Sustaining for 1971	540.00		
Sustaining for 1972	375.00		
Total Sustaining		915.00	
Subscriptions to the Wilson Bulletin			
For 1971	2,057.22		
For 1972	2,955.38		
Total Subscriptions		5,012.60	
Sales of back issues of The Wilson Bulletin		423.94	
Interest and dividends on savings & investments		3,729.51	
Royalties from microfilming back issues of The Wilson Bulletin		157.03	
Total Receipts		$22,701.58	

DISBURSEMENTS			
The Wilson Bulletin (Printing & Engraving)	$15,394.95		
Less contributions from authors	737.43		
Printing & Engraving Expense		$14,657.52	
The Wilson Bulletin (Additional Mail & Service)		636.18	
Editor's Expense		220.01	
Secretary's Expense		83.90	
Treasurer's Expense		439.80	
Foreign discount, bank charges and transfer fees		51.37	
Annual Meeting Expense		658.00	
Committee Expense		35.58	
International Council for Bird Protection (1970–71 dues)		55.00	
Transfer to Research and Other Grants		284.00	
Review Editor's Expense		28.38	
Miscellaneous Expense		2.00	
Total Disbursements		$17,151.74	
Excess of Receipts over Disbursements			5,549.84
GENERAL CASH FUND			
Checking Account			10,416.09
Savings Account			4,945.01
Balance in National City Bank, Cleveland, Ohio 31 December 1971			$15,361.10

JOSSELYN VAN TYNE MEMORIAL LIBRARY BOOK FUND

Balance as shown by last report 31 December 1970	171.23
RECEIPTS	
Sale of duplicates and gifts	316.00
Total Balance and Receipts	487.23
DISBURSEMENTS	
Purchase of Books	102.87
Balance in National City Bank, Cleveland, Ohio 31 December 1971	$ 384.36

LOUIS AGASSIZ FUERTES RESEARCH FUND, MARGARET MORSE NICE FUND, EDWARDS, AND W.O.S. PAPER FUNDS

Balance as shown by last report dated 31 December 1970		$ 104.00
RECEIPTS		
Contributions		232.00
Transfer from General Fund		284.00
Total		620.00
DISBURSEMENTS		
Grant to Flash Gibson	200.00	
Grant to William J. Maher	150.00	
Grant to John P. Ryder	50.00	
Grant to Kenneth P. Able	100.00	
Grant to T. A. Beckett, III	100.00	
Total		600.00
Balance in National City Bank, Cleveland, Ohio 31 December 1971		$ 20.00

SPECIAL FUND ACCOUNTS

Balance as shown by last report 31 December 1970		$ 199.50
RECEIPTS		
Prepaid Student Dues	0.00	
Advanced Renewals	200.75	
Discount Due Agencies	23.00	
Total Receipts		223.75
Total		423.25
DISBURSEMENTS		80.50
Balance in National City Bank, Cleveland, Ohio 31 December 1971		$ 342.75

ENDOWMENT FUND

Balance in Endowment Fund Savings Account as shown by last report dated 31 December 1970		$12,252.50
RECEIPTS		
Life Membership Payments	4,985.00	
Patronship Payments	750.00	
Total Payments		5,735.00
Total		$17,987.50
DISBURSEMENTS		
For Investments		7,250.00
Balance in Endowment Fund Savings Account National City Bank, Cleveland, Ohio 31 December 1971		$10,737.50
INVESTMENTS HELD AS OF 31 DECEMBER 1971		
United States Government bonds	4,996.09	
Canadian Provincial bonds	4,300.00	
Corporate bonds	8,925.00	
Convertible corporate bonds	3,462.50	
Convertible preferred stock	38,804.50	
Common stocks	17,186.25	
Investment trusts	8,310.32	
		$85,984.66
Total Endowment Fund 31 December 1971		$96,722.16

Respectfully submitted,
WILLIAM A. KLAMM, *Treasurer*

Report of the Secretary—1971

The Secretary of the Society answered a small amount of correspondence, forwarded several items to the Treasurer, and had the Society's stationery and envelopes printed and distributed. Utilizing volunteers the committee choices of the questionnaire respondents were tabulated on 3 × 5 index cards for the convenience of the President as he contacted committee chairmen. These were delivered to him in two portions.

A letter summarizing the duties of the Secretary was received from retiring Secretary Swinebroad which proved to be of great help. The *Guide to the Local Committee in Charge of the Annual Meeting* was sent at the same time. This was revised and updated. Copies were sent to the local committee. Events of the year rendered it partially ineffective.

President Hofslund appointed Elden W. Martin as Program Chairman in the anticipated absence of Second Vice-President Berger. With his help, and that of the local committee, the Secretary prepared, edited, and printed the announcement of the meeting. The announcement was mailed in late April. The program was printed and carried to the meeting by the Secretary.

From the Secretary's viewpoint it was an interesting, informative, and occasionally frustrating year. It was a pleasure to be of service to the Society.—James Tate, Jr., *Secretary*

Editor's Report—1971

Volume 83 (1971) consisted of 468 pages and included 34 papers, 45 Notes, 26 book reviews, one conservation paper, and the index. There were two colored plates, both of which had outside subsidy.

Two issues of Volume 84 have appeared totalling 228 pages.

During the past year 59 papers and 82 Notes have been submitted, and 27 papers and 48 Notes have been accepted. Fourteen papers and six Notes have been returned to the authors for substantial change before acceptance; 14 papers and 25 Notes have been rejected; and no decision has been reached on 8 papers and 3 Notes.

The current backlog of papers is a very comfortable one. The September issue is being set in type, and there is not quite enough material accepted as yet for the December issue. This issue should be filled shortly with the return of some papers for which change had been suggested. Thus the publication delay on some papers can be as short as six months, and on most no longer than one year. The average delay for papers in the June issue was 10 months, excluding one paper for which the author delayed six months in making revisions. The average delay for Notes was 9 months.

The members of the Editorial Board have continued in their excellent service, and once again I extend my thanks to them, and to the many other ornithologists who reviewed papers during the year.—George A. Hall, *Editor*

Reports of several of the committees which reported to the Council Meeting were then summarized, and are reproduced here:

Report of the Research Committee—1971

Your committee unanimously recommends that the Fuertes Award go to Donald E. Kroodsma, Department of Zoology, Oregon State University. The title of his research project is "Demes, dialects, and dispersal in the Bewick's Wren." Mr. Kroodsma was ranked well ahead of his closest competitors. In the committee's voting there was a tie for second place.

Thirteen people completed the application process, i.e., did more than write letters of inquiry or request forms. One of these later withdrew his name when he received other support. In addition to these thirteen, an approximately equal number of people wrote letters indicating an interest in applying.

For the Nice Award the committee recommends Rebecca L. Radcliffe, c/o Cranbrook Institute of Science, P.O. Box 801, Bloomfield Hills, Michigan 48013. Mrs. Radcliffe, who was the sole applicant having no affiliation with an academic institution (her husband is employed by the Cranbrook Institute, but not as a scientist), is working on a project entitled "A forty-year comparison study of nesting and migratory birds of Cranbrook Campus, Oakland County, Michigan."

It seems worth calling attention to the paucity of applicants for the Nice Award and suggesting that the Society take measures to encourage interest in it. This year, as in the past, applications for both the Fuertes and the Nice Awards were solicited only by means of repeated announcements in the major United States ornithological journals. It is possible that even amateurs who are serious enough to have research projects may not see these announcements. Perhaps the Bird Banding Laboratory at Patuxent might be asked to give publicity to the Nice Award.—VAL NOLAN, JR., *Chairman*

Report of the Membership Committee—1971

Even though I agreed in mid-summer to President Hofslund's request that I serve as chairman of the membership committee, I was unable to begin work on the membership drive until early October. My first efforts were directed toward increasing the number of committee members and the geographic representation on the committee. I contacted over thirty WOS members who had indicated a willingness to help with membership recruitment on the questionnaire circulated a couple of years ago. This resulted in the membership committee increasing from 14 to 41 members and increased our geographic representation from 13 states to 24 states and one Canadian Province.

In mid-January I sent each committee member a packet containing a two-page letter suggesting some possible techniques for recruitment, ten each of brochures and membership application cards, and an average of five names of prospective members gleaned from the AOU membership list. Since January, several committee members have requested a total of over 100 additional brochures and cards. Thus, assuming that most committee members contacted at least the number of names given them, a minimum of around 200 persons were approached about membership. If a substantial number of the members also turned up contacts on their own, this number could be as high as 400.

As of 6 June, I have received the cards of 104 new members from the Treasurer (list attached). Of this total, 36 were nominated by Treasurer Klamm, and 39 others were nominated by a total of 28 WOS members not serving on the membership committee. Unless some of the applicants whose cards were signed by the Treasurer were recruited by committee members, it appears that the committee has been responsible for the production of only 29 new members. While this number is embarrassingly low, particularly in view of the increased size of the committee, I do not know whether or not it is unusual. The recent annual reports of this committee have not reported the number of members recommended by committee members.

The 104 new members represents an increase of 7 over the number of new members reported in last year's annual report. However, we have lost 28 members from resignation, 9 from deaths, and 88 have been suspended for being delinquent in dues, for a total loss of 125. Thus, it appears at this time as though our total membership is down 21 from last year. The only encouraging aspect of this figure is that last year's decrease in membership, based on figures in the 1971 report, was 84. Treasurer Klamm also reports that we have 3 new life members and 2 new patrons.—NORMAN L. FORD, *Chairman*

Report of the Student Membership Committee—1971

After an initial special mailing in 1970 to all 429 WOS members at institutions of higher learning the Student Membership Committee has since then relied on college student nominations in response to a notice in the December *Wilson Bulletin*. The notice has been a complete failure. There were only two responses totaling two nominations in 1971, and so far in 1972 the two nominations received came from a single person. This compares to 55 responses providing 188 nominations and yielding 40 new members following the massive mailing in 1970. So it is apparent that a simple journal notice is ineffective. Instead an actual nomination form has to reach the membership. We suggest the possibility be explored of including such a form in the annual mailing for membership renewal since a special separate mailing to our members yearly is expensive. This approach could seek non-student as well as student nominees for membership.

In 1971 and again this year the Committee mailed letters to nature centers, municipal museums, Audubon Societies and the like in an attempt to find talented pre-college students with a keen interest in bird study to invite them to join the Wilson Ornithological Society at an early age. This quest is being conducted on a regional basis progressively covering the nation in successive years. In 1971 some 102 mailings to 10 northeastern states produced 11 responses and 27 nominees. This year 124 letters were posted in May to 13 states, mostly in the upper Midwest but extending to Virginia, and so far there have been four responses including 10 nominees.

The Committee will continue the pre-college search on a continuing regional basis, but it also feels it now is time to make a direct appeal to the college student again. We strongly recommend testing the procedure that provides nomination forms sent to members with the annual dues request.—Douglas A. James, *Chairman*

Report of the Library Committee—1971

The year has been relatively uneventful for the library but, on the whole, successful. The collection continues to grow.

Thirty-one gifts were received from 23 donors: 13 books, 81 periodicals and 300 reprints, in all.

Fifty-one loans were made by mail to 45 members; and, as always, the library had constant on-the-spot use.

Both the foregoing items represent an increase over last year.

The library receives 98 journals in exchange for *The Wilson Bulletin.*

An effort is being made to dispose of a rather large accumulation of duplicates. Success in this area is already considerably augmenting our New Book Fund, which will make possible the purchase of books still badly needed.

Our space problem may soon again become acute, where storage of back issues of the "Bulletin" is concerned. However, it is hoped that solutions will once more be found.

As always, members are invited to borrow, and also urged to contribute in any way possible.—William A. Lunk, *Chairman*

Continuing the summary of the Council meeting, Secretary Tate reported on the appointment of the Editor. The Council voted on the appointment of the Editor of The Wilson Bulletin, and selected George A. Hall. Editor Hall accepted the appointment, commenting that he would begin his tenth consecutive year with Volume 85 of The Wilson Bulletin. He reported that he would tender his resignation upon the completion of that Volume year.

The fifty-fourth annual meeting of the Society will be held at Chapel Hill, North Carolina from 17–20 May 1973.

There being no further business, the President closed the first business meeting at 09:47.

SECOND BUSINESS MEETING

President Hofslund opened the second business meeting at 14:20 on Saturday. The following resolution was read by Ernest P. Edwards:

WHEREAS, the Wilson Ornithological Society met in its Fifty-third Annual Meeting at Cape May, New Jersey, one of the famous ornithological sites of the east coast, and

WHEREAS, lodgings were provided and numerous special events were planned and offered, in addition to the papers sessions and business sessions,

THEREFORE, BE IT RESOLVED THAT the Society express its warmest appreciation for the hospitality of the City of Cape May, the Delaware Valley Ornithological Club, the New Jersey Audubon Society, and the Academy of Natural Sciences of Philadelphia, and particularly of the Local Committee on Arrangements who took care of the necessary arrangements to make the meeting possible.

The resolution was approved by the members in attendance.

Report of the Auditing Committee

We have examined the accounts of the Wilson Ornithological Society for the year 1971 and find everything in good order. We therefore approve the treasurer's report submitted by William A. Klamm.

We suggest that in the future the chairman of the Local Committee for any annual meeting be instructed to send all fees for attending the meeting to the treasurer and that the Local Committee be reimbursed for any expenses which it incurs, in our behalf, by the treasurer.—C. CHANDLER ROSS, *Chairman.*

Proposed new members of the Wilson Ornithological Society were elected as posted.

The report of the Nominating Committee was presented by the Secretary in the absence of any member of the committee. The nominations were as follows: Pershing B. Hofslund, President; Kenneth C. Parkes, First Vice-President; Andrew J. Berger, Second Vice-President; James Tate, Jr., Secretary; William A. Klamm, Treasurer; Harvey I. Fisher, Elected Member of the Council.

There were no further nominations, and a motion was made and seconded to close the nominations. The motion passed. A motion was made, seconded and passed that the Secretary be instructed to cast a unanimous ballot for the slate proposed by the Nominating Committee.

The President closed the Second Business Meeting at 14:40.

PAPERS SESSIONS

Jay M. Sheppard, California State College, Long Beach, *Movements of Color-marked LeConte's Thrashers* (Toxostoma lecontei).

W. Jon Richardson, Cornell University, *Spring Migration over Puerto Rico: A Radar Study.*

Robert C. Beason, U.S. Air Force, Kirtland AFB, New Mexico, *Aspects of Precision Radar in Monitoring Bird Behavior.*

Deborah V. Howard, Massachusetts Audubon Society, *Fall Migration of Black-capped Chickadees at Manomet Bird Observatory.*

Daniel D. Berger, Cedar Grove Ornithological Station, *The Fall Migration of Sharp-shinned Hawks Through the Western Great Lakes Region.*

Kenneth A. Youngstrom, Manomet Bird Observatory, *Applied Bird Banding: The Use of Banding to Facilitate Radiological Studies of Avifauna.*

William S. Clark, 7800 Dassett Court, Annandale, Va., *Cape May Point Raptor Banding Station.*

Charles F. Leck, Rutgers University, *The Expansion of the Monk Parakeet in New Jersey.*

Ralph E. Babcock, Western Michigan University, *Range Expansion of the Cardinal, Part II, Great Lakes States.*

Brian Sharp, Bird Banding Laboratory, Laurel, Md., *The Status of the Dusky Seaside Sparrow* (Ammospiza nigrescens).

Mary Heimerdinger Clench, Carnegie Museum, *Fall Migration Records of Kirtland's Warbler; The First Documented State Record for Pennsylvania.*

Frank B. Gill, F. J. Stokes, and C. C. Stokes, Academy of Natural Sciences of Philadelphia, *Contact Zones and Hybridization in the Jamaican Hummingbird,* Trochilus polytmus *(L.)*

Jon S. Greenlaw, C. W. Post College, *Habitat Differences in Territory Size and Clutch-size of the Rufous-sided Towhee in Relation to Food Supply.*

Roland R. Roth, University of Delaware, *A Case of Interspecific Aggression: Misdirected or Adaptive?*

Ernest A. Choate, Delaware Valley Ornithological Club, Academy of Natural Sciences of Philadelphia, *American Bird Names.*

William J. Francis, Patuxent Wildlife Research Center, *Reproductive Phenology of Blackbirds in Upland Nesting Habitat.*

Fred J. Alsop, III, University of Tennessee, *A Comparison of Eggshell Thickness in Contemporary Populations of the Red-winged Blackbird* (Agelaius phoeniceus) *with Populations Predating DDT.*

Elden W. Martin, Bowling Green State University, *Sensitivity of Starlings to Sulfur Dioxide as an Experimental Air Pollutant.*

George B. Reynard, Cornell Laboratory of Ornithology, *A New Collapsible Parabolic Reflector Convenient for Overseas Travel.*

Paul Spitzer, Cornell University, *Reproductive Failure of the Osprey in Southern New Jersey.*

Jerome A. Jackson, Mississippi State University, *Behavior of Nestling Woodpeckers.*

L. Irby Davis, 2503 Keating Lane, Austin, Texas, *Acoustic Evidence of Relationship in North American Potoos.*

Stephen I. Rothstein, Chesapeake Bay Center, Smithsonian Institution, *Egg Recognition in North American Passerines and its Relation to Cowbird Parasitism.*

Helmut C. Mueller, University of North Carolina, *The Role of the Specific Searching Image and Oddity in Prey Selection.*

Daniel S. McGeen, Oakland University, *The Kirtland's Warbler—Cowbird Interaction.*

ATTENDANCE

One hundred ninety members and guests were registered. Thirty states, the District of Columbia, two Canadian provinces, Germany, and Mexico were represented.

From ARKANSAS: 1—*Fayetteville*, Douglas James.

From COLORADO: 1—*Fort Collins*, Gustav A. Swanson.

From CONNECTICUT: 1—*Storrs*, George A. Clark, Jr.

From DELAWARE: 6—*Newark*, Roland R. Roth; *Wilmington*, Charles R. Conway, Mr. and Mrs. Albert E. Conway, Mr. and Mrs. Rodman Ward.

From DISTRICT OF COLUMBIA: 2—Richard C. Banks, Paul W. Woodward.

From FLORIDA: 1—*Winter Park*, Marjory Bartlett Sanger.

From HAWAII: 1—*Honolulu*, Andrew J. Berger.

From INDIANA: 1—*Dillsboro*, William Zimmerman.

From IOWA: 2—*Davenport*, Mr. and Mrs. Peter C. Petersen.

From KENTUCKY: 2—*Danville*, Mr. and Mrs. Frederick W. Loetscher, Jr.

From MAINE: 2—*Orono*, Mr. and Mrs. Edward J. Danforth.

From MARYLAND: 12—*Adelphi*, Brian Sharp; *Baltimore*, Richard D. Porter, C. John Ralph, Robert Wood; *Chestertown*, Mr. and Mrs. Edward Mendinhall, Mrs. James Plymire; *Columbia*, Charles J. Henry; *Edgewater*, Stephen Rothstein; *Gaithersburg*, Jeff Swinebroad; *Laurel*, Jay M. Sheppard; *Towson*, Gladys Cole.

From MASSACHUSETTS: 5—*Manomet*, Kathleen S. Anderson; *Petersham*, John and Rosalie Fiske; *Sherborn*, Richard T. Darby; *West Newton*, Deborah V. Howard.

From MICHIGAN: 11—*Alma*, Lester and Alma Eyer; *Ann Arbor*, Robert W. Storer (4); *Bronson*, Mr. and Mrs. Ralph E. Babcock; *Detroit*, Vivian Telford Anderson; *Pontiac*, Mr. and Mrs. Daniel S. McGeen.

From MINNESOTA: 1—*Duluth*, P. B. Hofslund.

From MISSISSIPPI: 5—*State College*, Mrs. W. L. Croft, Jerome A. Jackson (3), Miss Martha Ward.

From NEW HAMPSHIRE: 1—*New Hampton*, Robert W. Smart.

From NEW JERSEY: 35—*Audubon*, Clarence E. Stasz, James L. Stasz; *Blackwood*, James K. Merritt; *Bound Brook*, Robert C. Conn; *Cape May Point*, E. A. Choate; *Cranbury*, Bruce Adams; *Cranford*, Farris S. Swackhamer, Louise W. Swackhamer; *Delmont*, C. Brooke Worth; *Linwood*, Mr. and Mrs. William E. Savell; *Mt. Holly*, Katherine Price; *New Brunswick*, Charles F. Leck, Bertram G. Murray, Jr.; *Pennsauken*, Joseph Jacobs; *Piscataway*, John Kenny; *Princeton*, Miss Dorothy M. Compton, Charlotte A. DuBois, Mr. and Mrs. Charles H. Rogers; *Riverton*, George B. Reynard; *Rocky Hill*, Mr. and Mrs. Charles D. Allen; *Stone Harbor*, Herbert Mills, Miss Glosopy, Mark A. Pokras, Francis J. Singer; *Tenafly*, Mr. and Mrs. Dean Amadon; *Trenton*, Donald S. Heintzelman; *Turnersville*, James K. Meritt; *Verona*, Mr. and Mrs. Alfred E. Eynon; *Wenonah*, E. R. Manners, W. R. Middleton.

From NEW MEXICO: 1—*Albuquerque*, Robert C. Beason.

From NEW YORK: 19—*Buffalo*, Mr. and Mrs. Harold H. Axtell; *Dix Hills*, Jon S. Greenlaw; *Ithaca*, W. John Richardson, James Tate, Jr., D. Jean Tate; *Jamaica*, Frederick S. Schaeffer; *Lake Luzerne*, Elizabeth R. Thomas, Lester S. Thomas; *Long Island City*, Mr. and Mrs. Julius J. Keil; *Mamaroneck*, Robert S. Arbib, Jr.; *New York*, G. Stuart Keith, Helen S. Lapham, Lester Short, Doug Vageler; *Owego*, Ruth Williams; *Rye*, Devin A. Garrity; *Staatsburg*, Erik Kiviat.

From NORTH CAROLINA: 5—*Chapel Hill*, Helmut C. Mueller; *Montreat*, Mrs. Ira D. Holt, Miss Jane P. Holt; *Raleigh*, Thomas L. Quay, Vi Quay.

From OHIO: 15—*Ashtabula*, Howard E. Blakeslee; *Bowling Green*, Elden W. Martin; *Burton*, Robert McCullough; *Cleveland*, Ethel D. Surman; *Columbus*, Mrs. Vera Auten, Mr. and Mrs. Milton B. Trautman; *Gambier*, Robert D. Burns; *East Liverpool*, Mr. and Mrs. John Laitsh; *Lakewood*, William A. Klamm; *Sandusky*, William J. Francis; *Steubenville*, Mr. and Mrs. Clinton S. Banks; *Toledo*, J. M. McCormick.

From PENNSYLVANIA: 24—*Butler*, F. W. Preston; *Chester Springs*, Mr. and Mrs. Phillips B. Street; *Elizabethtown*, Mr. and Mrs. Robert S. Kennedy; *Flourtown*, Mr. and Mrs. Gene Stern; *Jenkintown*, Brad Gottfried; *Media*, Keith C. Richards;

Northbrook, Mrs. Frances H. Beach; *Philadelphia*, Frank B. Gill, Mr. and Mrs. Jeddu Keil, C. Chandler Ross, Robert H. Sehl, Mr. and Mrs. F. Joseph Stokes, Jr.; *Pittsburgh*, Mary H. Clench, Kenneth C. Parkes; *State College*, Dorothy L. Bordner; *Trout Run*, Mr. and Mrs. Walter K. Bigger; *Strafford*, Mr. and Mrs. Robert A. Livingston.

From SOUTH CAROLINA: 6—*Chester*, Mrs. Walker M. Atkinson, Mrs. B. Clyde Carter, James W. Crowder, Mrs. Catherine T. Moore, Mrs. W. C. Stone, Sr.; *McClellanville*, James B. Shuler.

Form TENNESSEE: 2—*Knoxville*, Fred J. Alsop, III; *Maryville*, Ralph J. Zaenglein.

From TEXAS: 2—*Austin*, Mr. and Mrs. L. Irby Davis.

From VERMONT: 1—*South Londonderry*, Mrs. James R. Downs.

From VIRGINIA: 7—*Annandale*, William S. Clark; *Arlington*, Mrs. Herbert M. Church, Jr.; *Manassas*, Mrs. Roxie C. Laybourne; *Portsmouth*, Gilbert S. Grant; *Richmond*, Charles R. Blem; *Sweet Briar*, Mr. and Mrs. Ernest P. Edwards.

From WASHINGTON: 1—*Seattle*, Karl W. Kenyon.

From WEST VIRGINIA: 7—*Inwood*, Clark Miller; *Morgantown*, Mr. and Mrs. Maurice Brooks, Mr. and Mrs. George A. Hall, Larry T. Schwab, Martha Schwab.

From WISCONSIN: 3—*Cedar Grove*, Daniel D. Berger; *Plainfield*, Frances Hamerstrom, Frederick Hamerstrom.

From GERMANY: 1—*Carlsruhe*, Ulrich Querner.

From MEXICO: 1—*San Miguel Allende*, Mrs. Lillian R. Birkenstein.

From ONTARIO: 3—*Hamilton*, Eric W. Bastin, *Parry Sound*, Mr. and Mrs. J. W. Robinson.

From QUEBEC: 2—*Westmount*, Mr. and Mrs. G. H. Montgomery.

This issue of *The Wilson Bulletin* was published on 29 September 1972.

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SUGGESTIONS TO AUTHORS

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The Wilson Bulletin

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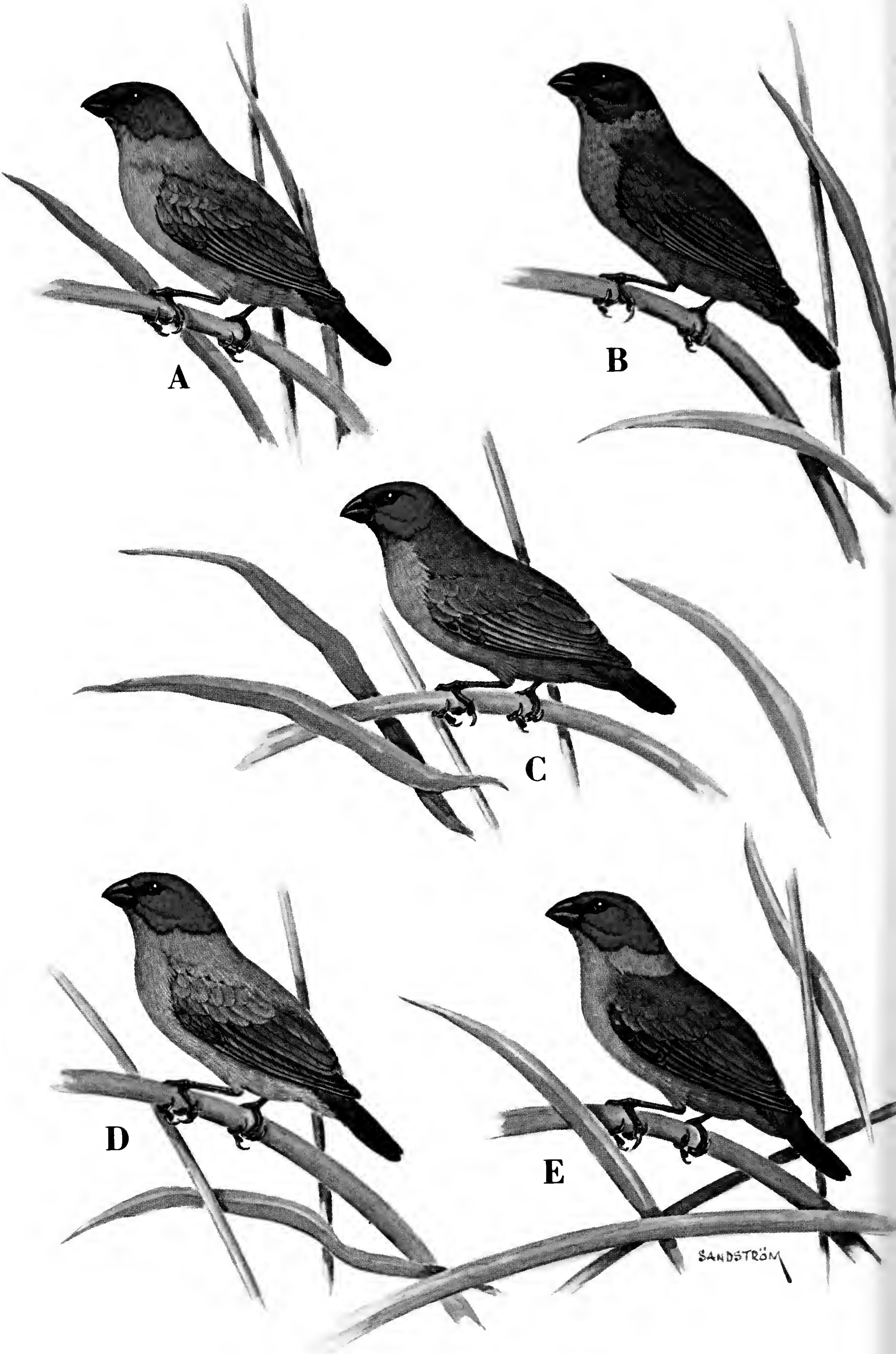

The subspecies of the Red-headed Parrot-Finch: (A) *Erythrura cyaneovirens cyaneovirens*, (B) *E. c. gaughrani*, (C) *E. c. pealii*, (D) *E. c. regia*, (E) *E. c. serena*. Painting by George Sandström.

NOTES FROM WESTERN SAMOA, INCLUDING THE DESCRIPTION OF A NEW PARROT-FINCH (*ERYTHRURA*)

JOHN E. DUPONT

IN 1970 the Delaware Museum of Natural History sent a field party to Savaii, Western Samoa, to carry out ornithological research, including recording the voices of some of the endemic species. The visit was made during the first three weeks of September by me and Dr. and Mrs. James Gaughran. We visited both the islands of Upolu and Savaii, concentrating on the latter, where we spent two weeks and ranged from sea level to the mountain tops (elevation 5,000 feet). One new subspecies was discovered, and records were obtained for three species new to Western Samoa.

I wish to thank Dr. Dean Amadon of the American Museum of Natural History and Dr. David Snow of the British Museum (Natural History) for lending specimens and assisting in other ways. Common names used are those suggested by Mayr (Birds of the Southwest Pacific, Macmillan Co., New York, 1945).

Peregrine (*Falco peregrinus*).—One adult bird seen on two occasions three miles inland from Lalomalava. Peregrines occur at least sporadically in Fiji (Viti Levu), some 750 miles WSW of Savaii, and may breed there (race *nesiotes*) (Mayr, op. cit.). Otherwise the species is virtually unknown in the Central Pacific.

Not previously recorded from Western Samoa.

Rock Dove (*Columba livia*).—A total of about 20 birds was seen on Savaii on two occasions, once at Lalomalava, and once at Satuiatua. The birds did not seem to stray far from the native huts and were not seen around large buildings in towns. Undoubtedly these were domesticated birds, but all were of the wild plumage type, i.e. gray coloration. The species may be expected to spread into other areas as a feral bird, but probably in settled areas only, as few cliffs are available in the wild.

Not previously recorded from Western Samoa.

Tooth-billed Pigeon (*Didunculus strigirostris*).—Found in virgin forest from 1,000 feet to 4,500 feet, where most often seen sitting on large limbs near tree trunk and not on the ground as has been generally recorded. Voice a slow *hoo*, *hoo*, *hoo*, low-pitched and infrequently heard.

This species is in no immediate danger of extinction so long as the forests remain intact. The bird was seen in original forests, sometimes quite near towns, but not in cut-over areas anywhere.

Red-vented Bulbul (*Pycnonotus cafer bengalensis*).—1 adult ♂ specimen was taken 6 September 1970, at Lalomalava. Birds seen in Apia, Upolu, and around Lalomalava, Savaii. These birds were numerous in Apia, but in Lalomalava only small numbers were seen. This species was undoubtedly introduced into Samoa, perhaps directly from India, but more likely from the introduced population of Fiji.

Not previously recorded from Western Samoa.

Samoan Starling (*Aplonis atrifusca*).—This bird was encountered in small to moderate numbers from the sea coast to the mountain tops. Nests, heretofore unknown, were found on two separate occasions about 40–50 feet up in cracks in old, dead trees, one in a limb and one in a trunk. A female carrying nest material was collected on 12 September 1970, at Lalomalava, Savaii. Soft part colors of four adults are: bill black, iris dark brown, feet black.

Red-headed Parrot-Finch (*Erythrura cyaneovirens*).—This colorful parrot-finch of the Central Pacific is separable into five subspecies, the nominate race being from Upolu, Western Samoa. Although some years ago Mayr (Amer. Mus. Novitates, 489:7, 1931) pointed out the Savaii population might be separable, only recently has material been collected that proves this suggestion to be valid. The Savaii race may be called:

Erythrura cyaneovirens gaughrani new subspecies

Type: DMNH 4868, male, Mt. 'O'a, Savaii, Western Samoa, 5,000 feet, 8 September 1970. Wing 64 mm, tail 32 mm, bill 13 mm, tarsus 18 mm.

Diagnosis: Male differs from *E. c. cyaneovirens* of Upolu by having the red on the head and tail decidedly darker; blue on the nape paler and less extensive; back green, lacking any blue; chin and throat green with a less extensive and paler blue wash; underparts green with only a slight trace of a blue wash; wing coverts greener lacking any of bluish edgings. Immatures from Savaii mirror the characters of the male by being green with very little blue. Adult female unknown.

Range: Savaii, Western Samoa.

Specimens examined: E. c. cyaneovirens—Upolu, 4 ♂, 1 ♀, 1 ?; *E. c. gaughrani*—Savaii, 1 ♂ (Type), 2 imm. ♂, 4 imm. ♀, 2 imm. ?.

Etymology: This new subspecies is named for Dr. James Gaughran of Stanford University.

The other races that I recognize of the species are:

Erythrura cyaneovirens pealii.— Geospiza prasina Peale, 1848, U.S. Expl. Expd. Bds., p. 116 (Vanua Levu, Fiji). *Erythrura pealii* Hartlaub, 1852, Arch. F. Naturg., p. 104 (new name for *Geospiza prasina* Peale, 1848). Range: Fiji Islands.

Erythrura cyaneovirens regia.—Erythrospiza regia Sclater, 1881, Ibis, p. 554 (Api = Epi Island, New Hebrides). Range: Bank Islands and northern New Hebrides.

Erythrura cyaneovirens serena.—Erythrospiza serena Sclater, 1881, Ibis, p. 544 (Aneiteum Island, New Hebrides). *Erythrura cyaneovirens efatensis* Mayr, 1931, Am. Mus. Novitates, 489:8 (Efate Island, New Hebrides).

E. c. efatensis is slightly and incompletely differentiated from *E. c. serena*, and I treat it as a synonym of the latter. Differences in the red coloration of the head and upper tail coverts seem to be due to differences in wear in the available specimens. The *serena* series was taken in February and appears to be more worn than the *efatensis* series, taken in June and July. Mayr (1931:10) also mentioned possible differences in the color of the secondary coverts, those of *serena* thought to be green versus bluish in *efatensis*. I found this character to be variable, with the fully adult *serena* being quite blue.

In wing length Mayr (1931:9) shows *efatensis* as being 61–65 mm in 26 adults, versus 66–67 in 3 adult *serena*. I have remeasured 16 of the *efatensis* and 2 of the *serena* and find that while the former average shorter-winged, there is overlap. My *efatensis* measurements are 62.5–66.5 and *serena* are 65–67.5, thus showing an overlap in the range 65–66.5 (4 birds). Range: Aneiteum and Efate Islands, New Hebrides.

DELAWARE MUSEUM OF NATURAL HISTORY, GREENVILLE, DELAWARE 19807, 10 APRIL 1972.

THE BEHAVIOR OF PLAIN-BROWN WOODCREEPERS, *DENDROCINCLA FULIGINOSA*

Edwin O. Willis

In forests of tropical America, woodcreepers of the genus *Dendrocincla* follow swarms of army ants persistently (Willis, 1960:158–159; Skutch, 1969:136; Oniki and Willis, 1972). Intensive studies of ant-following birds on Barro Colorado Island, Panamá Canal Zone, and brief studies in other areas show that Plain-brown Woodcreepers regularly follow army ants. The changes in foraging niche when these woodcreepers confront different sets of competing antbirds at some of the localities have been detailed elsewhere (Willis, 1966). Here social and individual behavior will be considered.

Feduccia (1970:1) lists many brief references, mostly in annotated lists, on the behavior of woodcreepers. The only extensive studies have been Skutch's (1969) of Tawny-winged and other woodcreepers. Slud (1960, 1964) and several others, including Johnson (1954) and Snow and Snow (1964) and Oniki (1970) among references not listed by Feduccia, have commented briefly on the natural history of Plain-brown Woodcreepers. The species and its genus and family are not well known ethologically.

Appendix 1 lists common and scientific names of birds mentioned herein, following Meyer de Schauensee (1970), except for Central American birds listed only in Eisenmann (1955) and for northern birds listed in the A.O.U. Check-list.

THE PLAIN-BROWN WOODCREEPERS

Plain-brown Woodcreepers wait on or hitch up the trunks of trees like slender woodpeckers or overgrown Brown Creepers. They live in the middle and lower levels of humid lowland forests from Honduras to central Brasil. Occasionally they wander to the edge of the forest, into cacao and coffee orchards, or into second growth more than 5 m tall. Instead of hammering or probing at bark or epiphytes, they peck prey off the surface of vegetation or sally out like flycatchers to snap prey off nearby vegetation, the ground, or out of the air. Commonly they follow army ants and capture arthropods they flush. Occasionally they flycatch away from ants, alone or with wandering interspecific flocks of insectivorous birds.

This is a brown bird with a dark malar streak below a pale gray face (Fig. 1); as in many woodcreepers, the flight and tail feathers are rufous. The yellow linings of wings and mouth and the pale throat seldom show as the bird waits stolidly. A dark streak from bill to eye and a yellowish streak behind the eye are similarly inconspicuous.

FIG. 1. Plain-brown Woodcreeper on Barro Colorado Island, Panama Canal Zone from slide; seen from below.

On Barro Colorado Island, weights of eight Plain-brown Woodcreepers ranged from 38.5 to 43.4 g (mean 41.6); these birds were captured over ant swarms, where food is abundant. James Karr (pers. comm.), netting mostly birds away from army ants nearby in the Canal Zone, found a range in seven birds (ten weights) from 35.0–44.4 g (mean 40.4). Culmens of 39 Panamanian birds in the American Museum of Natural History range from 27.1–32.5 mm (mean 30.2) without sexual differences.

Wing lengths (chord) for Panamanian specimens at the American Museum and at the Museum of Comparative Zoology are 96–106 mm (mean 101.4) for 21 females and 102–113 mm (mean 108.6) for 31 males. Some "males" with short wings and "females" with long wings may have been sexed incorrectly, since labels of these particular specimens indicate gonads were not enlarged. However, short-winged males may have been young. (Birds with very worn, damaged or molting wings were excluded from samples). Birds from other countries have different wing lengths, but males always average longer in

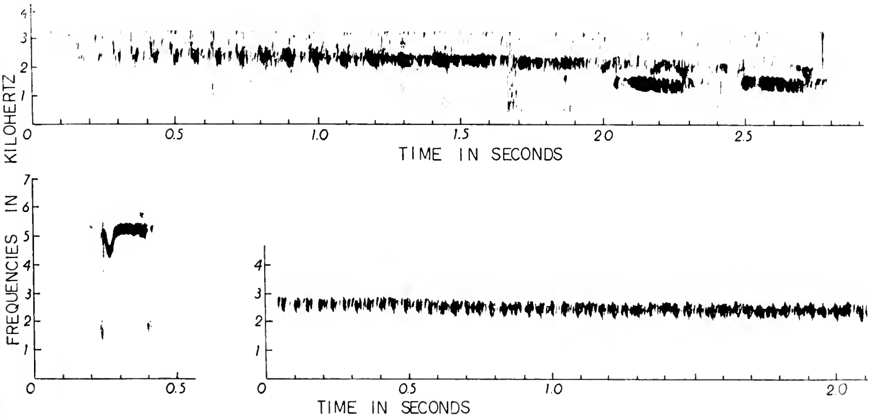

FIG. 2. Audiospectrograms of vocalizations of Plain-brown Woodcreepers. Above, "song"; two caws of a Slaty Antshrike overlap the end of the song. Below left, a "stiek" alarm note. Below right, "long rattling."

wing length than do females from any given region. The dimorphism in wing length helped me sex some birds captured on Barro Colorado Island. Eight adult females there had wings 101–105 mm long (mean 102.5), and four adult males had wings 108–110 mm long (mean 109). Two other birds, with wings of 104 and 106 mm, were judged by their later activity to be nearly-grown fledglings. Adult females also have vascularized, featherless brood patches while nesting.

THE STUDY AREAS

The climate, forest, and study area on Barro Colorado Island and several other localities where I watched Plain-brown Woodcreepers are described in Willis (1967). This reference also describes the behavior of army ants (especially the important species, *Eciton burchelli* and *Labidus praedator*) and methods of study. Many woodcreepers were banded with color bands; female RBYM, for instance, had a blue band above a red one on her left leg and a yellow band above red/white one on her right leg.

I studied woodcreepers over or away from army ants on Barro Colorado from 28 September, 1960 to 25 November, 1961, and for a few months each year to 1971. Information on Plain-brown Woodcreepers comes mainly from observations at swarms of army ants while I was watching many species. However, nearly as many hours have been spent censusing birds while looking for ants, so that the woodcreepers have occasionally been studied away from ants.

VOICE

Plain-brown Woodcreepers have only five calls that seem worthy of separate names, and none is varied, complex, or musical.

Stieking.—This is a piercing, sudden, high-pitched (Fig. 2) *scheek* or *stiek* given by an alarmed bird. The beak flaps open suddenly, showing the yellow lining more prominently than at any other time. The call is given at a rate of less than 40 per minute unless the bird is extremely disturbed.

Rattling.—This is a faint series of short grunting noises like the distant put-putting of an outboard motor or clacking of a train. The whole body quivers for the notes, but the bill is closed or barely open. The series may be brief ("rattlet") or continue for several minutes at a time ("long rattle"). *Chut-ut-ut-ut-u-u-u-u*, *a-a-a-a-a-a-a*, *ri'i'i'i'i chew-ew ri'i'i'i'i* and similar notations are in my field notes for this call. It often varies in pitch and speed, but usually is at about 23 notes per second (Fig. 2).

Singing.—The rough "song" of this species (Fig. 2) is a descending series of 25 or so notes, each one like a grunt during rattling but less rough in quality and given more loudly. Notes are longer toward the end of the song. *Whee-hee-he-hah-huh-huh-huh-huh-huh-huh-huh-hu-hu-hu-hu-hu-hu-hoo-hoo-hooh*, *wee-i-woo*! is one rendering. The sudden up-and-down ending, the greater speed, and the loudness of the song distinguish it from the rather similar but longer descending song of Black-striped Woodcreepers. Unlike rattling, singing is rather stereotyped. Males, females, and young birds all sing; songs occur in every month of the year, and seem communications of isolated birds hunting others rather than aggressive calls or sexual ones.

Hissing and Growling.—When a bird follows another closely a hissing or growling *chauhh* or similar sound is given. At increased speed the hissing or growling grades into rattling.

Screaming.—In the hand or when pecked by a supplanting bird, a woodcreeper screams roughly and piercingly. The burst of noise, *screeah* or the like, is more like hissing than like the clear and distinct stieking.

POSTURES AND MOVEMENTS

While clinging to a vertical trunk, the Plain-brown Woodcreeper often takes what may be designated the "standard posture" (Fig. 1 shows a slightly crouched bird, close to the standard posture). The slender and rather long body angles away from the trunk about 15 degrees and is clearly separated from it in side view. The bird is suspended by the front claws as it rests on the stiffened and somewhat incurved bare tips of the tail feathers. When seen from behind, as the bird clings to the trunk, the three front toes on each foot spray from just below the horizontal to 70 or so degrees above it, while the rear toe follows the line of the tarsus at about 60 degrees below the horizontal. The long, curved front claws dig into the thin and smooth bark usual on tropical trees, and the rear claws clamp in to some extent. Ordinarily the toes and sole of the foot are off the perch. The bill points about 15 degrees toward the trunk, or some 30 degrees from the line of the body. The wings meet above the base of the tail, and the bend of the wing is exposed.

TABLE 1

PERCH CHARACTERISTICS OF PLAIN-BROWN WOODCREEPERS

HEIGHT[a]		ANGLE[b]		DIAMETER[c]	
Height (m)	Records	Angle (deg)	Records	Diameter (cm)	Records
0.1	4	20 or less	31	0–1	11
0.2	19	40	37	–2	107
0.3	99	60	74	–3	206
0.4	242	80	284	–4	213
0.5	308	100	2525	–5	202
0.6	201	120	153	–15	1177
0.7	177	140	12	–25	471
0.8	218	160	4	–50	259
0.9	164			–100	138
1.0	148			100+	22
1	1580				
2	1676				
3	1167				
4	1084				
5	650				
6	497				
7	360				
8	340				
9	200				
10	158				
15	234				
20	14				
25	3				
30	3				
Totals	7966		3120		2806

[a] Barro Colorado Island, 1960–1964 data over army ants. Records are 0–0.1 or 0–1 m up to 26–30 m.

[b] Barro Colorado Island, 1960–1961 data over army ants. Records over 90° represent clinging to the underside of a perch. Records are for 0–20°, 20–40° etc.

[c] Barro Colorado, 1960–1961 data over army ants. Records are 0–1.0, 1.1–2.0 cm etc.

A tailless bird, in heavy molt, rests against the undertail coverts and upper parts of the legs when clinging to a vertical perch.

On the rare occasions (Table 1) when this woodcreeper perches on a horizontal or nearly horizontal perch, it frequently stands across it like a perching bird rather than along it like a woodpecker. Commonly the woodcreeper sits close, splay-legged and somewhat humped around the perch (Fig. 3,D), but at times one stands almost as upright as a thrush. One bird that tried to perch crosswise on a wet limb kept sliding backward (Fig. 3,E). A woodcreeper

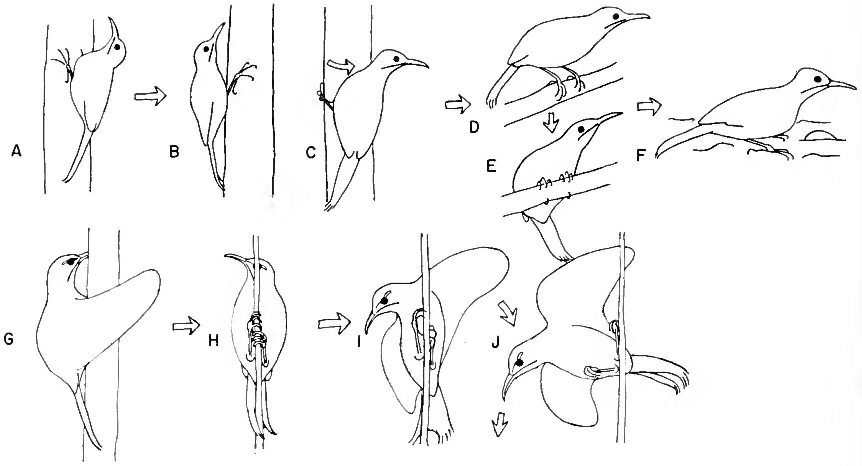

Fig. 3. Perching and travel of Plain-brown Woodcreepers. A bird alarmed by the stieking of another holds its head out (A), flies to another trunk and crouches (B), swings around the trunk (C) and on to another foraging area, where it perches briefly on a horizontal limb (D) but keeps sliding back on the wet bark (E); it flies to the ground briefly but has its crest raised (F). Another bird flashes its wing to flush a prey (G), waits on a slender sapling above ants (H), dives toward prey on the ground (I, J) by using its wings. From scattered field sketches at Simla, Trinidad.

perching crosswise reminds one of a leafscraper (*Sclerurus* sp.) or other furnariid. The plain brown leafscrapers often cling vertically to a tree trunk or buttress when first flushed, and then resemble Plain-brown Woodcreepers remarkably. Feduccia (1969) suggests from morphological studies that the genus *Dendrocincla* may have evolved from Furnariidae, but from the foliage-gleaners (Philydorinae) rather than from leafscrapers (Sclerurinae).

Plain-brown Woodcreepers stay on perches near the vertical far more often than they stand on horizontal perches or cling underneath perches (Table 1). Their woodpeckerlike adaptations also seem better suited for perching on trunks larger than 2 cm in diameter (Table 1), particularly for poles 5 to 15 cm in diameter. In this respect they differ from such competing birds as Bicolored Antbirds, which cling horizontally to vertical perches but cling to perches more than 4 cm in diameter only with great difficulty (Willis, 1967). The vertically-clinging types of birds and the horizontally-clinging types, both usual at swarms of ants, complement each other. Occasionally a Plain-brown Woodcreeper clings to slender saplings, especially on Trinidad where competing antbirds are absent. If the sapling is 1–2 cm in diameter, the bird simply interlaces its toes. On perches less than 1 cm in diameter the bird has to put one foot above the other (Fig. 3,H) or oppose the first and second toes of each foot while the outer toes hang freely. The outer feathers often slip forward and do not support the bird on such narrow perches.

Plain-brown Woodcreepers perch near the ground when few antbirds compete with them and high in the trees when antbirds are present (Willis, 1966). Table 1 summarizes the vertical distribution of the Woodcreeper over swarms of army ants on Barro Colorado Island.

HOPPING AND FLIGHT

Plain-brown Woodcreepers move up or down trunks by hopping or "hitching." In hitching upward, the bird catches itself with the tail at the end of each backward extension of the legs, then flexes the legs and catches hold of the bark again. In contrast to Barred Woodcreepers, hitching up and around perches is far more common than hitching downward. However, Plain-brown Woodcreepers do back downward occasionally. I have never seen hitching with head down like a nuthatch. On a horizonal perch or on the ground the bird may hop sideways, body angled at about 60 degrees from the line of progress; but the short legs force the bird to fly or flutter-hop for progressive movement. Adaptations for perching like a woodpecker definitely restrict freedom of movement on a perch compared with species like Bicolored Antbirds (see Willis, 1967).

In taking flight, the main push comes from the wings rather than from the short and forward-angled legs. These woodcreepers seldom hop from one perch to another without flapping the wings, and rapid movement up a trunk is often performed by fluttering vertically rather than by hitching. The long claws, which keep the feet off the trunk, probably do not permit rapid hopping or the effective use of the legs in taking wing in many situations.

Flight is strong. The long and broad wings flap rapidly, with occasional pauses, as a bird weaves rapidly through leaves and branches. The flight is slightly undulating. Long flights in one direction are rare, but the birds are expert at frequent changes of direction and at darting in and out of moderately dense vegetation. At times a fluttering or slow flight is adopted when one bird chases another. Flight is silent unless the bird hits leaves. These woodcreepers hover readily for brief periods: they can hover in any direction but backwards. In general, they combine speed with maneuverability very well.

In alighting, the Plain-brown Woodcreeper seldom glides up and in with wings outspread as do larger woodcreepers (especially the Barred Woodcreeper); it usually flaps as it comes to the perch, then quickly closes the wings when it alights. The yellow wing linings are seldom conspicuous in flight.

TABLE 2

ACTIVITIES OF PLAIN-BROWN WOODCREEPERS AWAY FROM SWARMS OF ANTS

Activity	Occasions	No. Birds	No. minutes
1. Wandering			
a. With other ant-followers[a]	12 (4.4%)	13	53
b. In to playback[b]	8 (2.9)	8	50
c. Singing	59 (21.5)	65	163
d. Rattling or quiet	38 (13.9)	48	159
2. Foraging			
a. With bird flock[c]	38 (13.9)	47	498
b. Not with flock	20 (7.3)	26	231
3. Bathing	8 (2.9)	11	54
4. Resting	1 (0.4)	1	7
5. Search for nest site	3 (1.1)	4	29
6. Sticking at predator or me	67 (24.4)	84	314
7. Activity uncertain	20 (7.3)	22	41
Total	274 (100.0)	329	1599

[a] Bicolored Antbird, Ocellated Antbird, Spotted Antbird, or Barred Woodcreeper. Recorded with Gray-headed Tanagers elsewhere (Rio Agua Salud, Panamá Canal Zone).
[b] Of songs of Bicolored Antbirds.
[c] Followed flocks of birds for at least one minute.

WANDERING AND INTERSPECIFIC FLOCKS

Johnson (1954:45) proposed that Plain-brown Woodcreepers typically follow the wandering interspecific flocks through the forest but are easily attracted to flocks of birds that follow army ants. I would reverse the order of importance. These woodcreepers follow army ants whenever they are available, even when no other bird is present, but occasionally join the wandering flocks when no ants are available. At other times the woodcreeper drifts through the forest alone, waiting and foraging as it goes, until it encounters a swarm of ants.

Away from swarms the Plain-brown Woodcreeper typically travels singly. Two adult birds together are generally unmated and unrelated birds, together for a short time. Most groups of two and three birds are a female with dependent young. Away from swarms on Barro Colorado, I have 210 records of one bird, 46 records of two, and 6 records of three together. The activities of these birds are listed in Table 2. For this table, a bird was considered to be "wandering" if it rapidly changed perches in a given direction and spent little time looking about at stops; a "foraging" bird stays and looks about from a perch, and changes perches first in one direction and then in another. Wandering birds forage to some extent.

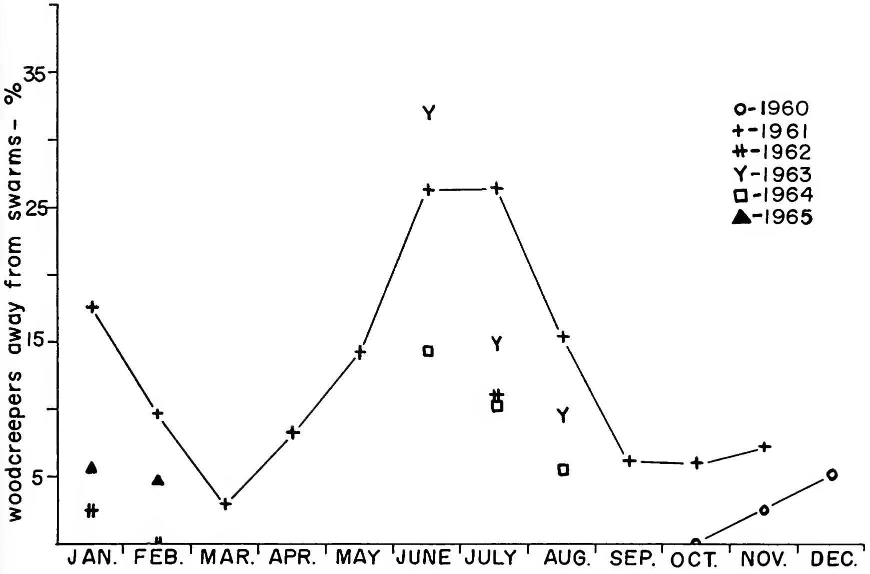

FIG. 4. Percentages of Plain-brown Woodcreepers away from swarms of army ants on Barro Colorado Island, 1960–1965.

Plain-brown Woodcreepers forage readily away from swarms of ants, in contrast to such ant-following species as Bicolored Antbirds (Willis, 1967). The percentage of woodcreepers away from swarms of ants on Barro Colorado rises during the rainy or nesting season (Fig. 4), when arthropods are more numerous away from swarms of ants. Highest use of swarms is in the late rainy season and in the dry season, when the young of the previous breeding season swell the ranks of ant-following birds (Fig. 5). There is some variation from year to year. In January and February of 1961 an unusually high percentage of woodcreepers wandered away from swarms. Perhaps this was a case of what Tinbergen (1946) calls "specific search images." During the preceding three months there had been an unusual number of swarms of *Labidus praedator*, which emerged frequently in the wet year of 1960. Disappearance of swarms of *praedator* in early 1961 apparently left many woodcreepers searching for them, even though swarms of *Eciton burchelli* were not overcrowded during these months (Fig. 5). In 1964 and 1965 there were unusually many swarms of *Eciton burchelli*, so that the percentage of woodcreepers away from swarms (Fig. 4) and number per swarm (Fig. 5) were both low.

On 58 of 255 occasions when Plain-brown Woodcreepers were recorded away from swarms and ant-following birds on Barro Colorado, they were

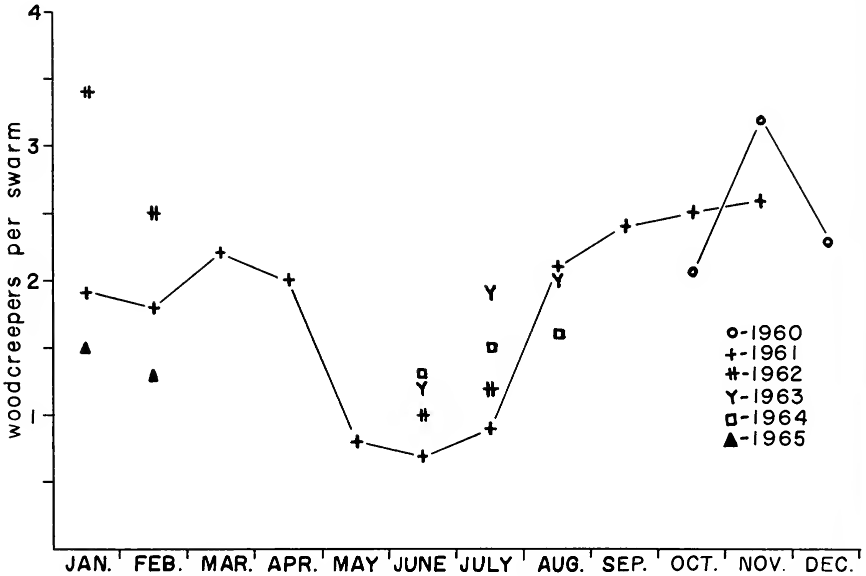

FIG. 5. Numbers of Plain-brown Woodcreepers at swarms of *Eciton burchelli* on Barro Colorado Island, 1960–1965.

with the wandering interspecific flocks of the forest interior (Willis, 1972). These flocks, which are entirely different from the ant-following interspecific flocks even though a few species occur in both, are characteristic of many forested areas in the tropics. Plain-brown Woodcreepers rarely lead such flocks or attract other species; they are desultory joiners and followers, or what Moynihan (1962) calls "active attendant species." Moynihan's term "active" implies joining rather than activity; the woodcreepers do not forage by moving actively, and often are rather inactive in following flocks about.

I doubt that other small birds often flush the large insects favored by woodcreepers. It is more likely that mixed flocks are efficient at detecting hawks and other predators, so that individual birds can then devote more time to finding food and specialize in foraging niches or use otherwise unsafe niches rather than watch in all directions for predators (see Willis, 1972). Plain-brown Woodcreepers stiek loudly from their elevated perches when hawks or distant ground predators such as tayras (*Eira barbara*) appear. The small birds near the forest floor are the first to call when predatory mammals pass in dense vegetation. Thus the high-foraging woodcreepers must often get advance warning of danger in a zone where they are not foraging actively.

I sometimes detected a Plain-brown Woodcreeper away from swarms by its loud stieking when I or a predator passed (Table 2). At other times woodcreepers sang as they wandered through the forest. Most singing birds wandered as if looking for a swarm of ants; such songs are sometimes answered by birds at swarms, and the singer homes on the replier. Females separated from their young also sing, and the young sing, stiek or hiss to their mother. The song is thus often used in the way Bicolored Antbirds use "loud-songs," (Willis, 1967), as a locating or "lost" call rather than as a territorial, agonistic, or sexual call. Songs occasionally follow agonistic encounters. Rattles and other calls were occasionally used by wandering birds, but silence was more usual if birds were not singing or stieking.

Playing recorded loud-songs of Bicolored Antbirds in the forest (see Willis, 1967:25 for methods) brought Plain-brown Woodcreepers up to the loudspeaker on 10 out of 79 trials. On several occasions the woodcreeper flew past the speaker and then flew back to it when the next loud-song was played. On a separate occasion the chirring of Bicolored Antbirds near their recently-fledged young brought up a Plain-brown Woodcreeper. A woodcreeper is thus able to home on the calls of the noisy Bicolored Antbirds, which as professional ant-followers usually are close to swarms of ants. It also homes on the calls of other species that follow army ants, especially the noisy and common Spotted Antbirds. On 3 October 1961 one woodcreeper arrived as two male Spotted Antbirds disputed away from a swarm. On several other occasions woodcreepers flew to the songs of Spotted Antbirds or associated with them in wandering flocks at points distant from known swarms; in some of these cases the two may have stayed together after leaving a folded or inactive swarm nearby, however. Plain-brown Woodcreepers occasionally follow other professional ant-followers when they move between branches of a swarm or to other swarms distant in the forest (Table 2).

Besides homing on the calls of other species that follow army ants or following those species about, Plain-brown Woodcreepers show several other behavior patterns usual among "professional" ant-followers. Interest in ants is not confined to swarms that are actively flushing insects, as is usual for the many "non-professional" ant-followers on Barro Colorado and elsewhere. Plain-brown Woodcreepers commonly visit "statary" (sedentary) army ant bivouacs, peer around the tree trunk, and follow any line of ants to the distant swarm. The woodcreepers occasionally wander near inactive bivouacs for hours until the ants finally start swarming. Plain-brown Woodcreepers, like other professional ant-followers, move along lines or trails of ants between nomadic bivouacs and swarms rather than stumbling on swarms by accident. Individual woodcreepers follow the same colony of the army ant *Eciton burchelli* for days or weeks at a time, return to it periodically during a statary period, and may resume following the colony when it becomes active again during the nomadic period. They shift readily from one colony to another, even when they have to travel a kilometer or more to do so.

Plain-brown Woodcreepers show by their behavior that they are strong ant-followers, and they are certainly "professional" ant-followers (ones that get more than 50 per cent of their food over ants) even though they forage readily away from ants. On Trinidad, where competing ant-following antbirds are absent, the woodcreepers rarely forage away from swarms. In other regions they probably depend on swarms of ants for most (60–90 per cent) of their food.

FORAGING BEHAVIOR

When following army ants a Plain-brown Woodcreeper waits on the trunks of trees or saplings, turning its head at intervals, until a large prey moves; then the bird darts over and snaps the prey out of the air or off the vegetation. Occasionally a bird hitches up or down, perhaps spiraling rapidly, and pecks prey while on a perch. These birds rarely poke in epiphytes or under bark as do many species of the Dendrocolaptidae. At times there is an involved aerial or semiaerial pursuit, with fluttering or hovering or rapid changes of direction.

When foraging off the ground, Plain-brown Woodcreepers forage most actively around rotten trunks and stubs, tangles of lianas in the crowns of saplings, near epiphytes, in the crowns of palms, at places where a dead limb or tree has jammed above the ground, and near other tangled places. Usually the birds wait on vertical lianas or saplings near the tangle or palm crown and sally to the periphery of the tangle for prey. At times, however, a bird hitches or flutters to deep within a tangle. The vicinity of a tangled treefall on the ground is another favorite site. When the ants pass through open forest, the woodcreepers scatter to vertical trunks and forage little unless competing antbirds are absent. Then they forage rapidly, and capture many prey items on the ground.

Table 3 lists foraging motions for Plain-brown Woodcreepers over ants on Barro Colorado Island. Birds take prey on the wing ("sallying") more frequently than they "lunge" or peck for prey from a perch. Prey taken on trunks is commonly pecked, however. Although these woodcreepers sally to the ground rather frequently, they take a large proportion of their prey from leaves and other vegetation above the ground. A greater proportion of prey is taken above the ground when such competing ground-foraging antbirds as Ocellated Antbirds are present (Willis, 1966).

The woodpeckerlike foraging position of the Plain-brown Woodcreeper seems a distinct disadvantage compared to the crosswise positions of competing ground-foraging antbirds. The woodcreeper uses small trunks only

TABLE 3

FORAGING MOTIONS OF PLAIN-BROWN WOODCREEPERS[a]

Place of capture	Foraging Motion			
	Sallying	Lunging	Leaftossing	Prying
Ground, root, log	328	5	3	–
Trunk	219	263	–	1
Stem or liana	230	83	–	–
Limb or twig	27	8	–	–
Leaf or petiole	410	23	–	–
Dead leaf or debris	26	7	–	–
Air	182	7	–	–
Unspecified	204	7	–	–
Total	1626	403	3	1

[a] From 1 October 1960 to 30 September 1961, over army ants on Barro Colorado.

with difficulty (Fig. 3,H). Large perches, besides being uncommon, block part of a bird's view. The woodcreeper must fly upward for a short distance or turn in midair (Fig. 3,I,J) to get away from the trunk if it is to capture prey below it, since it starts from a head-up position, but it is not delayed more than a fraction of a second by the conflict of adaptations for clinging with those for pursuing prey below it. Still, when a fast-leaping antbird and a woodcreeper go for the same prey the antbird usually captures it. The short legs and long toes of the woodcreeper also make hopping after prey on the ground rather difficult. If the woodcreeper misses prey on the first sally it must fly up again, fly short distances along the ground, or stay flopping, wheeling, and pecking in the midst of attacking army ants. A long-legged antbird hops nimbly about, exposing its feathers and body to the ants only rarely.

Away from swarms, I have never seen a woodcreeper sally to the ground. The woodcreepers forage 3–15 m above the ground at such times, in the mid-levels of the forest. Probably this is the zone in which the perching behavior and foraging motions of woodcreepers are most effective. Moreover, there probably are few prey items large enough on the ground unless ants flush them. Foraging strategy away from ants involves short waits on tree trunks, hitches upward to new waiting sites, flights to other trunks, and the like. To get food, a woodcreeper away from ants usually sallies to distant foliage or trunks, and hovers to catch the prey or chases it in flight. Less often it pecks off prey as it alights or as the prey alights, or pecks prey off a surface while hitching upward. They are unlike most woodcreepers (genera *Xiphorhynchus*, *Glyphorhynchus*, etc.), which forage by peering and pecking at or into trunks

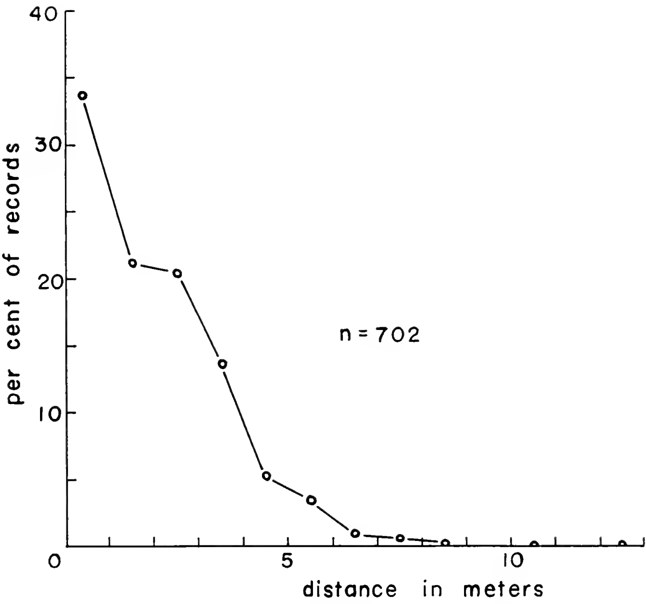

FIG. 6. Distances that Plain-brown Woodcreepers flew to try for prey ("sallying").

and epiphytes close-by, but are like other ant-following woodcreepers (genera *Dendrocincla*, *Dendrocolaptes* and *Hylexetastes*), in being "flycatchers" to distant surfaces.

Prey at and away from ants is captured both above and below a foraging bird. The distances of sallying are shown in Fig. 6. The Plain-brown Woodcreeper has a larger foraging radius than do such species as Bicolored Antbirds (Willis, 1967). However, 75 per cent of the prey of Plain-brown Woodcreepers is captured within 3 m from the perch and 98 per cent within 6 m.

Plain-brown Woodcreepers frequently use "wing-flashing" when prey stops and is concealed. The bird moves to the trunk where prey disappeared and briefly flashes one wing widely along the surface of the trunk. On slender trunks the bird may simultaneously sidle and peer around the trunk from the opposite direction (Fig. 3,H), so that it will run into prey fleeing the wing. At times a woodcreeper flashes its wings alternately, sidling and feinting back and forth around the trunk as if shadow boxing. The bird may also angle the head one way and then the other in the direction opposite the wing flashed instead of sidling bodily. On larger trunks the bird may crane the head or sidle in the direction of the flashed wing rather than in the opposite direction. Thus wing-flashing is not just a way to sidle more rapidly, although it could easily have originated from such rapid sidling motions.

TABLE 4
FOOD OF PLAIN-BROWN WOODCREEPERS[a]

	Size of prey in mm						
Food	?	0–10	10–20	20–30	30–40	40–50	50–125
Unspecified		110	60	34	4	1	
Sowbug	1						
Whip scorpions			2	3			
Scorpions			1	4	4		
Spiders	6		11	24	4	1	
Egg case	1						
Centipede				3	3	5	4
Millipede	1						
Roaches	7	3	18	23	6		
Orthopterans	12		15	32	17	4	6
Walkingstick							1
Mantids	1					1	1
Odonatans							1
Cicadas	6		1	3	1		
Heteropterans			1	2			
Beetles			2				
Beetle grubs	1			1			
Neuropteran				1			
Moths	10	2	7	4			
Caterpillars				2	1		
Ants	4	1	1	1			
Ichneumon			1				
Hymenopterans		1	3				
Lizards				1		2	3

[a] Barro Colorado Island, 1960–1971.

In 89 out of 105 recorded observations of wing-flashing, the presence or absence of foraging motions was noted. In 32 cases (36 per cent) the bird peered intently after wingflashing one to several times but made no try for prey. In one case the bird flashed at an insect covered by army ants; although unsuccessful here, wing-flashing may occasionally flush prey already captured by army ants. In a second of the 32 cases a Black-breasted Puffbird sitting above captured prey flushed by the wing-flashing woodcreeper. In 57 cases (64 per cent), the woodcreeper immediately sallied or lunged for fleeing prey. The woodcreeper is thus somewhat less successful at wing-flashing than is the Mockingbird which tries for prey after 74 per cent of its wingflashes (Hailman, 1960).

I recorded successful wing-flashing to flush prey by a White-chinned Woodcreeper at Cashibococha, Perú. Tawny-winged Woodcreepers flash the wings even more frequently than do Plain-brown Woodcreepers. Perhaps the conspicuous tawny wing patches of the Tawnywing and the yellow undersides of the wings of all three species are adaptations for flushing prey. There is some use of double wing-flashing in aggressive displays in all these species, however.

Orthopterans (mostly long-horned grasshoppers, katydids, crickets), roaches, and spiders are the primary large food of Plain-brown Woodcreepers at swarms of ants (Table 4). Moths, centipedes, scorpions, cicadas, and lizards (mostly *Anolis limifrons*) are also taken readily. Only prey that was held in the bill long enough for size to be estimated as a fraction of exposed bill length (about 25 mm) or for reasonably certain identification is listed in this table. The size range indicated is skewed toward the maxmum sizes of prey, since small prey was often swallowed before I could see it. This distribution of maximum-sized prey centers on the bill length of the species, although slender prey (centipedes, orthopterans, damselflies, lizards) were sometimes three to five times the length of the beak.

Small prey is swallowed at once. Large prey is frequently chewed vigorously and hammered or flailed against the trunk. The woodcreeper may hitch up the trunk now and then, hammering the prey at each stop, or fly to a new perch to continue work. The feet are never used for holding prey. One woodcreeper drooped its wings toward the trunk as it hammered prey, in the fashion of a hawk "shielding" its prey. Moth and locust wings are usually dropped. Legs and other small pieces of prey that fall are ignored, but the bird may dive after a major piece. If dropped prey falls to near the ground it is readily snapped up by Bicolored Antbirds. At other times other Plain-brown Woodcreepers may catch dropped prey.

Some small prey items are dropped or thrown away immediately or dropped after some chewing in the tip of the bill. These are probably prey with chemical defenses, for the woodcreeper often wipes the bill and shakes the head after such an encounter.

ANTING

Some small prey items elicit "anting" behavior. Instead of dropping the prey and wiping the bill, the bird chews the prey in the tip of the bill, brushes the prey through the rectrices or the under tail coverts (Fig 7,F), and resumes chewing. Often the bird shakes the prey before brushing it through the rectrices or regimes repeatedly. I recorded anting 67 times. On 35 occasions the prey was eaten. On one occasion the bird dropped the prey and bill-wiped repeatedly; on another, the prey was thrown away. On the 30 other occasions I did not record what happened to the prey, but think it was generally eaten. After a woodcreeper eats such prey, it often champs the beak or wipes it.

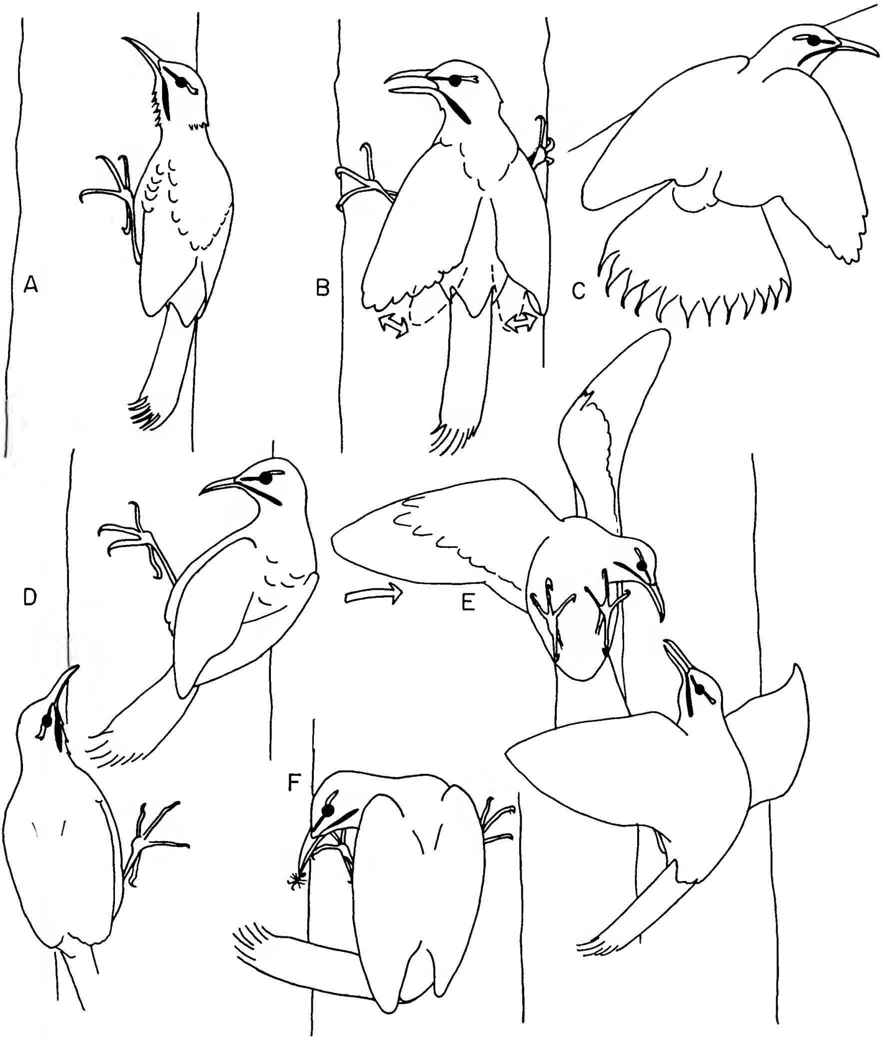

FIG. 7. Postures of Plain-brown Woodcreepers. A, during long rattling. B, wing-fluttering by a subordinate bird as a dominant one approaches. C, sunning on a log. D, a dominant bird takes an aggressive posture as a subordinate one hitches up below it, then (E) fights with it in the air. F, "anting" requires a C-shaped posture if the under-tail coverts or tail is to be used.

Anting in this species is probably a standard method for treating distasteful prey; it does not seem to reach the level of non-foraging anting as is recorded for some birds (see Whitaker, 1957; Simmons, 1966; and Potter, 1970, for summaries).

Southern (1963) and Potter (1970) suggest that anting soothes skin irritated by molt processes. Potter does not cite Dubunin's (fide Kelso and Nice, 1963) evidence that anting kills feather mites, nor my (Willis, 1967:33) evidence that subordinate Bicolored Antbirds have to take distasteful prey and ant with it. Perhaps there are two preening and one foraging uses for anting, rather than the single use suggested by Potter. Her main argument for anting as a molting poultice is that anting has been recorded more frequently in months when birds are molting.

I have recorded Plain-brown Woodcreepers anting every month of the year, but in 1960–61 I had more observations from September to November, 1961. (In summer visits later, I have obtained many records for July and August). September and October seem to be the main months of wing and tail molt in Panamanian Plain-brown Woodcreepers, judging from my observations and from the few specimes in museums. Some birds start molting in July and August. Although molting may be the reason for a peak of anting in the late months of an annual cycle, there are several alternatives that Potter does not consider: since molting follows nesting in most passerines, there are more birds present in molting months; the large number of young birds in months of molt means that more can make mistakes and pick up insects with chemical defenses; competition is high as young birds crowd in to local food sources, forcing some to take prey with chemical defenses; there may be more insects with chemical defenses about in late months of the annual cycle, since early insects of such a cycle are not so subject to predation and can be fast-reproducing ones without chemical defenses; observations of anting may be less frequent in spring and early summer because most observers are distracted by songs, bright colors, and territorial and reproductive activities of birds; winter observations are rare because few insects are out in northern areas and because few observers are out.

For Plain-brown Woodcreepers, the brief time of most anting episodes tends to indicate that care of the skin or use against feather mites is not as important as use as a part of a foraging strategy. Occasional sequences in which a bird anted with several prey usually seemed reactions to absence of more suitable prey rather than attempts to extend skin exposure to ants. Most anting episodes came when other Plain-brown Woodcreepers or Ocellated Antbirds were interfering with the bird's foraging, although some birds anted when few or no competitors were about. While young and subordinate birds sometimes anted, some adult and dominant birds also did so. There is not the clear correlation of subordinate status and anting that I found for Bicolored Antbirds. However, Plain-brown Woodcreepers are a subordinate species that uses a variety of prey items, and such birds might be expected to ant with prey with chemical defenses more often than do dominant species.

Simmons (1966) and I (Willis, 1967) have suggested that the original use of anting may have been wiping off distasteful secretions of prey, and that anting as a preening method may be learned individually. That such tropical species as Plain-brown Woodcreepers and Bicolored Antbirds show anting as a foraging pattern rather frequently may reflect the well-known diversity of tropical insects. Species of distasteful prey are likely to vary tremendously in appearance and to look like mimicking palatable prey rather often. It may be better strategy for a hungry or young bird to try for prey and then find if it is palatable rather than wait until species known to be palatable appear. Species of intermediate palatability may provide suitable prey for hungry birds if they are detoxified by chewing and by rubbing their secretions on the wings or tail.

MAINTENANCE BEHAVIOR

After chewing distasteful prey or large, juicy prey the bird often wipes the bill in the usual fashion: alternate sides, base to tip. Fluffing the head, a frequent movement in bill wiping in many species, was not detected. However, the feathers of the head are so short that it is difficult to detect head fluffing.

To egest fecal material, the Plain-brown Woodcreeper lifts the tail off the trunk by flexing the femora briefly, ejects the dropping forcefully, and quickly drops the tail to the trunk. Probably front and hind claws oppose each other at such times. Occasionally a woodcreeper coughs up parts of insect exoskeleta. It gapes one to several times as if choking, then shakes the head briefly as it is turned to one side; the exoskeleta drop out of the open beak.

Periods of inactivity or preening frequently interrupt periods of foraging. In addition, when competing antbirds are present, the woodcreepers are partly excluded from the continuous source of food near the ground and must depend on occasional probes of ants into tangles above the ground. During periods when ants are inactive above the ground the woodcreepers may cling and look about for long periods or wander widely about the swarms. They disappear for minutes at a time, but reappear as soon as the ants start up a tree. Johnson (1954:60) was also struck by similar behavior patterns when he watched these woodcreepers at swarms.

When preening interrupts periods of waiting or resting, the woodcreeper generally perches vertically in woodpeckerlike fashion. To preen the body, the feather tract is fluffed and the bird pokes the bill down in to the feathers, then out. In addition to movements of the feathers and neck, the bird extends the legs when it preens the underparts and flexes the legs when it preens its back. In the latter case the bird may rest on the ventral feathers for a time. There is also no difficulty when the wings are preened; extension of one wing at a time does not interfere with perching. However, preening the tail and scratching the head require awkward contortions. To preen the tail the bird raises it and directs it laterally, then falls back on the tail coverts or the sides of the tail so the body forms a C-shaped arc. Plain-brown Woodcreepers always scratch the head over the wing. When one foot is released from the trunk the bird seems to rest on the abdominal area on that side while the other foot grasps strongly and the tail forms the other leg of the tripod. Scratching the head is often awkward and hasty even when the bird rests in this position.

Perhaps the requirements of grasping during egestion and preening partly account for the large size of the rear toe, which Bock and Miller (1959) consider a hindrance or functionless in climbing birds that use the tail for support. In the Plain-brown Woodcreeper the rear toe is shorter and thicker than the front toe; the rear claw is less curved but is longer and thicker than a front claw. The rear toes and claws of this bird probably have a different function from the front ones rather than being vestigial, and in perching may act as wedges to prevent backward rotation. Perhaps a small bird that clings to smooth-barked tropical trees and to the under sides of smooth trunks or limbs occasionally clamps front and rear toes into the bark. Plain-brown Woodcreepers also use their rear toes to perch horizontally.

Woodcreepers stretch in the ways usual among birds: yawning, half-flexing both wings, or stretching fully on one side or the other (see Willis, 1967). When the bird does a left or right stretch the leg on that side is stretched and the bird swings against the trunk. I have not recorded toe-standing, which should be difficult for a clinging bird. After stretching movements the bird usually flies off.

Occasionally a woodcreeper suns itself on a log (Fig. 7,C) or on a limb of a tree. One wing and side of the tail are spread more fully than the others, and the face on the same side is turned toward the sun. Ordinarily Plain-brown Woodcreepers avoid full sunlight, although they readily cross clearings, openings in the forest, and esteros on Barro Colorado Island. They are by no means as strongly restricted to forest as are Bicolored Antbirds and similar species. On Trinidad, Plain-brown Woodcreepers follow swarms of ants through open cacao groves and to isolated trees in yards and pastures. Rivers and clearings should not be strong barriers to this species. There is little evidence of subspeciation across large rivers in the tropics, except across the “inland seas” of the Amazon, Tapajoz, and Madeira. There is much reason to suspect any subspeciation arose in isolated forest refugia during dry climatic periods, not because of the rivers (Haffer, 1969).

On many occasions woodcreepers bathed in holes in trees. I repeatedly found one or two woodcreepers bathing in one hole in a fig crotch in the evenings. On one occasion another bird drank after peering in the knothole, then backed in carefully and repeatedly, emerging and shaking briefly between dips. Investigation of cavities above ground is frequent, perhaps for roosting or nesting sites as well as for drinking or bathing.

Although this woodcreeper is a victim of the bites and stings of army ants less often than are birds that perch near the ground, one occasionally bends down quickly and throws an attacking ant into the air. Once a woodcreeper ate a soldier of *Eciton burchelli.* Occasionally a woodcreeper jitters, shaking one leg or shifting back and forth from one foot to the other rapidly, when ants attack. Normally the bird hitches a few centimeters away and waits in a position out of the stream of ants.

REACTIONS TO HUMANS AND PREDATORS

When predators appear, Plain-brown Woodcreepers occasionally freeze in place by clinging very close to the trunk and staying very still. Often the reaction includes loud stieking. In addition to the yellow flash from the gape as the lower mandible flaps down for each call, occasional flitting of the wings may betray the position of the bird. The yellow under wings flash inconspicuously when a bird flits. Often one wing seems to extend more than the other, but flitting never extends as widely or as close to the trunk as does wing-flashing, which is normally a movement of one wing. Commonly a stieking or silent bird whisks around the trunk so that it is hidden from the predator or the observer. At times it hitches up the trunk, flitting the wings at each jump, or darts suddenly and repeatedly from one tree to another, circling trunk after trunk. There is relatively little fluffing or sleeking, although a freezing bird is slightly more fluffed than usual and a hyperactive stieking bird is more sleeked and stands out farther from the trunk than it does in the standard posture. However, birds freezing on slender saplings seem sleeked, as if hiding behind the saplings. Often the bird jerks its head one way and then the other with or between stieking notes.

Stieking is commonly set off by a hawk, although it is also a common reaction when I first appear at a swarm unless the individual bird has seen me frequently. Stieking was recorded as reactions to hawks on 29 occasions involving seven species of hawks. Other records included stieking at a Spectacled Owl (1), Mottled Owls (2), Turkey Vultures (3), Collared Araçaris (1), Chestnut Woodpecker (1) in Brasil, a large bird flying over (1), the alarm note of a Buff-throated Woodcreeper (1) in Brasil. Once a woodcreeper stieked at a tayra, once at a jaguarundi (*Felis yagouaroundi*), once at running agoutis (*Dasyprocta punctata*), once at squawking of a squirrel (*Sciurus granatensis*), twice at the grunting and stick-dropping of white-faced monkeys (*Cebus capucinus*), once in Peru at red titis (*Callicebus cupreus*), and several times at my swinging my cap at mosquitos.

Many other birds react to stieking by freezing, fleeing, or giving alarm calls: Ocellated Antbirds (31 records), Bicolored Antbirds (43), Spotted

Antbird (12), Gray-headed Tanagers (3), Buff-throated Woodcreeper (1), Chestnut-backed Antbird (1), Streaked Flycatcher (1), and Barred Woodcreeper (1). In Peru a Lunulated Antbird keened; in Brazil, a Harlequin Antbird chipped. In Guyana, Rufous-throated Antbirds (2), White-plumed Antbirds (2), White-browed Antbird (1), and a Black-banded Woodcreeper (1) fled. At times, other Plain-brown Woodcreepers repeat stieking or flee when one bird starts calling. Usually only one or two birds stiek at a time while the others hide or stiek infrequently.

The reactions of Plain-brown Woodcreepers often precede those of other ant-following birds when a predator appears in the canopy, partly because these woodcreepers forage high in the vegetation rather than concentrating on ground prey as is the case for many ant-following birds. Once a woodcreeper, seeing a tayra approach on the other side of a hill, stieked and alarmed ground antbirds before the latter could see the tayra. However, Plain-brown Woodcreepers are also prone to hysterical outbreaks of stieking with no obvious cause after a hawk disappears or I take a position behind the swarm. Other birds at swarms may start a "dread," becoming hyperactive and giving alarm calls, when a woodcreeper continues stieking or resumes it long after danger has passed. Since the woodcreeper sometimes moves down and forages in the zone deserted by the antbirds even though it continues to stiek, one wonders if its seeming hysteria may help it by relaxing competition from domineering antbirds. I have suggested this for another subordinate bird, the Spotted Antbird (Willis, 1971). Another possibility is that the hair-trigger hysterics of Plain-brown Woodcreepers discourage types of predation which are probably quite common in tropical forests. In central Brasil the Lined Forest-Falcon, which occasionally follows ants for hours, often returns time after time to the same area. It sits and waits quietly for long periods. Although I have seen it capture only large insects, it undoubtedly gives the antbirds and woodcreepers reason for hysteria. Stieking may annoy such predators so that they move away, or keep the birds on their guard against still-hunters and hawks that return repeatedly. Plain-brown Woodcreepers, which work the middle levels of the forest in a zone where there is light and space for a hawk to maneuver, have to be more careful than do antbirds foraging in dim and tangled areas near the ground. On Trinidad, where the woodcreepers work near the ground on an island that has few species of forest hawks, they were far less prone to hysterical stieking than in other areas.

Plain-brown Woodcreepers react to the alarm calls of other birds. At chipping notes of Bicolored Antbirds or stieking of another woodcreeper, a woodcreeper often presses close to its perch, sleeks, and freezes. At chipping of Spotted Antbirds, one looked about quickly.

Woodcreepers that have had some experience with me quickly become tame, especially if I scare away Ocellated Antbirds or other domineering competitors so that the woodcreepers can forage near the ground. At times the woodcreeper changes from flitting and then sleeked hiding behind trunks to open foraging via the "displacement activity" of preening. However, I never saw any evidence of the "curiosity" or investigating behavior so characteristic of tame Bicolored Antbirds. Woodcreepers use peering and investigating behavior very little in foraging, in contrast to Bicolored Antbirds; the seeming lack of curiosity may be related to their noninvestigative type of foraging. Still, tame woodcreepers often hide behind trunks of trees when one tries to observe them closely.

Woodcreepers that were semi-tame or ones that I forced to fly from a swarm sometimes reacted with long rattles. Once long rattles were a reaction to marmosets (*Saguinus geoffroyi*). The bill is closed and the bird hardly moves, except for a pulsing low on the neck. The neck seems long, probably because of extending the angles between vertebrae (Fig. 7,A). The feathers of throat and forehead, possibly those of the entire head, are raised as the bird clings close to the trunk. The feathers of the vent are also fluffed. The bend of the wing is sometimes exposed. One bird ended its rigid display by ejecting feces, doing a half-flex of both wings, and spiraling up the trunk.

Woodcreepers held in the hand for banding commonly scream loudly and persistently. Some individuals squeak rather faintly or growl softly. Clawing stops if the bird is allowed to grasp a finger. Pecking is often vigorous, but these woodcreepers do not hold and twist so vigorously or for such a long time as do antbirds.

AGONISTIC BEHAVIOR

The frequent interspecific supplantings when Plain-brown Woodcreepers and other species compete over swarms of ants have been discussed elsewhere (Willis, 1966).

Large birds that follow army ants supplant (chase from its perch) or displace (cause to move off) the Plain-brown Woodcreeper (Table 5). It is rather nonaggressive, except to a few stolid moderately large birds and to small ant-followers. Buff-throated Woodcreepers are particularly pugnacious to it, and chase it about persistently on the rather infrequent occasions when Buff-throats follow army ants. Black-striped Woodcreepers are also rather pugnacious on the few occasions when they follow ants. Most of the large ant-following birds in Panamá, such as Barred Woodcreepers and Ocellated Antbirds, supplant or displace it rather regularly; but the Plain-brown Woodcreeper is good at keeping out of their way. In other countries, I have seen Plain-brown Woodcreepers supplant Scale-backed Antbirds and White-

TABLE 5

ANTAGONISTIC INTERACTIONS OF PLAIN-BROWN WOODCREEPERS

	Numbers of Wins/Losses by Species A[a]			
Species A	Fights	Supplantings	Displacings	Returns[b]
Plain-brown Woodcreeper	53	1196/	65/	
Barred Woodcreeper		109/	48/	
Ocellated Antbird		80/	28/	4/
Buff-throated Woodcreeper		85/2	18/	2/
Bicolored Antbird	1	60/16	8/11	
Black-striped Woodcreeper		42/	9/	
Gray-headed Tanager	2	9/9	6/1	
Squirrel Cuckoo		2/	7/	
Black-breasted Puffbird		4/	1/	
Bright-rumped Attila		2/1		
Rufous Motmot			1/	1/
Keel-billed Toucan			1/	
Broad-billed Motmot			/1	
Canada Warbler		/1		
Acadian Flycatcher		/1		
Wedge-billed Woodcreeper		/1		
Scaly-throated Leafscraper		/1		
White-whiskered Puffbird		/1		
Slaty Antshrike			/2	
Swainson's Thrush		/5		/2
Spotted Antbird		/9	/4	

[a] Barro Colorado Island, over ants, 1960–1971.
[b] One bird has to watch until other leaves before moving in.

throated Antbirds. Rufous-vented Ground-Cuckoos, Ruddy Woodcreepers, Red-billed Woodcreepers, Hoffmanns' Woodcreeper, Spix's Woodcreepers, Black-banded Woodcreepers, Rufous-winged Bare-eyes, Black-spotted Bare-eyes, Bare-crowned Antbirds, and Black-headed Antbirds supplant or displace Plain-brown Woodcreepers. Twice I saw White-chinned Woodcreepers displace Plain-brown Woodcreepers, and once a Plain-brown displaced a White-chin.

Generally a woodcreeper surprised by a larger species screams loudly if attacked or pecked but simply flees or sticks and flits as it hitches up a trunk if it is supplanted less strongly. It may ruff the throat, or cling close with feathers fluffed out. The woodcreeper gives rattlets or long rattles if it is gradually crowded out or displaced rather than attacked bodily. Once one shivered the wings as it approached a Barred Woodcreeper, which did not attack it.

Interactions with species close to its own size or dominance are frequently more varied. Once one supplanted a male Gray-headed Tanager (at 30 g, only three-fourths the weight of the woodcreeper) by spreading the wings and showing the yellow wing linings at it. A minute later the same tanager supplanted the woodcreeper when it did not spread its wings. On another occasion a tanager female, crest raised, gave faint notes as she pecked down repeatedly at a woodcreeper under the limb she stood on. The woodcreeper sidled back and forth, weaving and feinting at her with the beak, before it flew off. When Bicolored Antbirds (30 g) supplant the woodcreeper the latter sometimes stays and growls, pecking back at the smaller bird. However, the woodcreeper is usually forced to sidle back and forth around the perch by the repeated jabbing of the more agile antbird, so that the woodcreeper is often supplanted despite its initial resistance and larger size. Once a woodcreeper supplanted the antbird by flashing one wing at it and growling at it.

The intraspecific agonistic or competitive behavior of Plain-brown Woodcreepers seems as undistinguished as their plumage and voice. Simple avoidance, chasing, and fighting seem to replace aggressive and submissive displays most of the time. When two or more birds are present at a swarm of ants, they often stay apart. At times avoiding each other is not possible; the birds crowd around a palm or liana-covered tree the ants are ascending. At such times peck order is mainly evident in the well developed and rather diverse methods of fleeing and pursuing.

When a dominant bird flies up near a subordinate bird or supplants a third bird, the subordinate commonly sidles quickly behind its perch. If on a slender sapling, the subordinate bird may cling close and sleek the feathers as if to become as narrow as possible. Often one bird hitches up the trunk or around it when another alights below it. It may turn the head one way and then the other, looking down at the dominant bird (Fig. 7,D). When a subordinate bird flies, its flight seems normal unless it is hotly pursued by the dominant bird. It then twists and turns, zigzags in and around trunks, and quickly hitches or spirals around them on alighting. It may stiek at times, give rattlets in flight or on alighting, or end a series of rattlets with a song if completely driven away from the swarm.

Commonly a dominant bird ignores a nearby subordinate as long as it is quiet or sidles behind its perch. At times birds ignore each other even when three or four aggregate within a meter of each other for minutes at a time. Once a watching woodcreeper waited until another finished dissecting a tettigoniid, then hitched up and supplanted it. Most species that follow army ants wait until a subordinate finishes its meal before supplanting it, although Plain-brown Woodcreepers and other species commonly supplant subordinate birds during and immediately after prey capture. The position of dissecting birds in this and other species, hunched close to the perch and with necks retracted and bodies fluffed, may mimic submissive display and thus inhibit attack.

At other times a dominant bird may pursue the other bird by hitching or spiraling up the trunk after it, extending the neck to jab at it if it hesitates too long, or flying after it for as much as several hundred meters off into the forest or back and forth over the swarm. The pursuer or both birds may adopt a somewhat slow, flapping flight like a dove or a buzzy flight like a Spotted Sandpiper in the more protracted chases. Possibly such forms of flight display the yellow wing linings. At times the fluttery flight is accompanied by "tailgating," when the pursuer seems to slow and speed up when the pursued bird does so rather than try to overtake and attack it. Such flights may have sexual or parental connotations, as is discussed below.

Simple supplanting, often followed by long chases, is common. Fighting, or at least pecking and fluttering duels around and around a perch or down through the air (Fig. 7,E), is less common. Of 1,314 presumably agonistic displacings or supplantings, 53 (4.0 per cent) ended in fighting. This frequency is about ten times that for Bicolored Antbirds, a species with well developed aggressive and submissive displays. The contrast between these two species may support proposals that agonistic displays evolve to prevent dysgenic fighting. Fighting involves pecking with the bill as well as scratching at the opponent with the feet. Growling notes emerge during the more violent fights, which sometimes end on the ground.

A common display of subordinate birds is "rattleting." The beak is closed as a rattlet of 5 to 20 notes is uttered. The rigid, rather sleeked bird often ruffles the throat and lower face, sometimes the whole head. The neck is sometimes extended or ruffled, but more often the head is close to the body. At times the body seems ruffled. The wingtips commonly droop loosely. The legs are flexed, so the bird is close to the trunk. The eyes seem glazed, perhaps because they are diverged rather than focused binocularly. A bird that is consistently chased or forced away from a swarm by another woodcreeper or any other domineering competitor often extends rattleting into long rattles, as described under "reactions to humans and predators." At times the calling is omitted from the display of rattleting.

Another possibly submissive display is gaping and growling, or growling rattlets, during chases. Squealing comes from a bird losing a fight. Possibly growling is restricted to sexual and juvenile-parent chases, described below.

At times the subordinate bird flits the wingtips out sharply and repeatedly as it hitches jerkily up a tree after being supplanted. The dominant bird occasionally flits the tips of the wings. Such actions commonly accompany or lead into a stiek note or two, suggesting the bird may be panicking.

Occasionally the subordinate bird shivers or rapidly flutters the tips of the wings (Fig. 7,B). In seven out of 21 cases, however, the dominant bird shivered the wings and then chased the other off. In some of these cases the dominant bird seemed hesitant and initially unsure of its dominance, but the meaning of wing-shivering is unclear. Among Bicolored Antbirds it seems a juvenile or submissive activity (Willis, 1967, p. 47).

If there is an aggressive display in Plain-brown Woodcreepers, it is not frequent or conspicuous. Ordinarily the aggressor starts a chase from the standard posture, without calling. At times the legs are extended so that the body is far out from the trunk, as in the more conspicuous aggressive display of Barred Woodcreepers. If so, the head and neck are often arched, the head being flexed toward the neck (Fig. 7,D). Really aggressive birds fluff out the belly, chest, and back feathers; but I have not seen strong ruffling. The head is usually sleeked, so that the dark brown malar and presuperciliary lines seem more prominent than usual but the pale throat and yellowish postsuperciliary line less so. However, at times an attacking bird has the head ruffed; some such birds seemed unsure of their dominance. At times the attacker gapes, especially if defending a spot from an approaching bird. At times the yellow underwings are flashed out as well, especially if the approaching bird persists long enough to start a fight or chase.

One woodcreeper that preceded me to a swarm raised its back and chest feathers as it looked up at a bird one meter above; the latter dropped to half a meter below the new bird and shivered its wings. The newcomer then tailgated the other off. On another occasion an arriving woodcreeper went round and round a pole pecking and gaping at an unbanded bird; the latter tailgated the banded bird off after a pause.

MOVEMENTS AND TERRITORIES

Banding birds on Barro Colorado Island between 1960 and 1971 has given a moderately clear picture of territoriality and movements, even though many birds are not banded. Some banded individual birds (Fig. 8), especially birds known to be less than a year old, wander irregularly. Other banded birds, which I call "settled" birds, occasionally follow a swarm of ants outside the centers of their home areas but return to the areas year after year until they disappear. Settled birds with the long wings and feathered edges of the ventral apterium characteristic of males (Fig. 9) wander out from the centers of their home areas more frequently than do other birds (Fig. 10) with wing lengths characteristic of females; the latter are mostly birds that have vascularized, bare ventral brood patches during breeding seasons and birds that cared for one or more broods of young during the 1960–1971 period.

It is likely that the home ranges of these settled birds are territories, al-

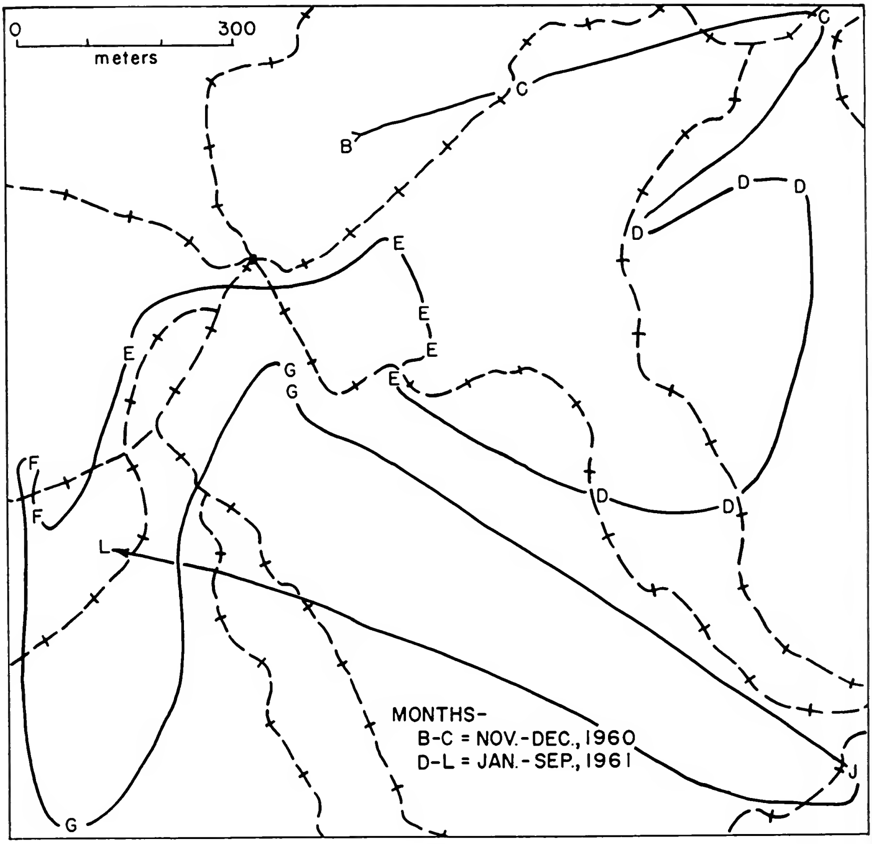

FIG. 8. Wanderings of Plain-brown Woodcreeper "XR" from November, 1960, to September, 1961.

though there is not enough evidence on supplanting and chasing to be certain of dominance. The known females have nearly exclusive ranges; I have yet to observe two banded ones together at the same swarm of ants or to observe two unbanded females with their broods at one swarm. The settled males have home ranges completely overlapping those of settled females. The ranges of settled males overlap each other, so that two or more settled males occasionally follow the same swarm. However, overlapping of ranges is no proof that animals are non-territorial (Willis, 1967); each male may be dominant over other males toward the center of his own range. The centers of ranges of settled males are different suggesting that males do have this form of territoriality.

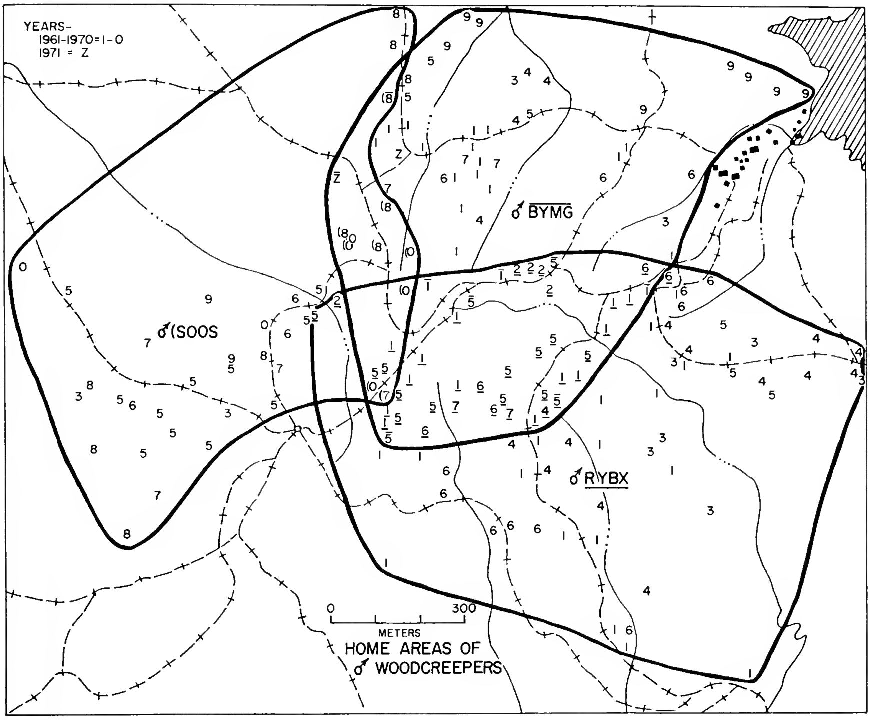

Fig. 9. Observations of three settled male Plain-brown Woodcreepers, 1960–1971. Within overlap zones, records of RYBX are underlined, of BYMG are overlined, and of SOOS start with a parenthesis.

There is some evidence that settled males are subordinate to settled females. The wider wanderings of settled males suggest this, since a subordinate bird must wander more widely than does a dominant one to find an unoccupied swarm. In 37 cases of supplantings involving settled females, the female was the victor in 35 cases. The exceptions may represent meetings of two females at territorial boundaries; in both cases the banded female was chased by an unbanded bird at a place where the neighboring female was unbanded. On 14 August 1961, female RBYM (Fig. 10) supplanted male BYMG (Fig. 9) within the ranges of both. Male RYBX rattleted whenever female BRYB came near him on 18 August 1964; the location was well within the area of the male but peripheral to the area of the female. On August 16 and 21 female PSPM repeatedly supplanted male RYBX; she was near the edge of her range, while he was well within the boundaries of his. On 2 October 1965 female BRYB displaced male RYBX at the edge of her range but well within his.

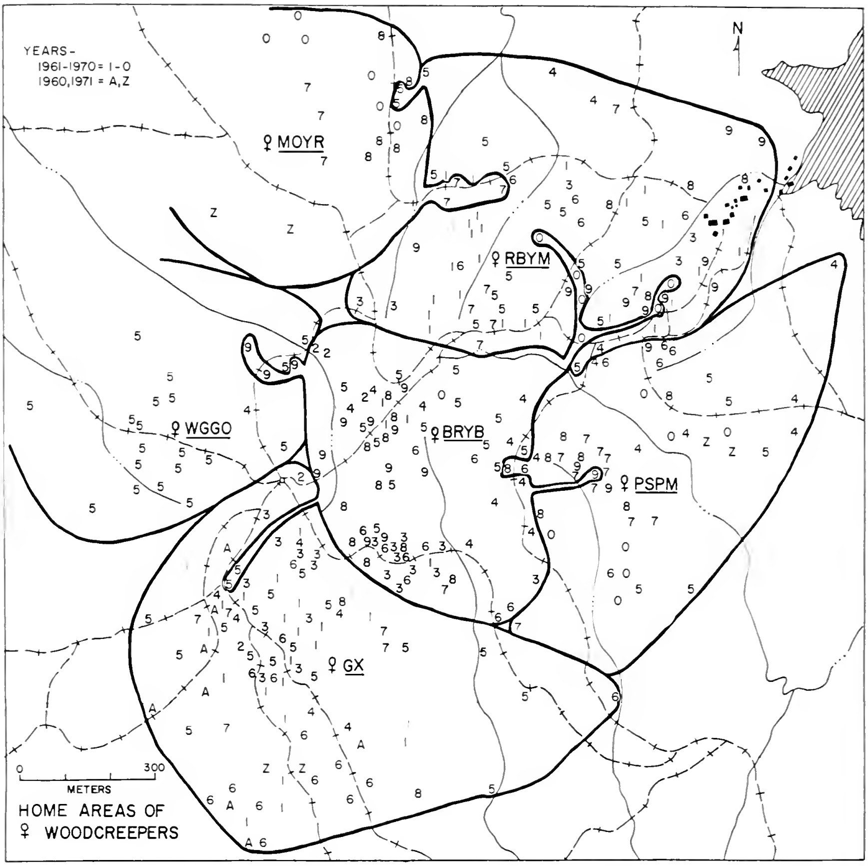

FIG. 10. Observations of five settled female Plain-brown Woodcreepers, 1960–1971. Dark lines separate records of individual females.

There were always unbanded birds wandering through the territories of these settled males and females. Probably most of them were either males with home ranges overlapping those of the banded birds or else wandering birds. I do not know how many years these birds wander before they settle down, for the only banded young rediscovered later (MGYY) was not found until nearly 10 years after banding. The extremely long lives of settled birds, especially settled females (of three females banded in 1961 as adults, two were still alive and on their territories in 1971 and the third disappeared after 1969) suggest that young may wander for years at times waiting for territories.

Preliminary evidence thus indicates that Plain-brown Woodcreepers have the kind of territoriality found in the European Cuckoo, some lizards, and some mammals. Females occupy exclusive territories, while the settled males have more or less separate ranges completely overlapping those of the females. The spacing system should be investigated further in an area where Plain-brown Woodcreepers are more abundant and easily studied, as on Trinidad.

There were 2.8 females and 1.8 males per square kilometer on the study area in 1960–1971. (Each female had an area of about 36 hectares.) At 41 grams per bird, this is a biomass of 188.6 grams per square kilometer or 1.9 grams per hectare. Possibly there were 1 or 2 wandering birds per square kilometer in May each year, or an additional 0.6 grams per hectare, for a total of 2.5 grams per hectare. The total population of Barro Colorado Island in May, at the low point of the annual cycle, would be about 90 birds. In December there would be somewhat over twice as many birds, or 180–200 birds (5 grams per hectare).

SEXUAL BEHAVIOR

Sexual behavior seems to grow directly out of agonistic behavior in this species. Pair bonds and courtship are certainly brief and rudimentary in nature.

Males chased by females in seemingly normal agonistic encounters sometimes growl or give soft rattlets, and allow tailgating or a pecking duel rather than flee to a distance. Gradually the two birds begin to associate in their chasing and to ignore trespassing birds. There are persistent chases during this period, but the two birds frequently alight close together and wait several seconds before resuming pursuit. The two may peck and spar back and forth before resuming a chase. Presumably the process involves an increasing tendency for the female to stay rather that attack the male when he approaches her, but these preliminary stages are difficult to distinguish from agonistic behavior. Occasional reverses of chases, in which the pursuer becomes the pursued, are the first clear sign that sexual behavior is involved and not just agonistic or parental chasing.

Over the course of a few days other elements enter the feuding. The chases become slower and more fluttery; there may be bursts of wingbeats so that the two undulate in flight. The male consistently alights below the female. Growling notes become more frequent than rattlets. Growling, whether by pursued or pursuer, is sometimes accompanied by fluffing of the throat, breast, and crown to a degree far surpassing the normal state among rattleting birds. At times the feathers of the breast part from those of the lower abdomen. The male may hitch up after the female at each stop, even though she pecks down at him and chases him off at times.

In the final days of the pair association, one bird consistently hitches up to the other and nibbles more and more vigorously into its lower back.

"Nibbling" is often accompanied by vigorous growling from either bird, at times speeding into a rattle. The throat of the chased bird is sleeked, but the chasing bird fluffs its throat as it growls. The chased bird often takes wing and is pursued by the other. The chased bird may jab downward repeatedly at the insistent other one, or hitch upward; but the chasing bird quickly follows the chased one. The chaser swings back and forth below the other when it jabs at him, then moves quickly in to nibble its back when it returns to the standard posture. Eventually it stays still for the nibbling. The male eventually nibbles her rump, then moves upward nibbling the female's back more and more rapidly and deeply. She gapes slightly and flattens herself against the vertical trunk as the male hitches up on her back and clings to her slightly spread wings. The male flutters rapidly as the tails of both birds are shifted off and on the perch rapidly. The female seems to rest on the side of her tail while the spread tail of the male remains on the trunk. Copulations I have observed were brief, generally less than a second, as both birds seemed to have difficulty copulating in this vertical position. In one case the male hitched up above the female after copulation, then hitched down past her and repeated the process of growling, nibbling, and copulation. He chased her to new perches and attempted or completed several more copulations during the course of the day.

On one occasion a female alighted just above an unbanded bird. As it growled faintly and gaped slightly, she looked down and gaped as she hitched down under it until she wedged up its breast with her tail. It gaped and finally started nibbling before she looked down and chased it off in a fluttering aerial flight.

On a few occasions wandering females were persistently nibbled by unbanded birds even though each female snapped down at the other bird or chased it off. On another occasion a female with young birds was persistently nibbled by an unbanded bird, although fluttering and pecking aerial duels were the result. Once a wandering young bird, independent less than two weeks, nibbled the back of another bird. Perhaps a male may attempt nibbling and copulation as soon as a bird it approaches fails to flee or attack, whether or not male or female are settled or in the appropriate stage of the nesting cycle. This may explain occasional cases where one bird nibbled another and the second nibbled back before there was a fluttering chase. However, female PSPM was observed to nibble the back of male RYBX in one pairing sequence, and to be the recipient of nibbling from an unbanded bird on another occasion, so the sex roles in nibbling must be reversed occasionally.

Most observations of sexual behavior were for unbanded birds, so that I do not know how many days the birds of a pair consort with each other or

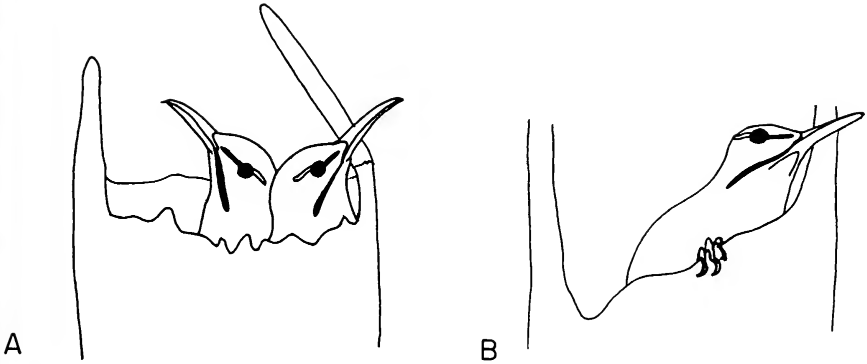

Fig. 11. A, "cavity-sitting" by two woodcreepers. B, female BXRB peers snakelike from the top of her nest cavity before leaving it and the single nestling. From field sketches.

whether the female accepts more than one male. Observations of another behavior pattern, "cavity-sitting," suggest that the interest of the male may extend somewhat beyond copulation. One bird flies to a cavity in the top of a pole-sized stub, peers down into it and around, then turns and backs down inside repeatedly. At times a second bird flies up and joins it in hitching up and down inside the cavity (Fig. 11,A). Growling sounds emerge as if a bumblebee is boring into the wood. After a minute or two of their jack-in-the-box behavior one bird and then the other emerge and fly off. It may be that copulations occur during cavity-sitting, for one wandering young female was mounted by an unbanded bird as both cavity-sat, despite much pecking when he first nibbled her back.

Male RYBX and female PSPM went through a sequence on 5 July 1966 in a way that suggested he was showing her a nest-hole. He gave a series of growls at a hole in a big stub; she flew up beside him and he hitched sideways, then flew off; she hitched up and flitted as she peered in several holes. Later he gave a rattlet as she hitched up to him. Both looked about, then she nibbled his back a few times. He flew off after looking down at her.

NESTING

A bird brought food to and carried a fecal sac away from a northwest-facing hole 4 m up in a stub 0.2 m in diameter in a new agricultural clearing in the forest at Tres Esquinas, Colombia, at 10:04 on 20 April 1962. One carried food to and a fecal sac away from a cavity in the top of a stub 0.2 m in diameter and 5.5 m tall, 25 m out in a manioc field in forest at Maloquinha, Brasil, at 18:02 on 25 February 1966. Pinto (1953) records an incubating female collected at a nest with a single white egg 2 m up in the trunk of a tree, 1 January 1924. Snow and Snow (1964) record dates of laying in nests in Trinidad from May to "September" (= early October). The latter record represents a young bird prematurely out of the nest on 10 November (D. W. Snow, in litt.). I noted adults still feeding grown young out of different nests on Trinidad on 4 and 15 December 1961, so that the nesting season extends later than the Snows indicate in their article and is essentially the whole rainy season.

Five nests the Snows located (their three other records are of birds carrying food to sites not exactly located) ranged from 1 to 9 m above the ground, in tree holes, the open tops of a bamboo stake and of a broken *Bactris* palm, and in a hollow tree branch. Two eggs were in each of three nests, two young in a fourth; none were successful (the fifth nest, high, was not revisted). Four of the nests were in forest and one near a house.

One nest on Barro Colorado was 3.5 m in a cavity in the top of a 0.2 m diameter stub in open forest. The nest-cup, a few dead leaves with a rhizomorph lining 0.5 m down inside the stub, held two small and downy young with areas of bare orange skin at 13:50 on 3 June 1966. They were probably two days old. One young left the nest about 16:30 on 25 June, so the nestling period was 23–25 days.

I watched from a blind 38 hours on 12 days, mainly in the afternoons because morning visits on 7 and 11 June (7.5 hours) showed no different patterns. Only female BXRB fed the young. She brooded them only during rain on 6 June and between 09:27 and 10:28 on 7 June; perhaps even small young are often allowed to cool off despite the longer developmental period lack of heat would require. Her visits with food were very irregular, from 4 to 162 minutes apart (mean, 46.0, n = 39). On 6 and 7 June the average interval was 87 minutes, then 48 minutes on 10–11 June, 30 minutes on 14–16 June, 40 minutes on 18–20 June, 54 minutes for 21–23 June, and 39 minutes for 25 June.

On nine occasions she brought variously colored cicadas, which probably were not taken over ants. Other prey were a lizard (*Anolis limifrons*), a lizard or a frog, a roach, and orthopterans (2), and several mangled insect abdomens. Usually she held the prey lengthwise inside her open bill, but the lizard projected back past her face and the roach was held in the bill tip. Prey was seldom less than the exposed bill length (25 mm). She was not known to follow ants during the nestling period, although other females feeding young in undiscovered nests have been known to do so.

She occasionally sang at a distance, but approached quietly otherwise. She often froze on a nearby sapling or the nest pole for a minute or two looking about, before hitching to the nest edge and looking about again. If I approached the nest as she did, she stieked and fled with wing-flitting, hitching up distant trees. Once a Chestnut-mandibled Toucan flew down and scared her away as it peered in the nest before I drove it off with difficulty. She froze or hitched behind the nest-stub at each whirr of toucan wings overhead, but on other days had ignored their sounds.

To feed, she looked inside and flipped head-first into the cavity. Once, returning in rain to brood without food, she backed tail first into the cavity. She sometimes gave faint rattlets as she looked in or went inside, and continued them if the young did not take the food. To rechew food, she sometimes reappeared at the nest entrance or flew off, then returned. Often she appeared at the nest entrance after a feeding and craned her neck about slowly like a snake (Fig. 11,B) for several minutes. At times her throat feathers were ruffed. Often she champed her bill, especially one day when toucans were flying overhead. Once she pecked and tossed a large ant (*Paraponera clavipes*) walking nearby. After peering, she often hopped to the inside top of the stub and waited before flying off, or flew off directly. A few times she flew off directly before waiting at the entrance.

She normally flew off directly when carrying a fecal sac, which she did on 12 of 26 visits between 14 and 24 June, but only three of 16 times 6 to 11 June and on one of five on 25 June. Presumably she ate most fecal sacs before emerging until the young were about two weeks old, and ignored fecal sacs on the last day.

The young gave a few hissing answers to her rattlets on 10 June and thereafter. On 16 June it gave a weak song inside the nest about three minutes before the female arrived. On 25 June, but not as late as 24 June evening, the young came to the nest entrance except during a rain. It seemed as big as the female, but had a rather short bill, a tail one quarter the normal length, and three-quarters-open remiges showing bare bases. It gave a rattly song once, but preened and looked about silently most of the time the female was away. It gaped widely for feedings and after one feeding. At 15:51 she watched as it flapped one wing out to climb up on the nest entrance after a feeding, then tapped twice on the nearby trunk with her bill. Both watched and waited as marmosets passed overhead, and it hissed at her a few times. She pecked into its open gape before leaving 16:08, and it gave squeaky rattlets as it looked after her. Later it fluttered atop the nest-stub. At 08:34 the next morning the female looked in the empty nest; at 09:14 she sang and rattled when I shook a nearby vine on which there was a snake (*Pseustes poecilonota*), discovered by scolding antwrens of a forest flock.

From 11 to 20 July the young and female were with army ants elsewhere in her territory. On 11 July the young had tail and bill three-quarters the normal lengths, and was "playing" by pecking off and dropping bits of moss

(Other young often pecked at leaves and billed them or other bits of debris, as if hungry or playing). It tried fluttery sallies for prey. On 16 July its tail and bill were nearly the adult lengths, and it caught one prey on its own. The female was by now in very worn plumage. (Female GX went into molt when her young were about this age, 14 July 1966). On 19 July she pecked it after it hissed near her, and it fled. On 20 July, however, she lured it away from me with rattlets.

There is no information on incubation except for Pinto's (1953) record of collection of an incubating female. Skutch (1969) records that one bird alone incubates and feeds the young in Tawny-winged Woodcreepers, another species with the attack-and-nibbling type of sexual behavior. Probably the female Plain-brown Woodcreeper also cares for eggs alone, as males lack incubation patches. Male and female do not associate during the period of nesting, as far as I have been able to determine.

Several other broods of young have been seen on Barro Colorado, including other broods of female BXRB. The young appeared as early as June and as late as September. One or two fledglings follow one female; no male associates with the group. The young are well grown and fly well before the female brings them to a swarm; the smallest young I have seen, those of female PXRP in 1964 and of an unbanded female in 1969, were fully feathered but had small beaks and half-length tails. At times these smaller young stay in one area and the female commutes to them from a swarm. The female more often stays nearby, even if no ants are available nearby. She stieks loudly as a human passes, but the young are silent at this stage.

The young birds forage little at this stage, but they gradually become independent over the next month or two (young were with female RBYM at least 17 August–11 October 1965). When the female catches food and has hammered or chewed it thoroughly, she utters a brief rattlet. If the young is busy preening, the female has to utter several rattlets. The young bird eventually flies up, takes the food in hitching past her, and eats it. The young may gape or flutter the tips of the wings briefly if the female holds the food or moves away at first. At times the young hisses or squeaks as it is fed. Larger, well-flying young hardly give the female a chance to rattle; they follow or chase her with hissing notes and hitch up to her as soon as she captures food. They gape at her head silently or with hisses. At times one nibbles the back of the female. She is forced to flee their hissing pursuit if she is to eat any food herself or even to forage in peace. Occasionally the female chases away larger young or snaps at them when they follow her closely. During feedings there is scarcely any display beyond gaping and squeaking by the young; the parent chucks the food into the open gape and bill-wipes or flies away.

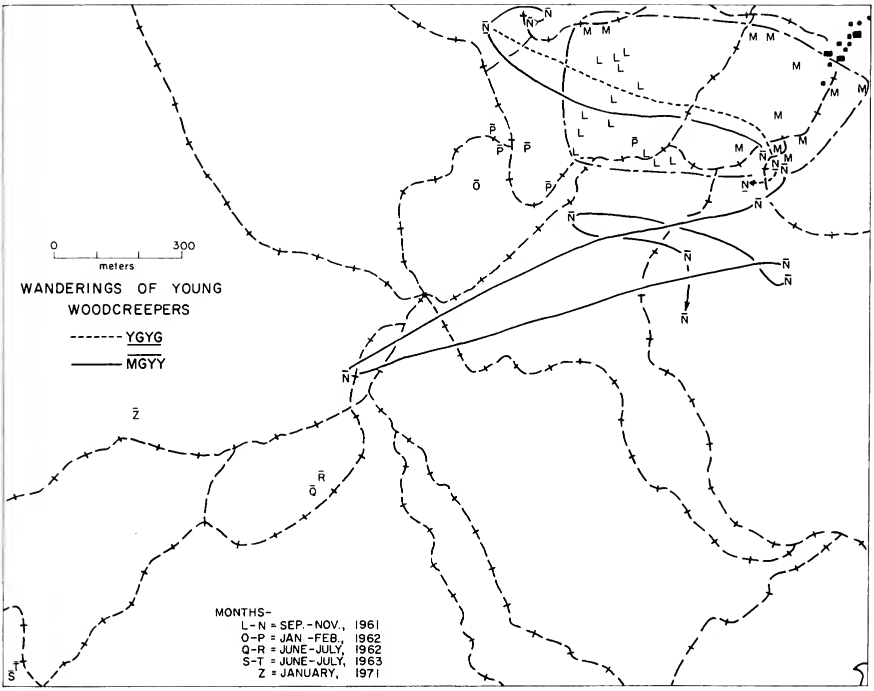

FIG. 12. Wanderings of two young Plain-brown Woodcreepers, the offspring of female RBYM, from September to November, 1961, and in 1962–1964 and 1971. Both young were with the female in her territory (inside the dot-dash line) in September and October, 1961; thereafter, records of YGYG are underlined and of MGYY overlined.

On one occasion a female Plain-brown Woodcreeper called *stiek* loudly nearby when an Ocellated Antbird briefly pounced on her screaming young. Females and juveniles sometimes sing back and forth when separated from each other. When the observer passes a female and her grown young all often start stieking and hide behind trees, and move off through the forest with occasional songs or stiek notes.

Sibling woodcreepers occasionally supplant each other, but they are usually so widely separated around a swarm that there are no chances for arguments at feeding times. In some of the broods I observed, the female fed one sibling frequently while the other was ignored and began to forage at an early age. This suggests that a female may sometimes have difficulty feeding more than one fledgling.

Young birds beginning to forage for themselves peck and pry at debris or even hit it on a perch as if to kill it; they examine epiphytes and nearby trunks actively in a fashion reminiscent of woodcreepers of the genus

Xiphorhynchus. One pecked at army ants (*Eciton burchelli*), and dropped them before fleeing with *stiek* notes. One tried backing down to a leaf-filled cavity as if to bathe or cavity-sit, but missed the cavity. Later the young woodcreepers wait more patiently and sally for prey in adult style.

The few birds banded as young wandered widely after leaving the female and did not associate with her or with each other even if they returned to her home area later (Fig. 12). Occasionally a young bird supplants wandering birds known to be older, although settled birds supplanted young birds in most cases.

DISCUSSION

Of all the birds that follow army ants on Barro Colorado, the Plain-brown Woodcreeper has the simplest and most individualistic social behavior. It is plain in this aspect of behavior as it is in voice and plumage.

Parental bonds involve little interaction between birds, except for persistent following of the parent by young birds. A long nestling period, typical of cavity-nesting birds, perhaps allows young to be relatively independent soon after they leave the nest. However, it seems more likely that having inconspicuous communication may protect young birds in a species that depends to a considerable extent on hiding or fleeing from predators in open vegetation rather than on keeping in or near dense cover.

Care of nests by one parent obviates the need for displays between parents and thus perhaps makes these open-cavity nesting birds even safer. Also, as Smith (1968) has pointed out for chickarees (*Tamiasciurus* spp.), the absence of the male means that there is one less animal to deplete food supplies or frighten prey near the nest. Skutch (1969:407) records that a female Tawny-winged Woodcreeper foraged actively near the nest in the evening; if the Plain-brown Woodcreeper ever does this a male and female caring for the nest together would compete rather strongly. Nesting Plain-brown Woodcreepers apparently do not travel much to distant ant swarms, and probably forage in areas near the nest on rather alert prey, such as lizards and cicadas; two birds might scare such prey more than would one.

The sexual behavior of Plain-brown Woodcreepers also involves little social display or interaction. Most birds with brief pair bonds have well-developed courtship ceremonies, plumage, or voice. Darwinian sexual selection, the necessity for correct recognition of a conspecific bird, and competition between males should lead to hypertrophy of male sexual behavior in such species. It is possible that insectivorous birds cannot develop a lek or similar time-consuming system of strong courtship display because their food is too widely dispersed or unpredictable (Snow, 1962). European Cuckoos, a species with a social system most like that of Plain-brown Woodcreepers, are also insectivorous. The necessity of not frightening alert prey by having too many birds about, and of not attracting predators, may make it advantageous to Plain-brown Woodcreepers to be retiring and inconspicuous in courtship behavior.

These birds have not developed the strong or conspicuous aggressive and submissive displays that would seem useful for establishment of dominance. Instead, there are fighting and long chases that seem to waste time and energy. Perhaps quick fights and unpredictable chases may reduce danger to birds that forage in rather open forest midlevels or open lower levels most of the time. Ignoring the opponent until there is a sudden chase makes maximum benefit of the protective coloration until the last moment. Moreover, a defeated bird has plenty of room in which it can forage. Such birds can escape in any direction from a dominant opponent or a predator. Ground-foraging antbirds could trap and hurt each other if they were to use fighting instead of displays. Thus the emphasis on displays instead of fighting in such species as Bicolored Antbirds and the opposite emphasis in these woodcreepers may reflect the ecological limitation of the former species to a narrow zone near the ground and to areas near safe cover. The woodcreepers, by contrast, must be fast at moving to unprotected sites not occupied by antbirds, and must behave inconspicuously or unpredictably in such sites. If so, it would be instructive to determine if the low-foraging woodcreepers on Trinidad, in an area with few competing antbirds or predatory hawks, show a relatively greater use of displays than do the woodcreepers on Barro Colorado. Another factor is that woodcreepers are generally less numerous at swarms than are Bicolored Antbirds; hence woodcreepers may have less need for frequent displays to set up and maintain peck orders. Again, the woodcreepers are very numerous at swarms on Trinidad and may use displays more.

Many patterns of submissive and evasive behavior are also inconspicuous in Plain-brown Woodcreepers, but are rather well developed. It is a bird that seems good at fleeing and hiding, whether from a competitor or from a predator. Submissive calls include rattleting, persistent rattling, and to a certain extent growling (which is more often a social call from fledgling to parent or from one sex to another in courtship). There is no clearly aggressive call, while in some antbirds the aggressive calls outnumber the submissive ones. Even song is rare and seldom seems to have an aggressive or territorial function in Plain-brown Woodcreepers.

The poor or inconspicuous development of forms of social behavior in Plain-brown Woodcreepers may have been favored as a result of their foraging behavior under conditions of competition with antbirds. These woodcreepers forage mainly above the ground during periodic probes of ants up trees or slip in and out at open and unsafe places where competing antbirds hesitate to go. Exploitation of such irregular sources of food at a swarm, in contrast to the regular feast enjoyed by ground-foraging antbirds, must place a selective premium on rapid movement of individuals. Antbirds, which lead mates or young about, have special calls and must be very active to get the mate or young to follow them to another part of a swarm. Not only is time wasted, but other birds of the same or other species quickly home on the calls and antics of the leading bird. Birds that work near the ground, where ants flush food regularly, need seldom use this kind of behavior; but if woodcreepers maintained close pair or parental bonds they would need it every few minutes. It is far better for them to wander individually, quickly move in at available sites as soon as they develop, and keep quiet so few competitors are attracted.

One form of social behavior, stieking and hyperactivity in response to predators, is well developed in Plain-brown Woodcreepers. Single woodcreepers stiek as readily as ones together, and stieking generally causes birds to scatter. Possibly the calling is a communication to the predator ("Here am I, alerted and a difficult catch"), or a call that irritates or disturbs predators; it may also drive off competing antbirds as has been suggested for a similarly subordinate species on Barro Colorado (Willis, 1972). In the past, alarm calls have often been assumed to be altruistic; stieking may also have such a function in Plain-brown Woodcreepers, especially when a family is together. Hamilton (1963) discusses how such "altruism" can evolve in situations where related animals are together.

In contrast to ground-foraging antbirds, Plain-brown Woodcreepers use the same call for terrestrial predators as for aerial predators. Probably there is no reason to develop a separate call for ground predators when a species normally forages well above the ground. Long rattling may represent a type of predator call, perhaps one that irritates or disturbs a predator, but this behavior is also used when a domineering competitor is present.

In contrast to most forms of social behavior, foraging and other types of individual behavior are well developed in Plain-brown Woodcreepers. The woodcreeper is peculiarly specialized in some ways and generalized in others. The woodpeckerlike perching and hitching restrict it in many ways; for instance, these woodcreepers tend to avoid perches below 3 cm in diameter. A bird that perches like a woodpecker is also relatively slow at catching prey below or behind it, and hence is at a disadvantage catching prey near the ground. When better-adapted horizontally-clinging antbirds are present, the woodcreeper scarcely uses the rich and constant source of food on the ground (Willis, 1966). As a result, it is very generalized and opportunistic in its vertical level of foraging. It uses wait-and-flycatch techniques, but moves from the ground to near the tops of forest trees as opportunities arise. Since the Plain-brown Woodcreeper is a generalist in at least two respects (variety of prey and level of foraging) but a specialist in others (woodpeckerlike perching, wait-and-flycatch techniques, relatively frequent attendance at swarms of army ants), it may be difficult to answer the question (Klopfer, 1962), are tropical avifaunas more diverse because the species have narrower niches? A species may have a niche that is narrow in one or more dimensions but broad in other dimensions. However, the niche of the Plain-brown Woodcreeper is broader on Trinidad, a "peripheral" tropical area with few competing species of ant-following birds, in the sense that the woodcreeper is more abundant there and catches a greater percentage of the total prey items flushed by ants there than in Panamá or Guyana (Willis, 1966).

Perhaps a simple objective way to say if a niche is broad or not is to see if a species captures a greater percentage of the total prey or other resource in a given area than does another species or does the same species in another area. Even though the Plain-brown Woodcreeper "narrows" its foraging niche on Trinidad by foraging mostly near the ground, the ground is such a rich source of food over army ants that the woodcreeper actually gets more prey and thus broadens its niche. It may lose to some extent the ability to forage above the ground, but it is certainly exploiting more of the available food supplies when competing antbirds are absent.

SUMMARY

Plain-brown Woodcreepers usually forage over swarms of army ants and capture arthropods flushed by the ants. The woodcreepers occasionally forage away from ants, at times with the wandering interspecific flocks of the forest interior. They generally wait on vertical perches 1–10 m above the ground and sally like flycatchers to capture orthopterans, roaches, spiders, and other prey from the vegetation or the air. When competing antbirds are absent, the woodcreepers descend and capture prey on the ground more frequently. They use "anting" and "wing-flashing" as foraging techniques; the former behavior pattern apparently wipes harmful secretions off prey and the latter flushes concealed prey.

Alarm behavior, especially fleeing and repetition of a loud call ("stieking") is well developed. In contrast, social behavior is as plain or inconspicuous as are voice and plumage. Agonistic behavior is mainly confined to ignoring conspecific birds, to sudden chasing, and to fighting. Submissive display is better developed but inconspicuous: there is wing-quivering, also a rigid posture during a "rattling" call; aggressive display is rarely seen. The relative lack of display or necessity for inconspicuous displays to avoid predators and competitors may be the reason for an observed high frequency of fighting, which in this species is perhaps not very dysgenic because the birds fight in the relatively open middle levels of the forest where entrapment is difficult.

Settled females occupy exclusive areas, and seldom visit ant swarms outside these areas. Settled males wander widely around the separate centers of their own areas; their mutually overlapping foraging areas overlap with but do not correspond to the foraging areas of females. Settled females apparently dominate settled males occupying the same

regions. There is no permanent pair bond. For a few days at the time of mating an individual female permits a male to come near her without fleeing or attacking. For a time the two squabble vigorously, but the female finally submits to mounting after the male "nibbles" her back repeatedly. "Cavity-sitting," a behavior pattern in which the two birds visit holes in stubs together, suggests that the pair association may extend for a short time beyond copulation. It is possible that the insectivorous niche of the species, and particularly its relatively irregular and marginal source of food, prevent evolution of lek behavior or hypertrophy of male voice or other characters by sexual selection.

Nesting and care of young are tasks of the female. Begging and parental behavior are inconspicuous. "Singing" is used when female and young are widely separated, as it is when adult woodcreepers are alone and wandering away from swarms. A kind of "rattlet" call notifies the young that the female has food. After a month or so the juveniles leave the female and wander separately.

The individuality of these woodcreepers and their relative plainness of plumage, voice, and social behavior may result from their irregularly available and exposed foraging niche. The woodcreeper depends upon irregular sources of food, when ants probe above the ground or when domineering antbirds happen to be absent near the ground. The premium this places upon rapid movement of individuals perhaps precludes development of pair bonds and parental behavior, which would require special calls and displays and thus attract domineering competitors. Moreover, these woodcreepers are adapted for using open sites in the forest midlevels and near the ground in places that antbirds hesitate to go; to use such unsafe sites the woodcreepers apparently depend on inconspicuousness of plumage and behavior, or sudden and unpredictable moves to get prey or chase competitors. They avoid fights with other species, or move in on them quickly or with wing-shivering, perhaps so neither predators nor competitors will be attracted. Individual woodcreepers seem successful at avoiding predation; some on Barro Colorado were over 10 years old.

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LITERATURE CITED

Bock, W. J., and W. D. Miller. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. Amer. Mus. Novitates, no. 1931.

Eisenmann, E. 1955. The species of Middle American birds. Trans. Linnaean Soc. N.Y., 7:1–128.

Feduccia, J. A. 1969. Evolutionary trends in the avian families Furnariidae and Dendrocolaptidae. Unpubl. Ph.D. Disser. Univ. Michigan.

Feduccia, J. A. 1970. Natural history of the avian families Dendrocolaptidae (Woodhewers) and Furnariidae (Ovenbirds). Grad. Res. Center, Southern Methodist Univ., 38:1–26.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science, 165:131–137.

Hailman, J. P. 1960. A field study of the Mockingbird's wing-flashing behavior and its association with foraging. Wilson Bull., 72:346–357.

Hamilton, W. D. 1963. The evolution of altruistic behavior. Amer. Naturalist, 97: 354–356.

Johnson, R. A. 1954. The behavior of birds attending army ant raids on Barro Colorado Island, Panama Canal Zone. Proc. Linnaean Soc. N.Y. 63–65:41–70.

Kelso, L., and M. M. Nice. 1963. A Russian contribution to anting and feather mites. Wilson Bull., 75:23–26.

Klopfer, P. H. 1962. Behavioral aspects of ecology. Prentice-Hall, Englewood Cliffs, New Jersey.

Meyer de Schauensee, R. 1970. A guide to the birds of South America. Livingston Publ. Co., Wynnewood, Pa.

Moynihan, M. H. 1962. The organization and probable evolution of some mixed species flocks of neotropical birds. Smithsonian Misc. Coll., 143:1–140.

Oniki, Y. 1970. Roosting behavior of three woodcreepers (Dendrocolaptidae) in Brazil. Condor, 72:233.

Oniki, Y., and E. O. Willis. 1972. Studies of ant-following birds north of the eastern Amazon. Atas Amazonica, (In press).

Pinto, O. 1953. Sobre a colecão Carlos Estevão de peles, ninhos, e ovos de aves de Bélem (Pará). Papeis Avulsos Dept. Zool., São Paulo, 2:111–222.

Potter, E. F. 1970. Anting in wild birds, its frequency and probable purpose. Auk, 87:692–713.

Simmons, K. E. L. 1966. Anting and the problem of self-stimulation. J. Zool., 149: 145–162.

Skutch, A. F. 1969. Life histories of Central American birds III. Pacific Coast Avifauna, 35.

Slud, P. 1960. The birds of Finca "La Selva," Costa Rica: a tropical wet forest locality. Bull. Amer. Mus. Nat. Hist., 121:49–148.

Slud, P. 1964. The birds of Costa Rica. Bull. Amer. Mus. Nat. Hist., 128:1–430.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of three (sic) squirrels *Tamiasciurus*. Ecol. Monogr., 38:31–63.

Snow, D. W. 1962. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. Zoologica, 47:65–104.

Snow, D. W., and B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad land-birds. Zoologica, 49:1–63.

Southern, W. E. 1963. Three species observed anting on a wet lawn. Wilson Bull., 75:275–276.

Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Arch. Néerl. Zool., 13:266–336.

Whitaker, L. M. 1957. A resume of anting, with particular reference to a captive Orchard Oriole. Wilson Bull., 69:195–262.

Willis, E. O. 1960. A study of the foraging behavior of two species of ant-tanagers. Auk, 77:150–170.

Willis, E. O. 1966. Interspecific competition and the foraging behavior of Plain-brown Woodcreepers. Ecology, 47:667–672.

Willis, E. O. 1967. The behavior of Bicolored Antbirds. Univ. of Calif. Publ. Zool., 79:1–132.

Willis, E. O. 1972. The behavior of Spotted Antbirds. A.O.U. Monographs, 10.

APPENDIX: NAMES OF BIRDS IN TEXT

Antbird, Bare-crowned.—*Gymnocichla nudiceps*
  Bicolored.—*Gymnopithys bicolor*
  Black-headed.—*Percnostola rufifrons*
  Chestnut-backed.—*Myrmeciza exsul*
  Harlequin.—*Rhegmatorhina berlepschi*
  Lunulated.—*Gymnopithys lunulata*
  Ocellated.—*Phaenostictus mcleannani*
  Rufous-throated.—*Gymnopithys rufigula*
  Scale-backed.—*Hylophylax poecilonota*
  Spotted.—*Hylophylax naevioides*
  White-plumed.—*Pithys albifrons*
  White-throated.—*Gymnopithys salvini*
Antshrike, Slaty.—*Thamnophilus punctatus*
Araçari, Collared.—*Pteroglossus torquatus*
Attila, Bright-rumped.—*Attila spadiceus*
Bare-eye, Black-spotted.—*Phlegopsis nigromaculata*
  Reddish-winged.—*Phlegopsis erythroptera*
Crane-Hawk.—*Geranospiza caerulescens*
Creeper, Brown.—*Certhia familiaris*
Cuckoo, European.—*Cuculus canorus*
  Squirrel.—*Piaya cayana*
Flycatcher, Acadian.—*Empidonax virescens*
  Streaked.—*Myiodynastes maculatus*
Forest-Falcon, Barred.—*Micrastur ruficollis*
  Lined.—*Micrastur gilvicollis*
Ground-Cuckoo, Rufous-vented.—*Neomorphus geoffroyi*
Hawk, Semiplumbeous.—*Leucopternis semiplumbea*
  White.—*Leucopternis albicollis*
Kite, Double-toothed.—*Harpagus bidentatus*
  Gray-headed.—*Leptodon cayanensis*
  Hook-billed.—*Chondrohierax uncinatus*
Leafscraper, Scaly-throated.—*Sclerurus guatemalensis*
Mockingbird.—*Mimus polyglottos*
Motmot, Broad-billed.—*Electron platyrinchum*
  Rufous.—*Baryphthengus ruficapillus*
Owl, Mottled.—*Ciccaba virgata*
  Spectacled.—*Pulsatrix perspicillata*
Puffbird, Black-breasted.—*Notharcus pectoralis*
  White-whiskered.—*Malacoptila panamensis*
Sandpiper, Spotted.—*Actitis macularia*
Tanager, Gray-headed.—*Eucometis penicillata*
Thrush, Swainson's.—*Hylocichla ustulata*
Toucan, Chestnut-mandibled.—*Ramphastos swainsonii*
  Keel-billed.—*Ramphastos sulfuratus*
Warbler, Canada.—*Wilsonia canadensis*
Woodcreeper, Barred.—*Dendrocolaptes certhia*
  Black-banded.—*Dendrocolaptes picumnus*
  Black-striped.—*Xiphorhynchus lachrymosus*
  Buff-throated.—*Xiphorhynchus guttatus*
  Hoffmanns'.—*Dendrocolaptes hoffmannsi*
  Plain-brown.—*Dendrocincla fuliginosa*
  Red-billed.—*Hylexetastes perrotti*
  Ruddy.—*Dendrocincla homochroa*
  Spix's.—*Xiphorhynchus spixii*
  Tawny-winged.—*Dendrocincla anabatina*
  Wedge-billed.—*Glyphorhynchus spirurus*
  White-chinned.—*Dendrocincla merula*
Woodpecker, Chestnut.—*Celeus elegans*

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RED-TAILED HAWK POPULATIONS AND ECOLOGY IN EAST-CENTRAL WISCONSIN

John M. Gates

This paper reports on a study of Red-tailed Hawk (*Buteo jamaicensis*) populations, reproductive success, and food habits in relation to Ring-necked Pheasants (*Phasianus colchicus*) in east-central Wisconsin. Information on the Redtail and other species of raptors was gathered as one phase of a population study of pheasants, concerned in part with pheasant mortality and with the possible influence of Red-tailed Hawk predation on pheasant survival (Gates, 1971). Although the Redtail is one of the most common birds of prey occupying the farmlands of the Midwest, comparatively few studies of its ecology have been published. In view of the alarming decline in population exhibited by many falconiformes in recent years, particularly in relation to biocides (Hickey, 1969), information on reproductive success and population density for all birds of prey is urgently needed as a reference point from which future population trends can be evaluated. Although Hickey (1969) still regards the Redtail as having normal reproductive success, Seidensticker and Reynolds (1971) have more recently uncovered evidence of post-DDT eggshell thinning in this species in Montana.

STUDY AREA

Observations of raptor ecology were made from December, 1959, to August, 1965, on the Waupun Study Area, a 42-square-mile tract in southwestern Fond du Lac County and adjacent parts of Green Lake and Dodge counties, Wisconsin (latitude 43° 45′ N; longitude 88° 53′ W). The topography of the area is level to gently undulating, with 78 per cent of the landscape under cultivation. Dairy farming is the principal farm enterprise; major crops include corn, oats, and hay. Twenty-two per cent of the land area is uncultivated, consisting largely of wetlands (10 per cent) and permanent pasture (7 per cent). Only 0.3 per cent of the area is covered by closed-canopy woodlots, predominantly bur oak (*Quercus macrocarpa*) and black oak (*Q. velutina*). Small groves of these species also occur in many pastures and on wetland edges. Most of the woodlots, and about half of the wetlands, are used to some extent for grazing. The most prevalent forms of wetland vegetation include sedge meadow (principally *Carex stricta*), canary grass (*Phalaris arundinacea*), and shrub swamps, the latter dominated by willow (*Salix* spp.) and dogwood (*Cornus stolonifera*; *C. Purpusi*).

In the winter of 1958–59 (December through March), observations were also made on the Springvale Study Area (15 square miles), approximately 3 miles northeast of the area described above. Except for greater abundance of woodlots on the Springvale Area (6 per cent), landscape features and cover composition were generally similar between the two.

To the best of my knowledge, use of insecticides during the period of study was light. I knew of only two crops that received regular foliar treatment—sweet corn (DDT) in late summer for control of corn earworm and peas (Parathion) in early summer for control of pea aphids. Collectively, these crops constituted about 12 per cent of the land area, but treatment was not applied to the total acreage in any one season and was highly variable between years. Dicke (1960), quoted by Hickey (1961), reported that only 12 and 7 per cent, respectively, of the statewide acreage of these crops was treated in 1959. These figures fall well in line with my subjective evaluation of the intensity of insecticide use during the study, suggesting that Redtails at Waupun probably were not being heavily contaminated by insecticides through the local food chain. Furthermore, since it appeared that the adult segment of the population was to large extent non-migratory, I also doubt that breeding birds were carrying high levels of pesticide residues accumulated elsewhere. Unfortunately, no egg or tissue analyses were available to support these conjectures, however.

METHODS

On the Springvale Area in February, 1959, Red-tailed Hawk and Rough-legged Hawk (*Buteo lagopus*) populations were determined by direct search. On the Waupun Area in subsequent years, winter populations of these species were estimated by the car-count method (Craighead and Craighead, 1956). A 45-mile transect was driven by two observers on two or three closely spaced afternoons between mid-January and mid-February. Counts were made on snow-covered ground, with wind velocities below 10 mph, and temperatures above 0° F. All Redtails and Roughlegs observed on the ground, perched, or in flight within ¼ mile of the transect were recorded, giving approximately 50-per cent coverage of the study area. The number of each species observed on successive runs was averaged and doubled as an estimate of mid-winter population size. Because of the area's open terrain, near-level topography, and scarcity of large woodlots, this method probably gave a reliable estimation of winter buteo numbers. The main criticism of the method was the small number of censuses run. Successive counts for individual winters showed an average variability of 41 per cent. Because each winter's population estimate was accordingly subject to considerable sampling error, attention in this paper is largely confined to the mean level of population for all winters of study combined.

Winter population data for other birds of prey were obtained from a daily log of all raptors sighted, from which the number of individuals was later inferred from the distribution of sight records. Snowy Owls (*Nyctea scandiaca*) were so conspicuous that a complete inventory of this species was doubtless obtained. Cooper's Hawks (*Accipiter cooperii*) and Horned Owls (*Bubo virginianus*), by comparison, were more secretive, and estimates for these species were necessarily regarded as minimum figures.

The breeding population of Red-tailed Hawks was determined over the 3-year period 1962–64 by systematic coverage of the Waupun Study Area for active raptor nests. Search was conducted during late March and early April, either on foot or by scanning for potential nest sites through binoculars and spotting scopes. Nests tended to be highly conspicuous at this season, and I believe that a complete census of breeding pairs was obtained. No estimate was made of the number of non-breeding Redtails on the area.

Redtail nests were periodically checked between the time of nest discovery and the time the young were fledged. After initially determining that eggs had been laid, no nest trees were climbed until the young were hatched. Prey remains were identified at each nest visit.

WINTER POPULATIONS

Red-tailed Hawks.—The estimated winter population of Redtails at Waupun varied from a high of 21 individuals in 1961–62 to a low of 9 in 1964–65

TABLE 1

ESTIMATES OF MIDWINTER RAPTOR POPULATION DENSITY ON TWO STUDY AREAS IN EAST-CENTRAL WISCONSIN[a]

Winter	Study area[b]	Red-tailed Hawk	Rough-legged Hawk	Cooper's Hawk	Snowy Owl	Horned Owl
1958–59	Springvale	14	8	4	0	6
1959–60	Waupun (2)[c]	19	21	–	–	–
1961–62	Waupun (2)	21	5	3	4	4
1962–63	Waupun (3)	17	28	2	2	5
1963–64	Waupun (3)	16	13	2	2	3
1964–65	Waupun (2)	9	13	3	3	4

[a] No raptor-census data available in 1960–61.

[b] Springvale Study Area 15 square miles in size; Waupun Study Area 42 square miles.

[c] Figures in parentheses represent the number of car-count census runs from which Red-tailed and Rough-legged Hawk population estimates were derived.

(Table 1). The number of winter residents showed comparatively little fluctuation between 1959 and 1964, during which period the average winter density was 0.44 per square mile. On the Springvale Area, 14 Redtails were censused in 1958–59, a density of 0.93 per square mile. Because of its larger size and longer period of study, the Waupun Area probably furnished more representative information on the density of wintering Redtails for the region. These data show an average winter population of 0.39 per square mile based on five seasons of field study.

In February, 1962, an immature Redtail was found dead where it apparently had been struck and killed by a motor vehicle while feeding on the remains of a road-killed cottontail rabbit (*Sylvilagus floridanus*). Aside from this single individual, all winter observations of Redtails in this study consisted of adult (= red-tailed) birds. Orians and Kuhlman (1956) reported much greater frequency of immatures wintering in Green County, Wisconsin. Fourteen per cent of the Redtails they encountered consisted of immature individuals as a 2-year mean. (Green County is located approximately 80 miles south-southwest of the Waupun Study Area.)

In general, I believe that most of the wintering Redtails at Waupun were mated pairs that eventually bred on the area. Two lines of evidence suggested that the majority were permanent residents. (1) The population of breeding Redtails for the period 1962–64 (Table 2) was only eight birds greater (62 versus 54) than the corresponding population totals of the preceding winters (Table 1). (2) In February and March of 1962 and 1963, seven Redtail pairs were maintained under near-daily surveillance. After mid-February in both years, each of these pairs was observed with increasing frequency in the vicinity of old nest trees that were eventually occupied. Five of the seven

TABLE 2

SUMMARY OF RED-TAILED HAWK BREEDING POPULATIONS AND REPRODUCTIVE PERFORMANCE, WAUPUN STUDY AREA

Year	Number of active nests	Number of successful nests	Total number of young fledged	Young fledged per successful nest	Young fledged per nesting attempt
1962	9	7 (78)[a]	13	1.9	1.4
1963	10	7 (70)	11	1.6	1.1
1964	12	6 (50)	11	1.8	0.9
Totals and means	31	20 (65)	35	1.8	1.1

[a] Figures in parentheses represent the percentage of total active nests.

were observed one or more times at the nest site proper, and two were also seen carrying nesting materials. No influx of migrant Redtails or other raptors was noted during the period of these observations.

In California, Fitch et al. (1946) similarly reported that Redtail pairs were permanently resident in definite hunting and nesting territories. Orians and Kuhlman (1956), in Wisconsin, reported that resident birds were on territory by the end of February; however, some migrants were also present that traveled singly or in groups. In central Iowa, Weller (1964) most commonly observed wintering Redtails in areas in which active nests were later located.

The winter density of Redtails in Green County, Wisconsin, averaged 0.46 per square mile in 1953–54 and 1954–55 (Orians and Kuhlman, 1956). On a study area in Columbia and Dane counties, Wisconsin, the 3-year mean density was 0.76 per square mile (Kabat and Thompson, 1963). All three Wisconsin study areas on which winter Redtail censuses have been conducted are located in roughly the southeastern quarter of the state. Available evidence suggests that Redtails regularly winter in this region at densities approaching, and locally exceeding, 0.50 per square mile. This compares with 0.37 per square mile as the three-winter mean density observed by Craighead and Craighead (1956) in southern Michigan.

Other raptors.—Midwinter population estimates of Rough-legged Hawks tended to be highly variable (Table 1). Comparatively small numbers of these hawks were observed during the two winters of heaviest snowfall, 1958–59 and 1961–62. Since the Roughleg's winter diet consists almost exclusively of small mammals (Bent, 1937; Craighead and Craighead, 1956; and Weller, 1964), lower vulnerability of small-mammal prey with heavier snow cover probably encouraged a higher percentage of these migrants to continue southward. In both winters, my recollection is that larger numbers of Roughlegs were present in early winter before build-up of heavy snow cover.

The minimum density of Cooper's Hawks and Horned Owls at Waupun was 0.06 and 0.10 per square mile, respectively, as a 4-winter mean (Table 1). On the Springvale Area in 1958–59, densities were 0.27 and 0.40 per square mile. These differences in population level doubtless stemmed from the greater abundance of wooded habitat on the Springvale Area.

Snowy Owls were present at Waupun each winter that an attempt was made to estimate their numbers (Table 1). Occurrence of these owls over the short period of study demonstrated no evidence of periodicity. Other birds of prey observed in winter included one Sparrow Hawk (*Falco sparverius*) in 1962–63 and one Barred Owl (*Strix varia*) in 1963–64. Screech Owls (*Otus asio*) were present in unknown numbers each winter of study. Short-eared Owls (*Asio flammeus*) were found in several day-roosting concentrations as large as 15 or 20 birds throughout the open winters of 1960–61 and 1963–64; however, no more than five Shortears were believed present during any other season of study.

Collectively, the average density of large raptors (Red-tailed Hawks, Rough-legged Hawks, Cooper's Hawks, Horned Owls, and Snowy Owls) in this study was slightly less than 1.0 per square mile.

OBSERVATIONS ON WINTER ECOLOGY

Intraspecific interactions.—I observed no overt sign of intraspecific intolerance between wintering Redtails; however, it was my definite impression that the hunting ranges of individual pairs tended to be mutually exclusive. Out of 41 birds encountered on winter car counts, 24 (58 per cent) were sighted no more than 0.50 mile apart. This seemed to imply a high degree of aggregation in winter Redtail distribution, which could be explained by a tendency for pairs to share home ranges that did not overlap those of other pairs.

One series of observations was particularly instructive on this point. In mid-February of 1962, at which time over 2 feet of snow blanketed the area and small-mammal prey were virtually invulnerable to avian predation, one pair of Redtails over an 11-day span killed at least eight hen pheasants out of a flock of 85–100 wintering birds. These pheasants were particularly vulnerable to predation, since they were concentrated around a bait-trapping station in a 0.15-acre grove of willow brush adjacent to several black willow (*Salix nigra*) trees that made ideal hunting perches. It ultimately became necessary to remove these hawks to continue pheasant trapping at the site, and on 17 February both members of the pair were trapped and dispatched. Three days later, a single Redtail was perched at the site, and on 23 February it too was captured and removed from the area. On 27 February, another pair of Redtails appeared on the scene, whereupon pheasant trapping was suspended. I was able to recognize one member of this second pair by conspicuous plumage variation. Earlier in winter, this individual had been consistently observed on a hunting range which centered approximately 1.7 miles northeast. At least in this particular instance, it seemed clear that removal of the original pair created a vacant hunting range that contained an attractive and highly vulnerable food source, and that this vacuum was almost immediately filled by individuals that were previously excluded from the site.

Interaction with pheasants.—Well before the conclusion of this study, I came to regard the Red-tailed Hawk as a skilled and highly capable pheasant predator. Out of 165 preyed-upon pheasants encountered in winter, 99 (61 per cent) were attributed to birds of prey. Of the 99, 50 were further assignable to individual species of raptor according to field sign described by Einarsen (1956) or from actual observations made at the kill site: Redtails 28, Horned Owls 11, Cooper's Hawks 9, and Roughlegs 2. At face value, these records suggested that Red-tailed Hawks were responsible for 55 per cent of all pheasants killed by avian predators and for 34 per cent of the overall winter predation loss. Twenty-one of the 28 Redtail records consisted of actual flushes from freshly made kills; in addition, I observed 2 successful and 17 unsuccessful attempts by Redtails on pheasants. From these observations, I believe that pheasants were an important component of the Redtail's winter diet, even though the actual percentage they comprised was not established through systematic food-habits investigation.

During the period 1959–65, winter (early January through late March) mortality of Ring-necked Pheasant hens at Waupun averaged 27 per cent. Predation accounted for 74 per cent of the winter loss (Gates, 1971), hence the kill by Redtails could be estimated at 7 per cent of the January pheasant population.

It is conceivable that this percentage was a somewhat inflated estimate. Because birds of prey generally do not cache prey remains, I believe that field evidence of avian predation tended to be more conspicuous than mammalian predation, probably leading to an over-estimate of the proportionate pheasant kill by raptors in general and Redtails in particular. Notwithstanding, I conclude that Red-tailed Hawks did in fact remove a substantial percentage of the hen pheasants at Waupun during the winter period.

The overall predation rate on pheasants, and I believe the Redtail rate individually, was highly variable between winters. During two winters of heavy snow cover (1958–59 and 1961–62), predation losses were calculated at 29 and 33 per cent, respectively, of the January population. Corresponding figures during two winters of virtually snowless conditions (1960–61 and 1963–64) were 2 and 17 per cent, respectively, and during three winters of intermediate snowfall (1959–60, 1962–63, and 1964–65) 13, 18, and 21 per cent, respectively (Gates, 1971). Of the 28 pheasant kills attributable to Redtails, 18 were recorded in 1958–59 and 1961–62.

During these particular winters, snow depths of 10 to 30 inches prevailed for at least a 70-day span between 1 January and 31 March. Pheasants during these periods were hard pressed for winter food and shelter, and virtually the entire population was concentrated at only 14 sites on the study area that still afforded protective cover. With small mammals well sheltered under the heavy snow canopy, it was clear that Redtails were taking full advantage of the increase in pheasant vulnerability. In February of 1962, for example, 13 out of 18 Redtails observed on winter car counts were sighted on hunting perches or in flight in the immediate vicinity of a pheasant concentration site. Although I could not measure the impact of Redtail predation on pheasants by individual winter of study, I conclude that it was highly variable between years, and that higher rates of pheasant loss resulted from a shift in food habits and hunting behavior as the small-mammal portion of the prey base became increasingly invulnerable with deeper snow cover.

Recent studies have characterized the Redtail as a versatile and highly adaptable predator, one capable of exploiting a wide variety of prey species (Craighead and Craighead, 1956; Orians and Kuhlman, 1956; and Luttich et al., 1970). For this reason, it doubtless enjoys considerable flexibility in adjustment of food habits to changes in prey vulnerability, at least in comparison with the more specialized feeders, e.g., the Rough-legged Hawk, which appears to be primarily a small-mammal specialist. The Redtail's ability to switch over to larger prey, including pheasants, during periods of heavy snow may be an important factor in this species' ability to successfully winter year after year in regions as far north as Waupun.

BREEDING POPULATIONS

Red-tailed Hawk.—The average number of active Redtail nests at Waupun during the breeding seasons of 1962–64 was 10.3, equivalent to one pair per 4.1 square miles or 0.54 breeding adults per square mile per year (Table 2). This was regarded as a minimum density, however, since no attempt was made to determine the number of non-breeding birds that may have been present. Of the 31 nesting pairs under observation, 30 comprised both adult (= red-tailed) individuals. The single remaining pair consisted of one adult paired with an apparent yearling (= brown-tailed) bird. The sex of the latter individual was unknown.

Breeding densities of the Redtail at Waupun were generally lower than reported elsewhere. In California (Fitch et al., 1946), New York (Hagar, 1957), Green County, Wisconsin (Orians and Kuhlman, 1956), and Alberta (Luttich et al., 1971), the number of breeding pairs averaged one per 0.5, 2.2, 2.8, and 2.7 square miles, respectively.

Other raptors.—One Horned Owl nest was found in 1963 and 1964; no nests of this species were found in 1962. Even though search for raptor nests may have been undertaken too late in the year for a complete inventory of Horned Owls, my conclusion was that the breeding density of this species at Waupun was extremely low. A sufficient amount of field work was conducted in February and March each year that I believe that most, if not all, Horned Owl nests would have been discovered before the spring search. Scarcity of woodlots at Waupun seemingly represented poor breeding habitat for this species. Many of the owls present in winter probably were non-breeding individuals.

BREEDING SEASON ECOLOGY

Nest sites.—Nineteen out of 31 Redtail nests under observation were situated in black oaks, five in bur oaks, three each in American elms (*Ulmus americana*) and black willows, and one in quaking aspen (*Populus tremuloides*). Only four of the 31 were located in closed-canopy woodlots. Eighteen occurred in open groves, generally less than one acre in size, and nine were situated in isolated trees along fencelines and ditchbanks. Aside from a single nest in an aspen swamp, all nest trees were located on well-drained upland sites.

Reproductive success.—A nesting attempt was considered successful if at least one young eventually fledged. Of the 31 nests in which eggs were laid in 1962–64, 20 (65 per cent) succeeded (Table 2). The cause of nest failure was known for only six of the 11 unsuccessful nesting attempts. Three were partly dismantled and blown down by high winds in 1964, two were destroyed by unidentified predators, and one failed when one of the adults was shot.

A total of 35 young were fledged from the 20 successful nests, an average of 1.8 young per successful clutch. Seven of the 20 nests produced one fledgling apiece, 11 produced two fledglings, and two produced three fledged young. The rate of fledging success at Waupun compared favorably with populations investigated elsewhere. In southern Wisconsin, the mean was 1.9 young per successful nest (Orians and Kuhlman, 1956); in New York, 1.9 (Hagar, 1957); in Montana, 1.7 (Seidensticker and Reynolds, 1971); and in Alberta, 1.4 (Luttich et al., 1971). I made no attempt to determine clutch size, nor brood size at hatching, for each of the nests under observation, hence information was not available on rates of egg mortality or nestling survival. From the average number of fledged young per successful clutch, however, rates of rearing success at Waupun appeared satisfactory.

The overall rate of reproductive success was 1.1 fledged young per breeding pair. Based on North American productivity and mortality data for the Redtail, Henny and Wight (in press) concluded that between 1.3 and 1.4 young must be raised per nesting attempt to maintain a stationary population. At Waupun, it might therefore be inferred that Redtail productivity was inadequate for population maintenance. If so, the problem seemed to center on the high rate of nest failure, since rearing success was very near the maximum recorded in the literature. Orians and Kuhlman (1956) reported 1.4 young raised per breeding pair in southern Wisconsin during 1953 and 1954.

Summer food habits.—Nineteen species were represented among the aggregate prey remains identified at seven Redtail nests (Table 3). These seven nests were visited at approximately weekly intervals between hatching and fledging. It is possible, however, that prey remains were collected too infrequently for a completely unbiased sample of summer food habits. Fitch et al. (1946) reported that adult Redtails sometimes remove unused prey items from the nest site, and English (1934) observed that smaller animals, particularly mice, were often eaten without leaving trace. Of the prey species listed in Table 3, I suspect that *Microtus*, passerine birds, and invertebrates were somewhat under-represented in the food-habits sample.

The five leading items of prey, which accounted for 63 per cent of the observed nesting-season diet, consisted of pheasants (23 per cent), *Microtus* (17 per cent), cottontail rabbits (11 per cent), Red-winged Blackbirds (8 per cent), and domestic chicken (5 per cent). Birds constituted 58 per cent of the observed diet by frequency of occurrence, mammals 38 per cent, and invertebrates 5 per cent.

Most other studies have revealed a higher incidence of mammalian prey than I observed in the Redtail's summer diet at Waupun. In Wyoming (Craighead and Craighead, 1956), Alberta (Luttich et al., 1970), and Michigan (Craighead and Craighead, 1956), mammals accounted for 93, 66, and 40 per cent, respectively, of the prey species taken. In southern Wisconsin, 85 per cent of diet reported by Errington (1933) consisted of mammals, among which thirteen-lined ground squirrels, *Microtus*, and cottontail rabbits were most important. The nesting-season prey of a single pair of Redtails observed in Michigan by English (1934) included 76 per cent mammals and 24 per cent birds.

It is interesting to note the close correspondence between Redtail food habits at Waupun and those observed in Green County by Orians and Kuhlman (1956). From evidence at nest sites, pheasants in their study also ranked as the leading item of prey (33 per cent), followed by cottontail rabbits (19 per cent), domestic chicken (14 per cent), crows (6 per cent), and *Microtus* (6 per cent). Sixty-five per cent of the nesting-season diet was made up of birds and 35 per cent of mammals.

To my knowledge, these two studies provide the only available information on Redtail food habits in areas that also represent good pheasant habitat. Green County, at the time of Orians and Kuhlman's investigation, was an area of comparative pheasant abundance by Wisconsin standards, as was the Waupun Area during the course of the present study. Although mammals seem

TABLE 3

FREQUENCY OF OCCURRENCE OF PREY REMAINS COLLECTED AT SEVEN RED-TAILED HAWK NESTS, WAUPUN STUDY AREA, 1963–64

Item	Number identified	Per cent occurrence
Birds		
Ring-necked Pheasant (*Phasianus colchicus*)	40	22.7
Red-winged Blackbird (*Agelaius phoeniceus*)	14	8.0
Domestic Chicken	9	5.1
European Partridge (*Perdix perdix*)	5	2.8
Crow (*Corvus brachyrhynchos*)	5	2.8
Yellow-shafted Flicker (*Colaptes auratus*)	4	2.3
Mourning Dove (*Zenaidura macroura*)	3	1.7
Common Grackle (*Quiscalus quiscula*)	3	1.7
Catbird (*Dumetella carolinensis*)	2	1.1
Blue Jay (*Cyanocitta cristata*)	2	1.1
House Sparrow (*Passer domesticus*)	1	0.5
Unidentified passerine remains	14	8.0
Mammals		
Meadow mouse (*Microtus* spp.)	29	16.5
Cottontail rabbit (*Sylvilagus floridanus*)	19	10.8
Thirteen-lined ground squirrel (*Citellus tridecemlineatus*)	8	4.5
Muskrat (*Ondatra zibethicus*)	4	2.3
Fox squirrel (*Sciurus niger*)	4	2.3
Norway rat (*Rattus norvegicus*)	2	1.1
Invertebrates		
Unidentified beetle remains (*Coleoptera*)	3	1.7
Unidentified crayfish remains (*Astacidae*)	5	2.8
Totals	176	99.8

to predominate in the Redtail's diet over much of its North American range, it is clear that this hawk is capable of exploiting pheasants as a major part of the spring and summer diet when this prey species is available in reasonable numbers.

Interaction with pheasants.—In 1963 and 1964, an attempt was made to determine the rate of predation on pheasants by nesting Redtails. Two procedures were relied upon. First, the number of marked hen pheasants recovered at Redtail nests was compared with the number of marked individuals present on the study area on 1 May. Pheasant marking was accomplished by leg bands and backtags. Pheasants were captured by autumn nightlighting and winter bait trapping, and estimates were made each year of the number of marked hens surviving on the area on 1 May (Gates, 1971). As an alternative procedure, the total number of hen pheasants identified at Redtail nests, including both marked and unmarked individuals, was compared with the 1 May census total for the study area at large.

In both years of study combined, 13 Redtail nests produced young and were periodically checked for pheasant marks. Twenty-seven sets of leg bands and/or backtags appeared at these sites, 6 per cent of the 443 marked individuals that I estimated to be alive on the area on 1 May. A total of 81 hen pheasants was represented among the aggregate prey remains identified. The 1 May hen population for the area in 1963–64 was 1,863, from which a predation rate of 4 per cent was calculated.

For two reasons, these percentages could not be accepted as unbiased estimates: (1) It is conceivable that backtagged pheasants were more vulnerable to Redtails than unmarked birds, which may have accounted in part for the higher rate of exploitation indicated by the first as compared with the second method. (2) In addition, proof was obtained that some of the pheasant hens whose remains appeared at Redtail nests had originally died or were seriously injured by mortality factors other than hawk predation. Leg bands from one marked hen that I initially found as a freshly made kill at the entrance to an active fox den I later recovered beneath a Redtail nest. Two other backtags were found at Redtail nests which belonged to hayfield-nesting hens that I knew had lost at least one leg as a result of hay-mowing accidents (the identity of these birds was established from leg bands attached to amputated legs at the nest site). The fact that some of the apparent Redtail kills actually represented carrion, and that certain other hens were severely incapacitated before being preyed upon, meant that both methods of calculation probably led to a somewhat exaggerated estimate of the rate of Redtail predation.

On the other hand, these findings applied exclusively to the nestling period when adult Redtails were rearing young. No allowance was possible for pheasants preyed upon outside the nesting season, nor for the kill by unsuccessful or non-breeding pairs. On balance, I conclude that Red-tailed Hawks probably removed close to 5 per cent of the spring population of pheasant hens in 1963–64.

The following figures perhaps provide some perspective in evaluating the overall impact of Redtail predation on pheasants. The average annual mortality rate of hen pheasants in this study between 1 October and 30 September was 76 per cent (Gates, 1971). Of those hens surviving in early January in an average winter, 27 per cent died before the end of March. Calculations suggested that a maximum of 7 per cent of the January population, or 26 per cent of all hens dying during the interval, were preyed upon by Redtails. Among those hens surviving on 1 May, 41 per cent disappeared by early

August (Gates, 1971). The estimated rate of Redtail predation on the 1 May population was approximately 5 per cent, equal to 12 per cent of the total loss.

Because predation rates were measured at only two seasons of the year, it is impossible to assess quantitatively the year-round importance of Redtail predation. I believe that this study has conclusively demonstrated, however, that where Red-tailed Hawks and Ring-necked Pheasants coexist, pheasants may comprise a significant proportion of the Redtail's winter and nesting-season diet, and that Redtail predation, in turn, may account for an appreciable fraction of the losses sustained by a pheasant population at these seasons. Under conditions of the present study, the number of pheasants killed by Redtails was nevertheless a modest fraction of total mortality, and the possible role of Redtail predation in regulation of pheasant density would have to be evaluated in context of other mortality factors which collectively accounted for a much larger proportion of total deaths.

SUMMARY

A study of Red-tailed Hawk populations, ecology, and predation on Ring-necked Pheasants was conducted in east-central Wisconsin in 1959–65. The average winter density of Redtails on a 42-square-mile tract was 0.39 per square mile; the average breeding density over a 3-year span (1962–64) was 0.54 per square mile. Wintering Redtails consisted almost exclusively of adults, the majority of which appeared to be paired and permanently resident.

Redtail nest success was 65 per cent, and the average number of young fledged per successful clutch was 1.8. The overall rate of productivity was 1.1 fledged young per breeding pair, well below the threshold of 1.3 to 1.4 young reportedly required for population maintenance in this species (Henny and Wight, in press). Rearing success was close to the maximum reported in the literature, the main limitation to breeding success being the high rate of nest mortality prior to hatching.

Pheasants were the leading item of prey in an analysis of spring and summer food habits. Pheasants were also preyed upon in winter, but the percentage they comprised of the winter diet, though considered substantial, was not quantitatively evaluated. Over a seven-winter period (1958–65), Redtails removed an estimated 7 per cent of the hen pheasant population between early January and late March. In 1963–64, Redtail predation during the spring and summer period was estimated at 5 per cent of the 1 May population. Under conditions of the present study, it was concluded that the Red-tailed Hawk was a highly capable predator on pheasants, and that Redtail predation accounted for a significant percentage of year-round pheasant mortality.

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LITERATURE CITED

Bent, A. C. 1937. Life histories of North American birds of prey (Part I). U.S. Natl. Mus. Bull., 167.

Craighead, J. J., and F. C. Craighead, Jr. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania, and Wildlife Management Institute, Washington, D.C.

Einarsen, A. S. 1956. Determination of some predator species by field signs. Oregon State Monogr., Studies in Zoology. No. 10.

English, P. F. 1934. Some observations on a pair of Red-tailed Hawks. Wilson Bull., 46:228–235.

Errington, P. L. 1933. Food habits of southern Wisconsin raptors. Part II. Hawks. Condor, 35:19–29.

Fitch, H. S., F. Swenson, and D. F. Tillotson. 1946. Behavior and food habits of the Red-tailed Hawk. Condor, 48:205–237.

Gates, J. M. 1971. The ecology of a Wisconsin Pheasant population. Unpubl. Ph.D. Thesis, Univ. Wisconsin, Madison, Wisconsin.

Hagar, D. C., Jr. 1957. Nesting populations of Red-tailed Hawks and Horned Owls in central New York state. Wilson Bull., 69:263–272.

Henny, C. J., and H. M. Wight. In press. Red-tailed and Cooper's Hawks: Their population ecology and environmental pollution. Symposium on the population ecology of migratory birds. Patuxent Wildlife Research Center. (Original not seen; cited by Luttich et al., 1971.)

Hickey, J. J. 1961. Some effects of insecticides on terrestrial birdlife in the Middle West. *In* Report of the Subcommittee on Relation of Chemicals to Forestry and Wildlife for the State of Wisconsin. Madison, Wisconsin.

Hickey, J. J. 1969. Peregrine falcon populations: Their biology and decline. Univ. Wisconsin Press, Madison, Wisconsin.

Kabat, C., and D. R. Thompson. 1963. Wisconsin quail 1834–1962/Population dynamics and habitat management. Wisconsin Conservation Dept. Tech. Bull. No. 30.

Luttich, S., D. H. Rusch, E. C. Meslow, and L. B. Keith. 1970. Ecology of Red-tailed Hawk predation in Alberta. Ecology, 51:190–203.

Luttich, S. N., L. B. Keith, and J. D. Stephenson. 1971. Population dynamics of the Red-tailed Hawk (*Buteo jamaicensis*) at Rochester, Alberta. Auk, 88:75–87.

Orians, G., and F. Kuhlman. 1956. Red-tailed Hawk and Horned Owl populations in Wisconsin. Condor, 58:371–385.

Seidensticker, J. C., IV, and H. V. Reynolds, III. 1971. The nesting, reproductive performance, and chlorinated hydrocarbon residues in the Red-tailed Hawk and Great Horned Owl in south-central Montana. Wilson Bull., 83:408–418.

Weller, M. W. 1964. Habitat utilization of two species of buteos wintering in central Iowa. Iowa Bird Life, 34:58–62.

WILDLIFE RESEARCH SECTION, STATE OF WISCONSIN DEPARTMENT OF NATURAL RESOURCES, MADISON, WISCONSIN 53701 (PRESENT ADDRESS: DEPARTMENT OF WILDLIFE AND FISHERIES SCIENCES, SOUTH DAKOTA STATE UNIVERSITY, BROOKINGS, SOUTH DAKOTA 57006), 20 MARCH 1972.

PREDATOR-PREY RELATIONSHIPS AND REPRODUCTION OF THE BARN OWL IN SOUTHERN TEXAS[1]

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This study was designed to reveal the ecological interactions existing between the food habits and breeding of Barn Owls (*Tyto alba*) in southern Texas. Specific areas of investigation included determination of (a) Barn Owl food habits, (b) relative abundance of prey populations, and (c) Barn Owl nesting biology. Certain portions of the study began in 1965, whereas intensive field work was initiated and continued in 1969 through 1971.

STUDY AREA

Field work was conducted on the Rob and Bessie Welder Wildlife Foundation (hereafter referred to as the Welder Refuge), eight miles northeast of Sinton, San Patricio County, Texas. The Welder Refuge covers 7,800 acres of a broad ecotone between the Coastal Prairies and Rio Grande Brushlands. The region supports a complex biota of nearly 1,400 flowering plants and more than 500 animal species. A subhumid climate prevails; hot summers and mild, short winters are characteristic together with frequent late summer and fall hurricanes. Rainfall averages about 31 inches per year, but the fluctuation between years is highly variable with the extremes, rather than the average, influencing the permanent vegetation.

Box and Chamrad (1966) described the soils and plant communities of the area. The vegetation can be generally considered a brush-grass complex developing on (a) clay and clay loam sites, (b) sandy and sandy loam sites, (c) bottomland sites, and (d) semi-permanent lake sites. Our work centered on eight of the major plant communities present at the Welder Refuge.

METHODS

Capture and handling of owls.—Most adult Barn Owls were caught in nest boxes erected throughout the Welder Refuge. Snares set on top of the nest boxes were also used if the resident owl could not be captured inside the box. Nesting owls were returned to the box and detained for several minutes by blocking the entrance hole. This usually was sufficient to calm the bird and inhibit its flushing.

Adult owls were banded with standard aluminum leg bands. Juveniles of sufficient size were also banded. The sex of adults were determined only during the breeding season by cloacal examination. The female Barn Owl develops an incubation patch and, if still in the laying period, also has an enlarged, reddened vent. No reliable method was otherwise found to determine the sex of either adult or immature owls.

Periodic inspection of the nest boxes yielded information on clutch size, nesting success, breeding chronology, and general nesting behavior.

Analysis of owl foods.—Barn Owl foods were determined from an examination of pellets collected on a monthly basis from nest boxes and roost sites. The analysis included the

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frequency (percentage) and the minimum number of prey items in the pellets. Prey species were identified by comparison with museum specimens and by the mammalian skull key developed by Glass (1951). Bones from birds were compared with specimens at the U.S. National Museum.

Prey census.—Small mammal populations were estimated in eight of the major plant communities described in part by Box and Chamrad (1966): Bunchgrass-Annual Forb; Mesquite-Buffalograss; Chaparral-Bristlegrass; Pricklypear-Shortgrass; Paspalum-Aquatic Weed; Live Oak-Chaparral; Annual Forb Disclimax (i.e. disturbed sites); Texas Wintergrass Stands.

Trapping stations at 25-foot intervals formed a grid of eight by six trap lines. Trapping periods consisted of 48 traps checked for three consecutive nights. Sex, age, species, and trapping station were recorded for each captured mammal which was ear-tagged and released at the point of capture. The composition and relative abundance of each population were determined using the marking-and-recapture method (Davis, 1959). Details of the habitat preferences and other ecological aspects of the small mammal populations not directly relevant to the present study are as yet unpublished.

The blackbird population, consisting of Red-winged Blackbirds (*Agelaius phoeniceus*), Boat-tailed Grackles (*Cassidix mexicanus*), Brown-headed Cowbirds (*Molothrus ater*), and Bronzed Cowbirds (*Tangavius aeneus*), was also estimated with the mark-and-release method. Large (5 × 16 × 18 feet) poultry-wire decoy traps containing live decoy birds, food, and water were used to capture blackbirds.

RESULTS

Dynamics and composition of prey populations.—No attempt was made to fully estimate the rodent densities on the Refuge because of non-random sampling bias inherent in the trapping procedure (cf. Krebs, 1966). Instead, the objective was to measure trends important to the availability of prey to Barn Owl predation. Trap success provided an adequate measure for these fluctuations (Table 1).

Rodent populations declined from the summer of 1969 to the following winter and spring of 1970 (Table 1). The lowest level of trapping success was reached in May 1970, and thereafter it increased to 48 per cent success in the fall of 1970. This peak was again followed by a period of decline that stabilized during the winter and spring of 1971.

In 1969, prior to live trapping, small mammals were snap-trapped in the major plant communities to gain a cursory view of the composition of the rodent population. The results showed the highest percentage of rats found during the duration of the study (Table 2). Following the summer of 1969, the rat population declined to less than 1 per cent of the catch.

Mice dominated the catch throughout the study; they varied from 78 to 99 per cent of the overall rodent population. These data indicate that the decline in the rodent population was strongly influenced by a disproportionate reduction in the rat populations that was not accompanied by marked losses of mice.

Table 1

Fluctuations in Rodent Populations as Shown by Trap Success, Welder Wildlife Refuge, 1969–1971

Date	Number		Percentage trap success
	Traps set	Traps entered	
July, 1969	540	154	28.5
January, 1970	288	37	12.8
February, 1970	192	24	12.5
March, 1970	288	57	19.8
April, 1970	288	26	9.0
May, 1970	864	17	1.9
June, 1970	2,160	83	3.8
July, 1970	1,296	84	6.5
August, 1970	2,160	178	8.2
November, 1970	288	139	48.3
January, 1971	2,160	388	19.3
February, 1971	432	83	19.2
March, 1971	1,584	351	22.2
May, 1971	1,584	299	18.9
Total	14,124	1,920	$\bar{x} = 13.6$

Blackbird populations.—Our estimates indicate that about 50,000 resident and migratory blackbirds roosted each winter in sites dominated by roundstem rushes (*Scirpus californicus*). The spring and summer population was estimated at 15,000 birds. The population included Red-winged Blackbirds and lesser proportions of cowbirds and grackles.

An attempt to measure the rate at which Barn Owls preyed on the blackbird population employed the methods of Southern (1955). Birds were trapped, banded, and released, and although 2,413 blackbirds were marked, no bands were subsequently recovered from the owl pellets. Thus it was not possible to directly assess the proportion of blackbirds taken as prey by the owls. However, as noted above, the availability of blackbirds was never limited.

Bias in Barn Owl food habits studies.—Barn Owls as well as many other species of raptors, regurgitate pellets of bone, feathers, and fur. These form in response to the mechanical barrier posed by a small pyloric opening (Reed and Reed, 1928); the materials are ejected in virtually an undigested mass because of the absence of free acidity in the owl stomach. Hence, examination of the pellets generally provides a reliable technique for determination of owl food habits. However, at least two sources of error may occur. First, there is the potential failure to collect one of the two pellets usually formed in each 24-hour period. A small pellet is formed and regurgitated during the night

TABLE 2

PERCENTAGE COMPOSITION OF LIVE- AND SNAP-TRAPPED SMALL MAMMALS, WELDER WILDLIFE REFUGE, 1969–1971

	1969	1970				1971		Total individuals
Species	Summer	Winter	Spring	Summer	Fall	Winter	Spring	
Pigmy Mouse	72.7	89.9	82.5	85.1	94.9	82.6	91.6	1,749
Harvest Mouse	4.1	9.3	4.8	3.8	1.4	14.9	6.4	184
Deer Mouse	1.0	—	6.3	3.4	—	1.5	1.0	15
Hispid Pocket Mouse	—	—	—	0.7	—	—	—	2
House Mouse	—	—	0.8	—	—	0.1	0.3	3
Sub-total	77.8	99.2	94.4	93.0	96.3	99.1	99.3	1,953
Wood Rat	9.6	—	0.8	0.4	—	—	—	30
Rice Rat	8.3	—	1.6	0.4	1.4	—	—	29
Cotton Rat	—	0.8	2.4	2.7	—	0.1	0.3	12
Sub-total	17.9	0.8	4.8	3.5	1.4	0.1	0.3	71
Least Shrew	4.1	—	0.8	3.4	2.2	0.6	0.7	32
Total Individuals	290	118	126	262	139	822	299	2,056

while the birds are still foraging whereas a second and larger pellet is deposited at the diurnal roost (Guerin, *in* Wallace, 1948:25). In our study, the nesting boxes were the sites of diurnal roosting so that we were able to collect and examine only these pellets and not those scattered elsewhere. Secondly, errors may occur when soft-bodied foods (invertebrates, nestling birds, etc.) were eaten (Glading et al., 1943). These foods may be overlooked or not accurately identified. Errington (1932) noted that the foods of very young owlets may be masked because of their temporary proficiency at digesting calcium and thus dissolving many of the bones otherwise diagnostic of their food habits.

Year-to-year variation in Barn Owl foods.—Variations in fundamental predator-prey interactions due to environmental factors often complicate a full understanding of Barn Owl food habits. Physical changes in the habitat (floods, rainfall, etc.) as well as biological changes have much to do with the pressure exerted on prey populations (Craighead and Craighead, 1956: 147). However, we are able to evaluate the Barn Owl diet in southern Texas over a seven year period, 1965–1971, inclusive, using the pellet analysis technique. This method permits us to determine the frequency of each prey's occurrence in the diet, but not directly, determination of either volume or availability.

Mice represented 4,715 or 40 per cent of the 11,625 items identified as owl foods. The species included pigmy mice (*Baiomys taylori*), fulvous

TABLE 3

PERCENTAGE FREQUENCY FOR BARN OWL FOODS ON THE WELDER WILDLIFE REFUGE, 1965–1971

Species	1965	1966	1967	1968	1969	1970	1971
Mammals							
White-footed Mice	1.3	1.8	1.5	3.5	2.0	2.2	0.6
Pigmy Mice	27.5	23.7	8.6	2.6	14.8	30.0	20.0
Fulvous Harvest Mice	12.9	30.9	5.7	2.0	2.5	2.0	5.1
Pocket Mice	31.1	5.2	3.3	0.5	1.8	1.2	—
Mice Sub-total	72.8	61.6	19.1	8.6	21.1	35.4	26.7
Cotton Rat	2.3	14.0	20.8	9.2	12.9	11.1	2.0
Rice Rat	1.1	1.2	2.2	5.7	17.7	7.1	5.4
Wood Rat	—	1.1	12.1	25.9	1.6	0.7	—
Rat Sub-total	3.4	16.3	35.1	40.8	32.2	18.9	7.4
Least Shrew	10.0	11.9	9.8	9.0	24.5	24.0	34.0
Cottontail	1.4	4.4	7.6	4.3	0.1	0.7	0.4
Pocket Gopher	7.1	2.7	8.7	2.4	0.5	0.4	0.8
Unidentified	4.2	—	0.2	0.4	1.7	—	—
Mammal Sub-total	98.9	96.9	81.4	65.5	80.1	79.6	69.3
Birds—Roosting							
Over Water	—	1.0	13.7	17.2	13.4	16.4	17.0
Over Land	1.1	1.6	4.4	17.1	3.2	1.3	3.3
Bird Sub-total	1.1	2.6	18.1	34.3	16.6	17.7	20.3
Insects							
Grasshopper	—	0.3	1.0	—	2.6	2.6	10.4

harvest mice (*Reithrodontomys fulvescens*), white-footed mice (*Peromyscus leucopus*), and hispid pocket mice (*Perognathus hispidus*). Of these, all but white-footed mice were subject to pronounced fluctuations in the owl diet during the seven year period (Table 3). A crash in the mouse populations was particularly noticeable in 1968, following the earlier (October 1967) inundation by Hurricane Beulah.

Gray wood rats (*Neotoma micropus*), rice rats (*Oryzomys palustris*), and cotton rats (*Sigmodon hispidus*) represented 21 per cent (2,430 individuals) of the diet. Gray wood rats were not present in the pellets in 1965, nor were they important in 1966. Their numbers began to increase in 1967 (12 per cent of the diet), and in the year following the hurricane, they were a major food item (26 per cent). The principal habitat of the wood rat, clay soil communities, was not flooded by Hurricane Beulah. Rice rats were particularly evident only in 1969.

Least shrews (*Cryptotis parva*) were a relatively stable food throughout the study. Overall, the pellets contained 1,861 individuals (16 per cent) and varied from 9 to 34 per cent in annual occurrence. Pocket gophers (*Geomys bursarius*) comprised 4 per cent (458 individuals) of the total diet. Cottontail rabbits (*Sylvilagus floridanus*) made up 318 separate items or 3 per cent of the diet. Adult rabbits are likely less vulnerable as Barn Owl prey because of their comparatively large size; all of the rabbit skulls taken from the pellets between 1969 and 1971 were from sub-adults, and it is probable that Barn Owls select only the smaller, and thus younger rabbits as food.

Birds roosting in association with aquatic communities at the Welder Refuge occurred 1,066 times (9 per cent) in the owl pellets. These were primarily members of the Icteridae: 182 grackles, 390 Brown-headed Cowbirds, and 435 Red-winged Blackbirds. The Barn Owls apparently used the abundant icterid populations as a buffer group when the availability of rodents was low (Table 3). With the decline of mice in 1967, icterids in pellets increased from less than 1 per cent in 1966 to 14 per cent in 1967. Further declines in the rodent population in 1970 and 1971, indicated in both the live trapping census and in the pellet analysis, were again compensated by increased use of blackbirds as food.

Other birds contributed 403 individuals (3 per cent) to the owl diet. Non-passerine species included Sparrow Hawks (*Falco sparverius*), Mourning Doves (*Zenaidura macroura*), Inca Doves (*Scardafella inca*), Yellow-billed Cuckoos (*Coccyzus americanus*), and 81 Bobwhite (*Colinus virginianus*). An additional 308 individual passerine birds were identified; these were primarily 111 Dickcissels (*Spiza americana*) and lesser numbers of 28 other species. The occurrence of Bobwhite and other landbirds in the Barn Owl diet was prominent only in 1968.

Grasshoppers of the family Acrididae were infrequently found in the pellets although, in 1971, 10 per cent of the pellets contained grasshopper remains. Other invertebrates were of even rarer occurrence.

Seasonal variation.—The seasonal food-habits picture is least representative in late summer and early fall, when few pellets were collected. At this time, young Barn Owls were awing and expanding their range, and the adult birds used established roosts less than before.

There were pronounced seasonal changes in the percentage of prey species. Predation on birds, predominantly those that roost over water, was characterized by a seasonal variation. In the winter, predation on birds was directed toward adult migratory blackbirds, whereas in late spring and early summer predation on nestlings increased. Likewise, there was an inverse relationship

TABLE 4

SEASONAL VARIATION IN BARN OWL FOODS, WELDER WILDLIFE REFUGE, 1969–1971
Data are percentage frequency.

	1969		1970				1971	
Species	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring
Mammals								
Mice	42.2	62.3	47.8	5.9	2.7	16.6	24.7	27.9
Rats	7.2	2.2	10.6	22.5	30.5	13.7	7.1	8.6
Shrews	28.3	33.3	27.0	16.8	42.0	34.3	34.6	32.5
Birds Roosting Over								
Water	0.4	2.2	6.0	41.7	17.0	6.0	12.8	27.4
Land	0.8	—	—	1.5	3.0	9.8	3.8	2.0
Insects								
Grasshopper	21.1	—	1.9	0.8	—	14.7	15.7	—

in the proportion of rats versus mice. The greatest number of rats in the diet (summer, 1970) corresponded to the lowest number of mice. Conversely, the period when mice were consumed in great numbers (fall, 1969) coincided with a small amount of rat foods. These relationships, shown in Table 4, reflect opportunistic hunting by Barn Owls in various habitats as seasonally characterized by prey availability.

Biomass.—Pellet analysis alone provides only an index to the numbers of food items taken, but if the average weight of individual prey species can also be determined, an index of biomass can be developed. Biomass is ecologically significant because small species (pigmy mouse, etc.), while numerically abundant in the pellets, may provide relatively little bulk to the Barn Owl diet. Hence, using the weights of specimens collected in live traps, the mouse population which numerically contributed 41 per cent of the owl foods actually comprised only 11 per cent of the biomass (Table 5). In contrast, the rat population contributed 50 per cent of the biomass and, numerically, only 21 per cent of the diet.

Using the biomass estimates shown in Table 5, we found that a strong relationship exists between the percentage frequency of each class of food and the percentage biomass in the Barn Owl diet. Mammals comprised 85 per cent of the individual prey and 87 per cent of the biomass and birds, 13 per cent of the individuals and 13 per cent of the biomass.

Barn Owl breeding biology: nest sites.—The Barn Owl primarily nests in tree cavities, holes in river banks, and in crevices in cliffs although nests in towers, barns, and other buildings are common. At the Welder Refuge, Barn

TABLE 5

NUMERICAL AND BIOMASS COMPOSITION OF BARN OWL FOODS AS DETERMINED BY PELLET ANALYSIS, WELDER WILDLIFE REFUGE, 1965–1971

Species	Number individuals	Percentage of individuals	Estimated weight (grams)	Estimated biomass	Percentage of estimated weight
Mammals					
Pigmy mouse	2,252	19.7	9.5	21,394	2.9
White-footed mouse	208	1.8	20.5	4,264	0.6
Fulvous harvest mouse	1,161	10.2	10.5	12,190	1.6
Hispid pocket mouse	1,094	9.6	42.0	45,948	6.1
Cotton rat	1,232	10.8	170.0	209,440	28.0
Rice rat	660	5.8	56.0	36,960	5.0
Wood rat	538	4.7	236.0	126,968	17.0
Least shrew	1,861	16.3	4.5	8,374	1.1
Cottontail	318	2.7	250.0	79,500	10.6
Pocket gopher	458	4.0	229.0	106,256	14.2
Unknown mammals	166	1.4			
Sub-total	9,740	85.4		651,294	87.1
Birds					
Boat-tailed Grackle	182	1.6	120.0	21,840	3.0
Brown-headed Cowbird	390	3.4	40.0	15,600	2.1
Red-winged Blackbird	435	3.8	65.0	28,275	3.8
Dickcissel	111	1.0	150.0	16,650	2.2
Miscellaneous birds[a]	291	2.5	50.0	14,000	1.9
Unknown birds	69	0.6			
Sub-total	1,478	12.9		96,365	12.9
Insects					
Grasshoppers	190	1.7	2.0	380	0.1
All species	11,408	100.0		748,039	100.0

[a] Birds each providing less than 1.0 per cent total biomass include a wide range of passerines and 81 individual Bobwhite (*Colinus virginianus*) and 38 Virginia Rails (*Rallus limicola*), among other non-passerine species.

Owls made extensive use of nesting boxes described elsewhere (Bolen. 1967). Of the 112 Barn Owl nests found in this study, 109 were located in 36 nesting boxes situated on the Welder Refuge; the additional three nests were located in a small shed also on the Refuge grounds.

Nest materials.—Pellets regurgitated in the confines of the nest boxes are subsequently trampled underfoot and in time become a thick, coarse mat of organic debris underlying the eggs. Wallace (1948) also reported that Barn

TABLE 6

MONTHS OF NEST INITIATION FOR BARN OWLS, WELDER WILDLIFE REFUGE, 1965–1971

	Number of nests							All years		
Date	1965	1966	1967	1968	1969	1970	1971[a]	Number	Mean	Per cent
January	3	7	–	–	5	–	–	15	2.1	13.4
February	2	2	10	4	2	4	–	24	3.4	21.4
March	3	3	7	7	7	7	4	38	5.4	33.9
April	1	1	2	–	–	2	1	7	1.0	6.2
May	1	–	–	1	–	1	–	3	0.4	2.7
June	5	7	–	–	2	–	–	14	2.0	12.5
July	5	2	–	–	–	–		7	1.2	6.2
August	1	1	–	–	–	–		2	0.3	1.8
September	1	–	–	–	–	–		1	0.2	0.9
October	–	1	–	–	–	–		1	0.2	0.9
Total	22	24	19	12	16	14	5	112	—	100.0

[a] Field study ended in June, 1971.

Owls crushed many of their pellets when nesting; no other materials are involved in nest construction.

Nesting chronology.—Nests were initiated four times in January, twice in February, and once in March (Table 6). These differences suggest that the onset of nesting may be regulated by the availability of food more so than by such environmental features as photoperiod or temperature.

The length of the Barn Owl nesting season in south Texas was determined from the beginning dates of each year's first and last nests. The last nests, respectively, were started in September of 1965, October of 1966, April of 1967, May of 1968, June of 1969, May of 1970, and April of 1971. The average nesting season lasted 5.3 months during the period 1965–1971. Nesting attempts increased rapidly as each season began and reached their peak in March (Table 6).

Number of broods per season.—At the Welder Refuge female Barn Owls usually produce only one brood per year. However, there was one instance (1965) of a banded Barn Owl raising two broods in the same calendar year. Male Barn Owls feed their mates while the latter incubates, whereas after hatching both parents tend the flightless young and remain with the brood for some time even after flight is attained. This pattern of events does not usually permit time for a second clutch during the nesting season unless the male were to divide his efforts between the re-nesting female and the owlets of the first nest.

Clutch size.—Of 112 separate clutches under study, 91 were considered as

Table 7

Mean Clutch Size for 91 Barn Owl Nests, Welder Wildlife Refuge, 1965–1971

Clutch size	No. clutches	Total eggs
3	19	57
4	12	48
5	29	145
6	24	144
7	4	28
8	3	24
Totals	91	446
Mean clutch size		4.9
Standard deviation		1.3

completed sets. The size of these varied from 3 to 8 eggs per nest with a mean clutch size of 4.9 eggs (Table 7). The additional 21 nests, 11 with 1 egg and 10 with 2 eggs, were excluded from the analysis as incomplete clutches.

Lack (1947) found a tendency for the mean clutch size of owls to increase with latitude and with an increased abundance of rodents. Henny (1969) reported a mean clutch size of 5.3 eggs for Barn Owls nesting in Switzerland (Lat. 46–47 N) and 4.9 eggs for those in Maryland (Lat. 38–43 N). Clutch sizes for the 68 Maryland nests and the 91 nests in this study (Lat. 28 N) thus yielded identical results. It thus appears that clutch sizes in Barn Owls are more closely associated with factors other than with latitude. Lack (1954: 22) also suggested that the number of eggs laid by each species (i.e. average

Table 8

Nest and Egg Success for the Barn Owl, Welder Wildlife Refuge, 1965–1971

	Nests			Eggs			
Year	Attempts No.	Hatched No.	Percentage successful	Layed No.	Hatched No.	Percentage successful	Clutch mean
1965	19	10	52.6	95	45	47.3	5.0
1966	21	12	57.1	106	57	54.2	5.0
1967	16	13	81.2	86	60	69.7	5.4
1968	12	11	91.6	62	38	61.2	5.2
1969	14	11	78.6	63	35	55.5	4.5
1970	6	2	16.6	23	8	34.7	3.8
1971	3	1	33.3	11	2	18.1	3.7
Totals	91	60	65.9	446	245	54.9	4.9

Table 9

Influence of Prey Availability on Barn Owl Breeding Success, Welder Wildlife Refuge, 1965–1971

	Abundance of prey (scale 1–14)[a]	
Reproductive effort	Abundant (3 years) 14–7	Scarce (4 years) 6–1
Number of pairs breeding	14.0	11.5 N.S.
Mean clutch size	5.0	4.4 N.S.
Young fledged/pair	2.5	1.0*

[a] Abundance scale defined as biomass per year divided by total biomass for all years, rounded to nearest whole number.

* $P < 0.05$.

clutch size) has been established by natural selection to correspond with the largest number of young that can be successfully raised. Successful rearing, in turn, is based on the amount of food that is available and provided to the young by the adults. This hypothesis as it relates to the clutch size of the Barn Owls nesting in southern Texas, is discussed in a following section.

Nesting success.—Nesting success of the Barn Owls was 66 per cent for the seven year period of our study. Losses occurred because of abandonment (10 per cent), swarming bees (1 per cent), and disturbances associated with our periodic inspection of the nests during incubation (23 per cent). Of 446 eggs laid in these nests, 245 (55 per cent) later hatched. Year-by-year details are shown in Table 8.

Evaluation of prey biomass and Barn Owl reproduction.—Juvenile Barn Owls remain in the care of their parents for more than two months after fledging. Prey populations during this time must, therefore, be sufficient to provide food for the adults and the young. Food supplies are thus critical to Barn Owl reproductive success for about 18 weeks.

The ultimate measure of breeding success is the average number of young raised per pair (Lack 1966:142). Accordingly, we found that Barn Owls raised 1.5 times as many young per pair in years when prey was abundant than in years when prey populations were more limited (Table 9).

A statistical comparison between the biomass of mammals in the Barn Owl diet and the number of young owls raised per pair indicated that mammals were a dietary requirement for successful reproduction. Declines in the biomass of mammals were significantly correlated ($r = 0.913$) with a corresponding decline in the number of owlets fledged (Fig. 1). The otherwise abundant bird population alone did not sustain successful Barn Owl reproduction.

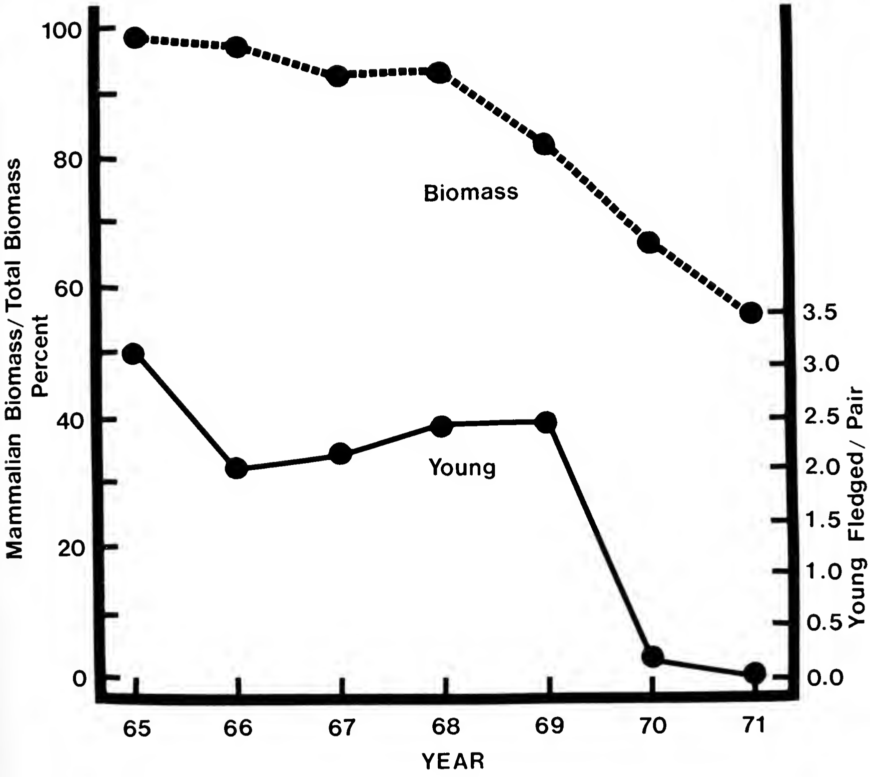

FIG. 1. Reproductive success of the Barn Owl relative to the percentage of mammalian biomass in the owl diet. Statistical correlation of these data was highly significant ($r = 0.91$, $P < 0.01$).

The Welder Refuge supported 12 to 17 breeding pairs of Barn Owls from 1965 through 1970. During this time, the pellet analysis indicated that the mammalian biomass was abundant through the breeding season of 1969. Thereafter, however, rodent numbers and their biomass rapidly declined in the winter of 1969–70. The 12 pairs of Barn Owls attempting to breed at this time experienced a marked reduction in the number of young fledged: fully 92 per cent more young were successfully raised in 1969 than in 1970 (Table 10).

The three owlets actually fledged in 1970 were indeed nourished by a diet of 91 per cent blackbirds. Two owlets of another nest—abandoned at 5 weeks of age—were fed a diet of 72 per cent blackbirds prior to the time of parental abandonment. The significant amount of birds in the diet of these owlets was further evidence that rodents were not available in the spring and summer

TABLE 10

BREEDING HISTORY OF BARN OWLS, WELDER WILDLIFE REFUGE, 1965–1971

Year	Breeding pairs	Mean clutch	Young fledged	Young fledged per pair	Abundance index of prey based on pellet analysis[a]	Biomass ratio of mammals to birds
1965	12	5.0	38	3.2	8	99–1
1966	17	5.0	35	2.0	6	98–2
1967	16	5.4	32	2.1	14	92–8
1968	12	5.2	25	2.4	6	93–7
1969	14	4.5	34	2.4	7	83–17
1970	12	3.8	3	0.2	4	67–32
1971	5	3.7	0	0.0	1	55–45

[a] Abundance index defined as biomass per year divided by total biomass for all years, rounded to nearest whole number. The index reads from 14 (abundant) to 1 (scarce).

months of 1970. The amount of rodent biomass available to the Barn Owl population continued to decline after 1970 (Table 11).

In 1971, 58 per cent fewer pairs nested than in 1970 (five vs. 12 pair). This again indicated that the Barn Owl population had adjusted their reproductive efforts to the lower population level of rodents. The mean clutch size was slightly reduced whereas the number of completed clutches was 50 per cent lower than in 1970. The information from both the trapping and

TABLE 11

SEASONAL VARIATION IN BIOMASS AND NUMBERS OF LIVE-TRAPPED MAMMALS, WELDER WILDLIFE REFUGE, 1969–1971.

	1969	1970				1971		
Species	Summer	Winter	Spring	Summer	Fall	Winter	Spring	Total
Pigmy Mouse	2,004	1,007	988	2,118	1,254	3,059	703	11,133
Harvest Mouse	126	115	63	105	21	1,302	199	1,931
Deer Mouse	61	—	164	184	—	246	61	716
Hispid Pocket Mouse	—	—	—	84	—	—	—	84
House Mouse	—	—	10	—	—	10	10	30
Wood Rat	6,608	—	236	236	—	—	—	7,080
Rice Rat	1,344	—	112	56	112	—	—	1,624
Cotton Rat	—	170	510	1,190	—	170	170	2,210
Least Shrew	54	—	5	40	13	22	9	143
Total Biomass	10,197	1,292	2,088	4,013	1,400	4,809	1,152	24,951
Number Individuals	290	118	126	262	139	822	299	2,056
Biomass/No. Individuals	35.2	10.9	16.6	15.3	10.1	5.8	3.8	12.1

from the pellet analysis showed the lowest biomass of rodents during the winter and spring of 1971 (Tables 10 and 11).

Predator–prey relationships.—The Barn Owl population on the Welder Refuge seemed well adjusted to the carrying capacity of the area, and did not change greatly until the crash of all small mammal populations in 1970. Prior to 1970, some individual prey species occurred at high population levels while others were low. However, the overall prey population of mammals during the Barn Owl breeding seasons appeared sufficient to meet the requirements of the owls. The total owl population maintained a constant rate of food consumption during years preceeding the 1970 rodent crash. A year-to-year increase in Barn Owls was not apparent because of the balance between the predator and prey populations. Thereafter, however, a decline in the total owl population was preceeded by a decline in the populations of rodents.

Thus the increase or decrease in any one small mammal population appeared to have had no immediate effect on Barn Owl nesting density or success, but the productivity of the Barn Owl population was greatly reduced when the overall small mammal population decreased in availability to a point where the Barn Owls depended on birds for 32 per cent or more of their food.

SUMMARY

A study of Barn Owl ecology was begun in 1965 at the Welder Wildlife Refuge, Sinton, Texas, and continued to the summer of 1971. Additional study of the small mammal prey populations took place between 1969 and 1971.

The seasonal fluctuations of the rodent populations were severe, and trap success ranged from 48.3 to 1.9. Blackbird populations varied between an estimated 50,000 birds during the winter to 15,000 in the spring and summer. The availability of blackbirds as owl food was not limited.

Food habits of the Barn Owl were determined from pellet analysis. This material contained 11,408 food items of which mammals comprised 85 per cent, birds 13 per cent, and insects 2 per cent. A strong correlation existed between the percentage frequency and the percentage biomass of these foods.

Barn Owls initiated their nests in the first three months of the year with a peak of activity in March. The nesting season was irregular, lasting from two to ten months. Clutch size was calculated as 4.9 eggs per nest. Nesting success over a 7-year period was 65.9 per cent.

There were 1.5 times as many young raised per pair in years when rodent prey populations were abundant than in years when prey was less available.

Both the quantitative and qualitative nature of Barn Owl foods are important as the otherwise abundant blackbird population did not sustain successful Barn Owl breeding as measured by fledged owlets per pair. The changes occurring in a single small mammal population had no immediate effect on Barn Owl nesting density or success. However, when the overall small mammal population decreased in their availability as prey, the productivity of the Barn Owl population was greatly reduced. This point was reached when birds made up at least 32 per cent of the Barn Owl diet. Mammals, rather than birds, were the key staple on which Barn Owl reproduction depended.

ACKNOWLEDGMENTS

We express our gratitude to Marshall White and C. Robert Watts for use of their unpublished data on the food habits of owls from 1965 to 1968. Steven Labuda assisted with inspections of the nest boxes and Ronald Cherry helped with the rodent census. An early draft of the manuscript benefited from the reviews of Robert Packard, Donald Klebenow, and Billie E. Dahl; the final revision was reviewed by M. Kent Rylander.

LITERATURE CITED

Bolen, E. G. 1967. Nesting boxes for Black-bellied Tree Ducks. J. Wildl. Mgmt., 31: 794–797.

Box, T. W., and A. D. Chamrad. 1966. Plant communities of the Welder Wildlife Refuge. Welder Wildl. Foundation. Contrib. 5. Series B.

Craighead, J. J., and F. C. Craighead. 1956. Hawks, owls and wildlife. Wildlife Management Institute, Washington, D.C.

Davis, D. E. 1959. Manual for analysis of rodent populations. School of Hygiene and Public Health. The John Hopkins Univ., Baltimore, Maryland.

Errington, P. L. 1932. Technique of raptor food habits study. Condor, 34:75–86.

Glading, B., B. F. Tillotson, and D. M. Selleck. 1943. Raptor pellets as indicators of food habits. California Fish and Game, 29:92–121.

Glass, B. P. 1951. A key to the skulls of North American mammals. Oklahoma State Univ., Stillwater.

Henny, C. J. 1969. Geographical variation in mortality rates and production requirements of the Barn Owl (*Tyto alba*). Bird-Banding, 40:277–290.

Krebs, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr., 36:239–273.

Lack, D. 1947. Significance of clutch size. Ibis, 89:302–350.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford.

Reed, C. I., and B. P. Reed. 1928. The mechanism of pellet formation in the Great Horned Owl. Science, 68:259–260.

Southern, H. H. 1955. Nocturnal animals. Sci. Amer., 193:88–98.

Wallace, G. J. 1948. The Barn Owl in Michigan; its distribution, natural history and food habits. Michigan Agr. Exp. Sta., Tech. Bull. No. 208.

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SEED SIZE PREFERENCE IN FINCHES

Mary F. Willson

Seed preferences of several finch species have been explored in the laboratory (Willson, 1971; Willson and Harmeson, in press) using both wild and commercial seeds. Choice among a variety of seed types necessarily involves many variables such as color, flavor, size, nutritional value and so forth. In an effort to eliminate some of these variables, I conducted series of choice experiments using different sizes of the same species of seed (from the same commercial shipment or gathered from the same areas locally). Most of these trials used Cardinals (*Richmondena cardinalis*) but a few observations are available for other species. Hespenheide (1966) earlier made similar observations on a few individuals of two species.

METHODS

Birds were captured locally, kept in fairly large, individual cages in the laboratory (see Willson, 1971), and fed on a diet of mixed seed plus supplements. Equal numbers of different size classes of seed, placed in small dishes, were presented to the birds. Since the position of the dishes relative to the perches in the cage influenced choices, the relative position of each seed size was changed between trials. Four sizes of sunflower seed (*Helianthus annuus*) were tested: long and fat (LF), long and thin (LT), short and fat (SF), and short and thin (ST). Seeds were divided into length categories of 12 mm or less and 13 mm or more, and thickness categories of 4.7 mm or less and 5.2 mm or more; width in all categories was similar. Wild hemp (*Cannabis sativa*), sorted into the two size classes by sieving, was also used. Seed dishes were placed in the cages and left for a short period, depending on how fast the seeds were eaten: the dishes were removed before any one of them was completely empty. Ten trials for each bird were run on both sunflower and hemp.

The significance of differences in seed choice were tested by chi square, $P \leqslant 0.05$.

RESULTS

Five male and five female Cardinals were tested; there was no significant difference between male and female choices. Nine birds showed no preference, individually, and one avoided class LT. Taken as a group, however, the ten manifested a significant preference for class ST and against class LT (Table 1A). Cardinal preferences for certain sizes of sunflower, when shown, were not based solely on thickness or length for either males or females: when all seeds of the same thickness or length classes were pooled, no difference between classes were evident.

In a set of earlier tests, four Cardinal females and two males were given ten trials each. This group preferred thin seeds to fat, regardless of length.

Nine birds were tested on hemp. Two males and the four females had no

TABLE 1

A. SUNFLOWER SEED SIZE PREFERENCES

	ST	SF	LT	LF	*n*
Cardinal*					
1. 5 ♂♂, 5 ♀♀	29	25	20	26	1,391
2. 4 ♀♀, 2 ♂♂	30	18	29	22	1,568
Tree Sparrow* (4)	55	9	4	32	22
Song Sparrow* (4)	57	28	11	4	54
Slate-colored Junco* (4)	71	21	4	4	24
Purple Finch* (3)	39	7	39	14	635
Rose-breasted Grosbeak* (2)	57		43		212

B. HEMP SEED SIZE PREFERENCES

	Large	Small	*n*
Cardinal (5 ♂♂, 4 ♀♀)	52	48	2,675

* Indicates significant differences among the choices by χ^2, $p \leqslant 0.05$. The percentage of all seeds eaten that were of each size class is given, with the total number of seeds eaten in all trials.

preference for either large or small hemp seeds, two other males preferred small and one preferred large seeds. Males as a group, however, showed no significant preferences (Table 1B).

Both male and female Cardinals husked and ate large and small hemp at the same rate, but females husked large hemp faster than males (Table 2). Males husked all sizes of sunflower at the same rate; for females, husking rates were also similar except that seeds of class ST were husked significantly faster than those of LT (t-test, df = 50). Males husked large sunflower seeds, both LF and LT, somewhat faster than did females.

Several other finch species were tested in fewer numbers and with fewer trials (summarized in Table 1). Tree Sparrows (*Spizella arborea*), four birds in four trials each, ate mostly class ST, but class LF was second choice, which seems peculiar, and is probably a result of the small sample size. Song Sparrows (*Melospiza melodia*) and Slate-colored Juncos (*Junco hyemalis*) (four birds of each species, eight trials per bird) preferred class ST, with class SF in second place, so that in general both species preferred short to long seeds. The small number of seeds eaten by all the small birds reflects the difficulty with which they handled even the smallest sunflower seeds. Of two Rose-breasted Grosbeak (*Pheucticus ludovicianus*) males in ten trials between long and short sunflower seeds, one bird preferred long, the other short ones.

TABLE 2

CARDINAL: SEED HUSKING-AND-EATING TIMES, IN SECONDS

	♂♂				♀♀		
	$\bar{x}$	SE	N		$\bar{x}$	SE	N
Sunflower							
ST	28.8	2.3	25		32.2*	3.1	24
LF	29.1	2.8	25	**	39.2	5.0	26
SF	35.0	3.1	25		43.3	4.9	25
LT	33.9	2.4	26	**	39.0	2.3	28
Hemp							
Large	6.9	0.87	15		4.1*	0.32	15
Small	6.2	0.60	15		6.0*	0.98	15

** Indicates a significant difference between males and females.
* Indicates a significant difference between seed sizes.

Three Purple Finches (*Carpodacus purpureus*), probably females, 10 trials, preferred thin seeds to fat ones; length preferences varied among the individuals. Husking times for Purple Finches were similar for all sizes of seeds (Mann-Whitney U, $P \geqq 0.05$; $\bar{x} = 83.1$ sec., $n = 10$ seeds of each size category), but fat seeds were obviously more difficult to handle since over 50 per cent of those picked up slipped out of the bill before cracking.

DISCUSSION

In the main, the results for Cardinals indicate a highly variable choice of sunflower seed sizes. Many individuals showed no particular preference, but the collection as a whole was inclined to favor short-thin seeds, and sometimes long-thin. Correspondingly few differences were found in husking times, except that females could handle class ST more quickly than class LT. Also, no strong preference was seen for size of hemp seed, and there was no difference in husking time of different sizes. This suggests that all the sizes used may have been well within the average capacities of the Cardinals to handle. Any individual preferences could be the result of individual differences in morphology, learning, physiology, etc. J. R. Jehl (pers. comm.) has recently emphasized the importance of such individual variability among the experimental birds.

Song and Tree Sparrows and juncos chose class ST especially, in keeping with their smaller bills (see Willson, 1971 for average dimensions). Purple Finches are intermediate between Cardinals and the smaller birds in bill size (length 10.0 mm, depth 8.3 mm, width 6.9 mm, $n = 12$). They selected seed primarily on the basis of thickness rather than length. Purple Finches have

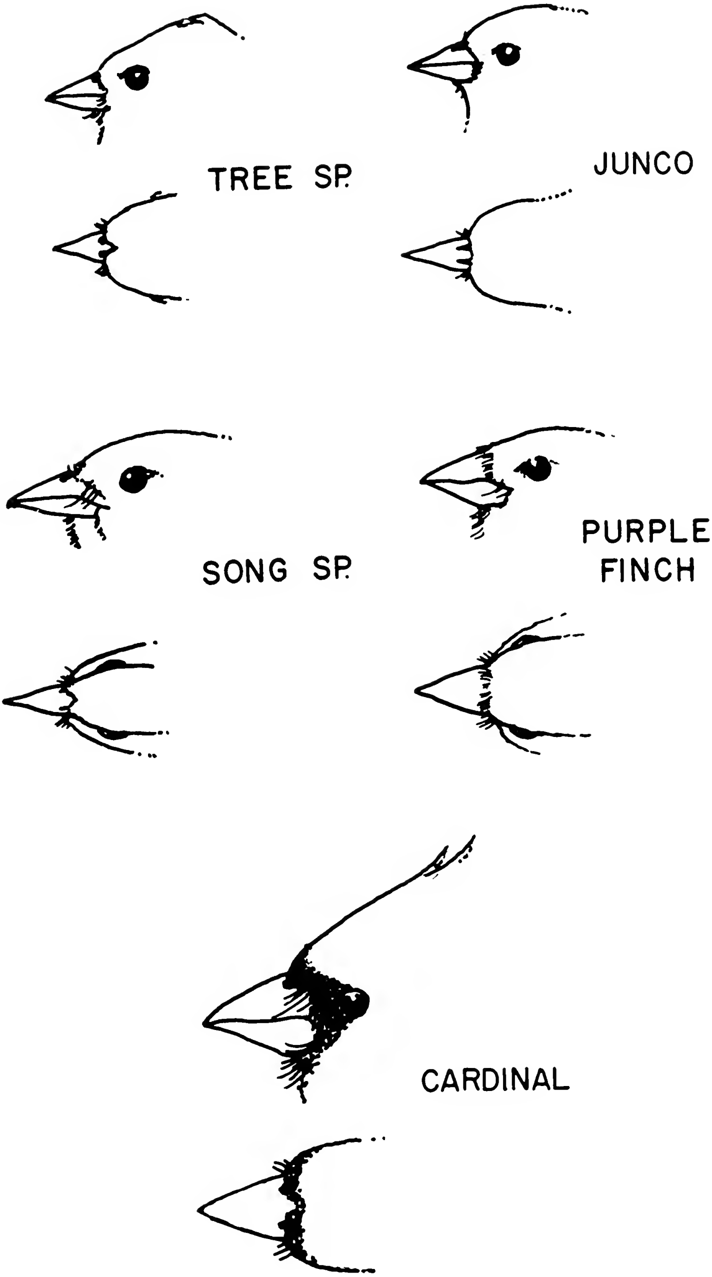

Fig. 1. Top and side views of the bills of the primary experimental species, to scale.

an average bill length equal to that of juncos, intermediate between Tree and Song Sparrows, but much shorter than Cardinals (see Fig. 1). The ability of Cardinals to handle experimental seeds of all sizes with almost equivalent facility is probably a function of their larger bill size. The shorter bills of Purple Finches and the small-billed species may make difficult the handling of thicker seeds by providing a smaller "pocket" for the holding of thick seeds, so that they slip out more readily. The greater bill depth and width of Purple Finches (and Cardinals) may facilitate handling of long seeds by providing a broader base for holding the seeds while they are rotated during cracking and by permitting greater forces to be applied to the seed so that even if long seeds can't be balanced as well as short ones, the greater forces permits them to be cracked before they slip away. Bill characteristics and related morphological characteristics concerned with food handling are discussed in some detail by Bowman (1961, 1963) and Ziswiler (1965).

Measurements of the force delivered by the bill in cracking seeds would be most useful. At present, the only information available came from a Gilson polygraph "physiograph," which transforms physical pressure into electrical impulses to be recorded on a moving graph. The birds were held in such a manner that either the upper or the lower beak pressed against the transducer as the bird "bit." The largest response so generated was used as an index of maximum pressure generated, and converted to force/unit area. These estimates of force refer to the middle of the bill, not the tip where the pressure would be greater. Although in absolute terms the estimates of force applied may not be accurate, they are probably adequate *relative* indices.

Six species were so measured: Cardinal, Purple Finch, Song Sparrow, White-throated Sparrow (*Zontrichia albicollis*), Fox Sparrow (*Passerella iliaca*), and junco. At least two individuals of each, sometimes four, were measured. Invariably the lower jaws exerted a somewhat greater pressure than the upper, but for purposes of Figure 2, all measurements were averaged. All bill dimensions are significantly correlated with the average force applied (Spearman rank correlation, $p \leqslant 0.05$), but Figure 2 suggests that force exerted by the bill is more closely associated with depth or width than with length. Width and depth are more closely correlated with each other than with bill length and it seems reasonable to suppose that depth is more important in determining the force applied than is width (Bowman, 1961). Obviously the presence of palatal bosses or keels or other special structures could confound this tendency.

Average kernel weights of the different sunflower seed sizes varied significantly (Mann-Whitney U, $p \leqslant 0.05$): LF > LT = SF > ST. The mean weights of 10 kernels of each size class were as follows: LF, 0.084 g; LT, 0.065 g; SF, 0.063 g; ST, 0.053 g. Making the reasonable assumption that

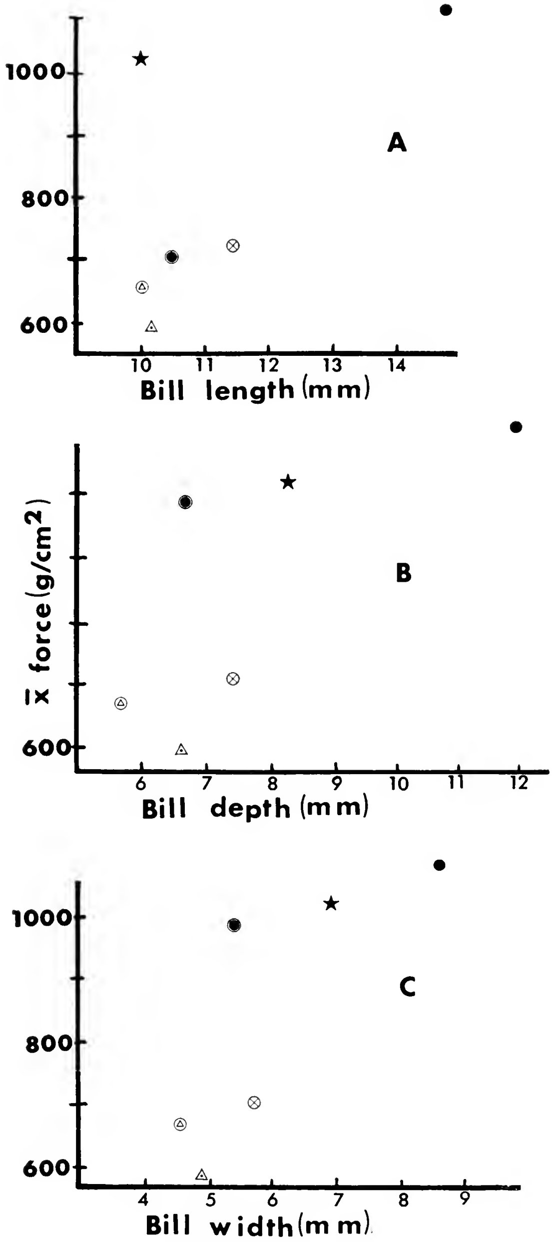

FIG. 2. Association of each bill dimension with the average force exerted by the bill: all correlations are significant, but there is less scatter for width and depth, which are themselves closely correlated. Cardinal, ●; Purple Finch, ★; Fox Sparrow, ⊗; Song Sparrow, ◉; White-throated Sparrow, △; Slate-colored Junco, ◬.

the per-gram caloric content of different-sized kernels is similar, the small-billed species were limited in their food intake by their apparent inability to handle large seeds. In the wild they seldom tackle such large seeds. However, Cardinals, which could handle all sizes offered, certainly did not exercise their ability to maximize caloric intake.

SUMMARY

Cardinals showed few preferences for seed (sunflower or hemp) size and little difference in ability to handle different seed sizes. A slight tendency to prefer short and thin sunflower seeds may be associated with the ability of females to husk this size more rapidly.

Other species tested usually preferred small (short and thin) sunflower seeds corresponding to their small bills and general inability to handle larger seeds. Purple Finches preferred thin sunflower seeds to thick ones, regardless of length. Thick seeds were apparently difficult to hold in relatively short bills, long ones difficult for more slender bills.

Relative forces applied by the main portion of the bill may be correlated more closely with bill depth, and perhaps width, than with length.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galapagos finches. Univ. California Publ. Zool., 58:1–302.

Bowman, R. I. 1963. Evolutionary patterns in Darwin's Finches. Occas. Papers California Acad. Sci., 44:107–140.

Hespenheide, H. A. 1966. The selection of seed size by finches. Wilson Bull., 78:191–197.

Willson, M. F. 1971. Seed selection in some North American finches. Condor, 73: 415–429.

Willson, M. F., and J. C. Harmeson. Seed preferences and digestive efficiency of Cardinals and Song Sparrows. Condor, in press.

Ziswiler, V. 1965. (Toward an understanding of seed-opening and the structure of the horny palate in grain-eating oscines) (in German). J. Ornithol., 106:1–48.

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NESTLING DEVELOPMENT OF BOAT-BILLED HERONS (*COCHLEARIUS COCHLEARIUS*) AT SAN BLAS, NAYARIT, MEXICO

Carlos Juarez L. and Robert W. Dickerman

Although the Boat-billed Heron (*Cochlearius cochlearius*) is a widespread species in the New World tropics from Mexico south to Peru and southern Brazil. and is widely maintained and recently bred as a zoo bird (Bell, 1966), little has been written on its sub-definitive plumages and to date few data are available on its nestling development. A study of the nesting biology of the Boat-billed Heron has recently been published (Dickerman and Juarez, 1971). This report on the growth of the nestlings is the second part of that study.

METHODS

The field work was carried out from August to October 1964, the period of nesting activity in the large colony of mixed heron species, 3 kilometers NNE of San Blas, Nayarit (Dickerman and Gavino, 1969; Dickerman and Juarez, 1971). The field work was largely carried out by Juarez, and provided in part the basis of his professional thesis submitted to the Facultad de Ciencias of the Universidad Nacional Autonoma de Mexico (Juarez, 1967). The junior author provided the outline for the project and translated and amplified the manuscript.

Nesting was well underway when the study was initiated on 19 August. At that time 31 nests contained 65 eggs and one newly-hatched chick (Dickerman and Juarez, 1971). All nests and eggs then present were marked. On subsequent daily visits to the colony new nests and eggs were labeled and as chicks hatched they were color coded with a dab of paint. When the young were large enough (usually about 15 to 19 days), they were banded with leg bands provided by the U.S. Fish and Wildlife Service. Each day all new eggs, and as many young as time permitted, were weighed and measured.

Measurements taken were: weight in grams, and the lengths in millimeters of the 3rd and 8th primaries, the tarsus, the upper mandible from the tear duct and from the anterior edge of the nostril, and the width of the upper mandible at the base (Fig. 1). Measurements for the upper mandible from the tear duct and of the third primary were modeled after the study by McClure et al. (1959). The vane and sheath of the 3rd and 8th primaries were measured because of the doubt as to which feather McClure et al. referred to as the 3rd primary. Later W. F. Scherer, one of the co-authors, informed us (pers. comm.) that in the Japanese study they measured the third large primary from the outside (i.e., 8th primary). Measurements were taken with vernier calipers reading to a tenth of a millimeter. Weights of small young were taken with an Ohaus triple-beam balance. Young of a few days and older were weighed in a plastic bag on an Ohaus spring scale read to the nearest gram.

The subspecies of Boat-billed Heron nesting at San Blas, Nayarit, is *Cochlearius cochlearius zeledoni* (type locality Mazatlan, Sinaloa). As in other New World species of the family Ardeidae, there is only a minor degree of sexual dimorphism in wing and tail measurements (1–3 per cent) within populations of the Boat-billed Heron. However

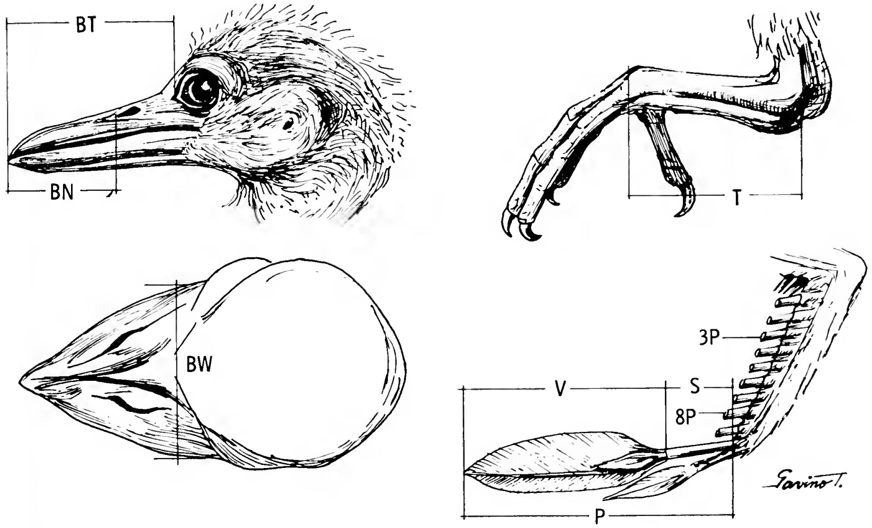

FIG. 1. Method of measuring nestling Boat-billed Herons. BT = culmen from tear duct; BN = culmen from anterior edge of nostril; BW = width of bill; T = tarsus; P = primary (third and eighth); V = vane and S = sheath.

measurements of the tarsus and the exposed culmen vary about 8 per cent between the sexes, with males slightly larger (Table 1). Still, sexual dimorphism in size, even of tarsal and culmen measurements, did not constitute a significant variable in making field measurements of the young. This is supported further by the nearly parallel growth curves for male and female nest mates (Fig. 2).

Carpenter (1971) presented measurements of randomly selected nestlings and older birds raised in the New York Zoological Park and measurements of "mounted specimens" from the collection of the American Museum of Natural History. Because the zoo colony included birds from both Central America and South America, and because the subspecies of the "mounted specimens" measured was not given, comparisons are not made with that study.

TABLE 1

MEASUREMENTS OF ADULT BOAT-BILLED HERONS FROM THE PACIFIC COASTAL LOWLANDS OF MEXICO FROM SINALOA SOUTH TO OAXACA

	Males				Females			
	No.	Range	Mean	SD	No.	Range	Mean	SD
Wing (chord)	16	259–280	269.3	5.4	11	258–273	264.5	4.2
Tail	15	102–110	106.5	2.2	11	100–111	104.6	3.8
Tarsus	16	71–83	79.4	3.0	11	73–78	75.4	1.8
Exposed culmen	16	78–88	83.7	2.8	11	74–82	78.2	2.2

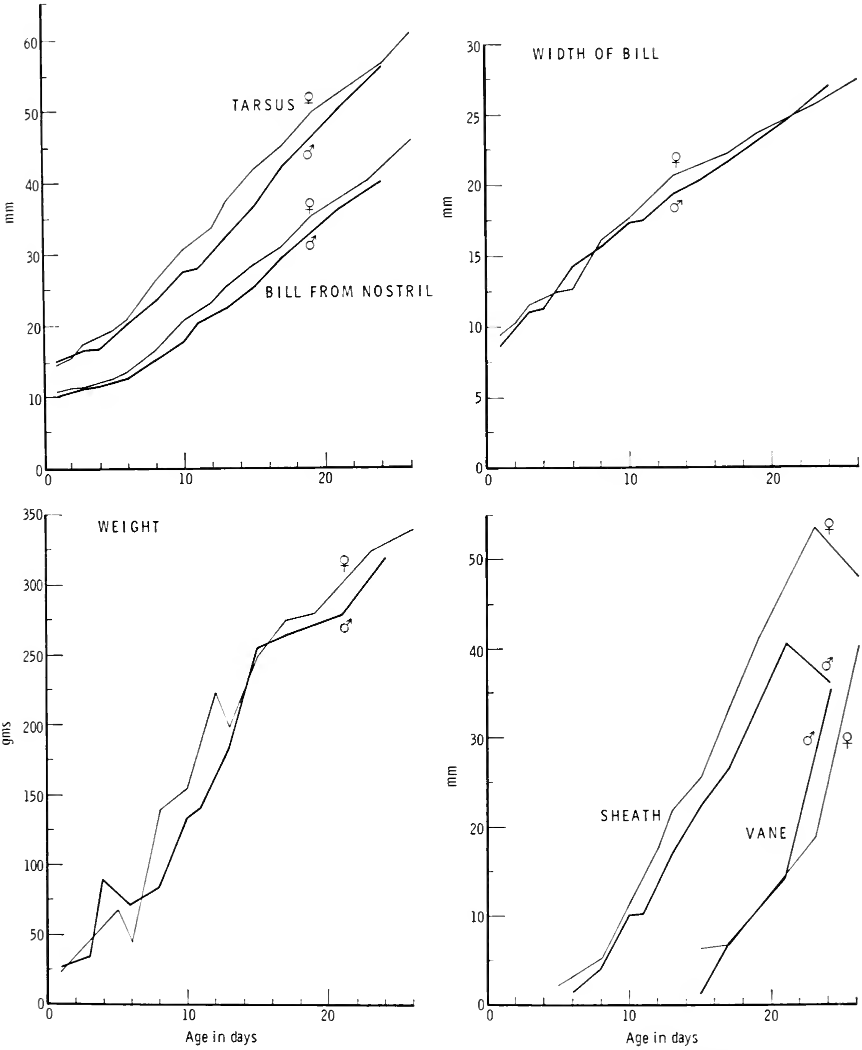

FIG. 2. Growth rates of two Boat-billed Heron nest mates at San Blas, Nayarit. August–September 1964.

NESTLING DEVELOPMENT

Weight.—Gross weights as taken in the field (Fig. 3) were far more variable than were those for young Green Herons (*Butorides virescens*) in the same habitat (Gavino and Dickerman, 1972). Boat-billed young, like those of Black-crowned Night Herons (*Nycticorax nycticorax*), were especially prone

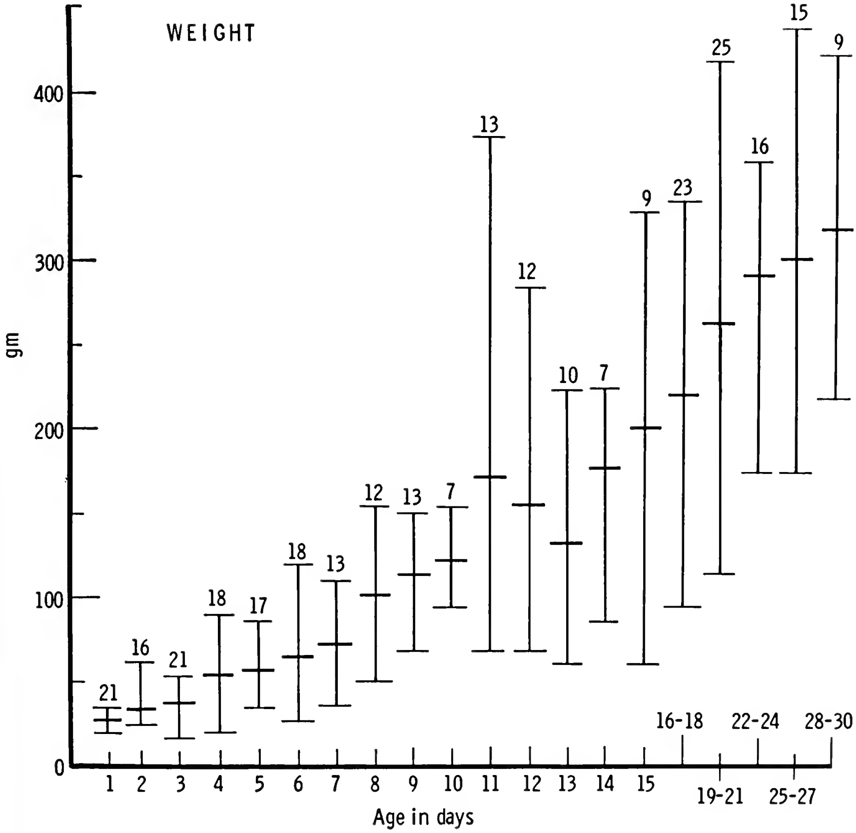

FIG. 3. Daily weights of nestling Boat-billed Herons at San Blas, Nayarit, with range, mean, and number of young in sample.

to regurgitate their food. However it was not always feasible or possible to stimulate regurgitation uniformly. Thus weights for an individual bird might increase (or decrease) by as much as 50 per cent over two consecutive days, due largely to the volume of food in the bird's stomach. Nestlings 20 days of age regurgitated 90–100 g of food, over 30 per cent of the weight of an average nestling at that age.

Secondly, due to the initiation of incubation with the laying of the second egg, hatching was similarly spread out over a several-day period (Dickerman and Juarez, 1971). Thus, for example, young no. 3 in nest 10, weighing 31.8 when two days old, had to compete on the same date with a sibling 7 days old that weighed 110.0 grams! In nest 33 one chick was two days younger than the other. When 10 and 11 days of age respectively, they weighed 110

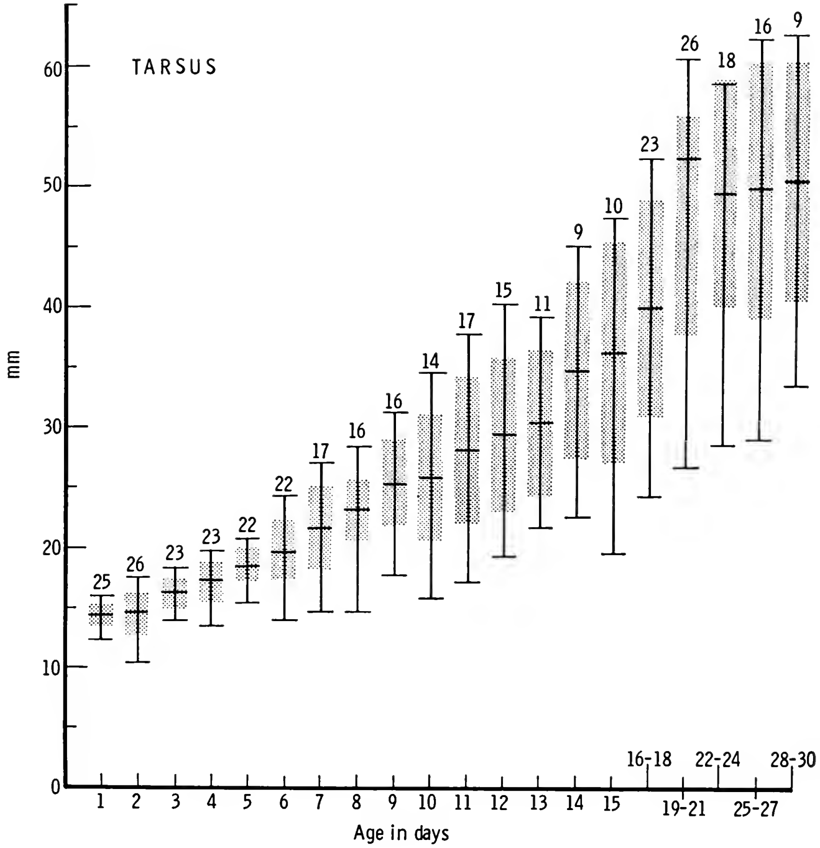

FIG. 4. Daily measurement of length of the tarsus of nestling Boat-billed Herons at San Blas, Nayarit, with range, mean, one standard deviation (gray bar) on either side of the mean, and number of young in sample.

grams and 203 grams; yet at age 25 days they weighed 325 and 260 grams, respectively.

A third cause of low weight gain was poor attendance by the parent bird. In nest 12, three eggs hatched but two young had disappeared by the time the last chick to hatch was 4 days old. Even this single young was apparently poorly fed, for on Figure 3 it represents the minimal weight figure for days 9, 14, 20, and 30! In other nests with two or three young, all developed a pace with at times exceedingly little variation (see Fig. 2 for development of two siblings in nest 6). Because of the great extent of variations in weights, they are of little value as age criteria. Some young 6 days old equaled or

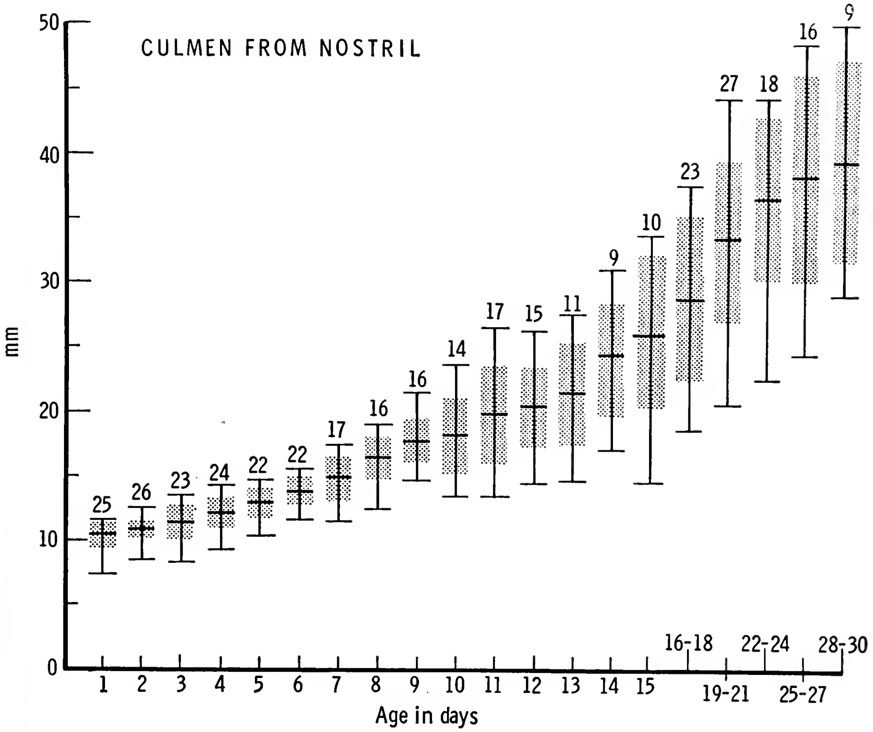

FIG. 5. Daily measurement of length of culmen, from the anterior edge of the nostril, of nestling Boat-billed Herons (key same as Fig. 4).

exceeded in weight other young 19–21 days of age. Conversely, some young 28–30 days of age weighed no more than other young 11 days old.

Gross (1923) in his detailed study of the Black-crowned Night Heron did not mention great disparity in weights among young of the same age. Unfortunately McClure et al. (1959) did not record weights of their large series of aged young Black-crowned Night Herons; and Wolford and Boag (1971) only plotted mean values in their growth curve for weight without giving ranges or sample sizes.

Growth in bony structures.—Growth rates of bony structures that were measured (length of tarsus, length of bill from anterior edge of nostril and width at base and from tear duct) for some individual birds were exceedingly uniform (Fig. 2). However, the measurements of these structures for the population studied showed a moderate to great amount of variation, in part because of the variation in nutrition mentioned above (Figs. 4–6). A running average of the mean values shows that the tarsus grew from 1.0

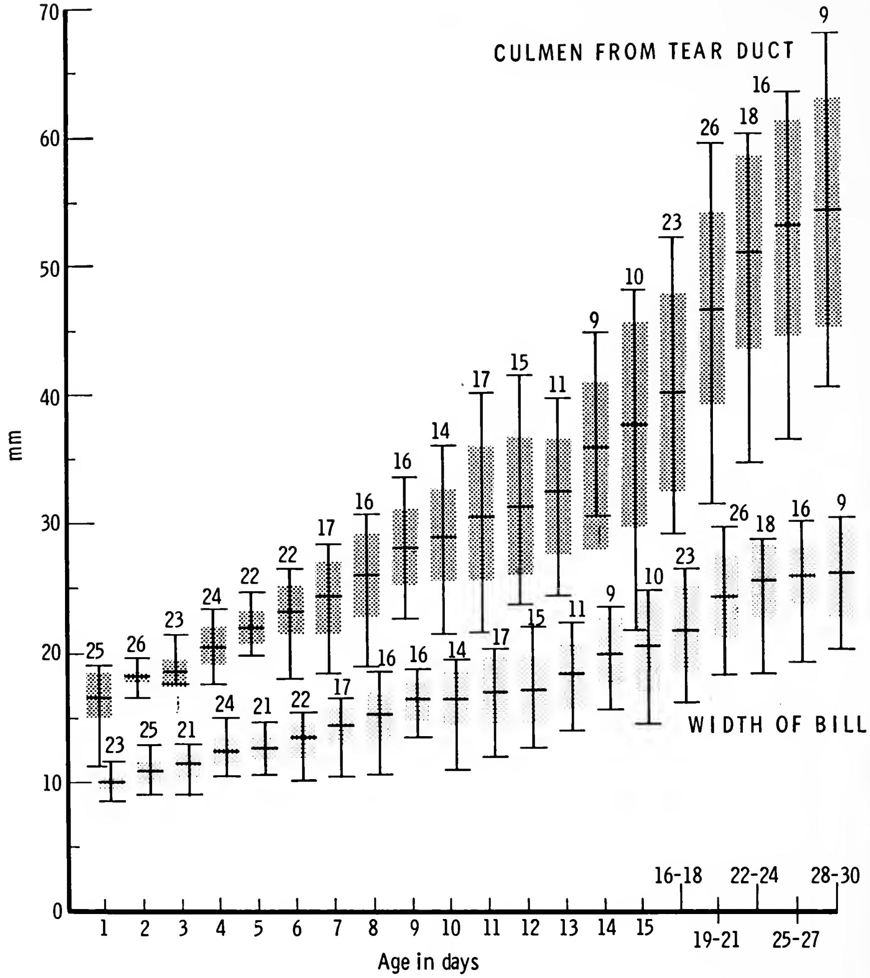

Fig. 6. Daily measurement of length of the culmen from the tear duct and the width of the bill at the base of nestling Boat-billed Herons (key same as Fig. 4).

to 2.9 mm per day to age 18 days. Between day 18 and day 30 the rate stabilized at about 1 mm per day. In contrast, the bill measurements show a slightly increased growth rate after day 14–15, averaging less than 1.5 mm per day before then and over 2.0 per day after that age. The growth rate of the width of the bill was uniform throughout the time studied. Measurements for these structures in the oldest young measured fall considerably below the minimal measurements of comparable measurements for adults (Table 1). This, in the case of the tarsal measurements, is in contrast to the Green Heron,

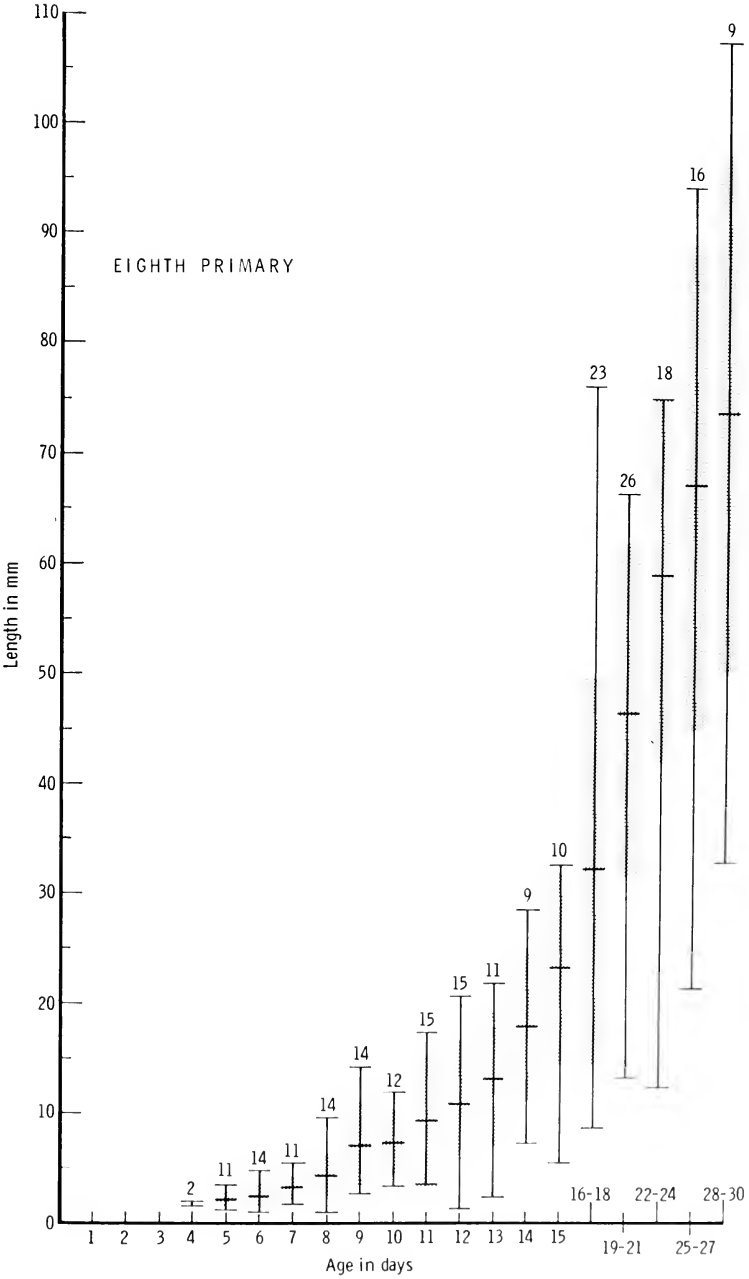

FIG. 7. Daily measurement of length of the eighth primary of nestling Boat-billed Herons (key same as Fig. 4).

where minimal adult measurements were reached by some individuals by day 17 (Gavino and Dickerman, 1972).

The mean growth curve for the culmen (method of measuring unstated) of nestling Black-crowned Night Herons in Alberta is rapid and uniform up to about day 22, but the extent of individual variation was not plotted (Wolford and Boag, 1971). McClure et al. (1959), in studying growth in nestling Black-crowned Night Herons in Japan, also found great variation within an age class in growth rates of bony structures. In their study some young 21–22 days of age had tarsi and mandible measurements similar to other young only 9–10 days old.

Remiges.—The third and the eighth primaries erupted on days 4–6, rarely on day 3. Because growth rates were similar, only data on total length (sheath plus vane) of the eighth primary are presented. When the pinfeathers reached a length of about 20–22 mm on day 13–14, the vane began to emerge. By day 20–21 the sheath was disintegrating (Fig. 2). Variation in nutrition apparently influenced the growth rate greatly as shown by the amount of variation in this measurement exhibited both by the population (Fig. 7) and to a lesser extent by individual birds (Fig. 9). At the oldest age for which we have measurements, 28–30 days, the 8th primary had reached barely half of the adult length (Table 1). Unfortunately, series of fully-grown young in the first basic plumage are not available for a more meaningful comparison. Young Black-crowned Night Herons 30 days of age in Alberta had a mean wing chord of about 250 mm (Wolford and Boag, 1971), nearly within the range of measurements of the wing chord for adults, 285–315 mm (Palmer, 1962).

NATAL AND "JUVENAL PLUMAGE"

The following description of the juvenal plumages is based on a series of 24 young, mostly of known ages, from newly-hatched to 40 days of age, from San Blas, Nayarit or from near Minatitlan, Veracruz.

The natal plumage has been described by Wetmore (1965) and Dickerman, in Dickerman and Juarez (1971). The Boat-billed Heron is unique among the herons in having a tricolored downy plumage with sharply marked bicolored head (Fig. 8). The ventral surface is white, the back (neutral) gray, and the crown dark sooty gray. The color of the crown and back appear to fade rapidly even by the 4–6th day post hatching; however, this may be due to the increase in size of the chick and less dense covering of down. The mandibles are nearly black with lighter tips and white egg tooth. The latter is still present in one young 4–6 days old.

By the fourth day rudimentary pinfeathers are visible in most tracts except in the ventral. The sheaths of the primaries begin to emerge on the 4th day, and by the 8th day all tracts except the caudal anal and powder-down tracts

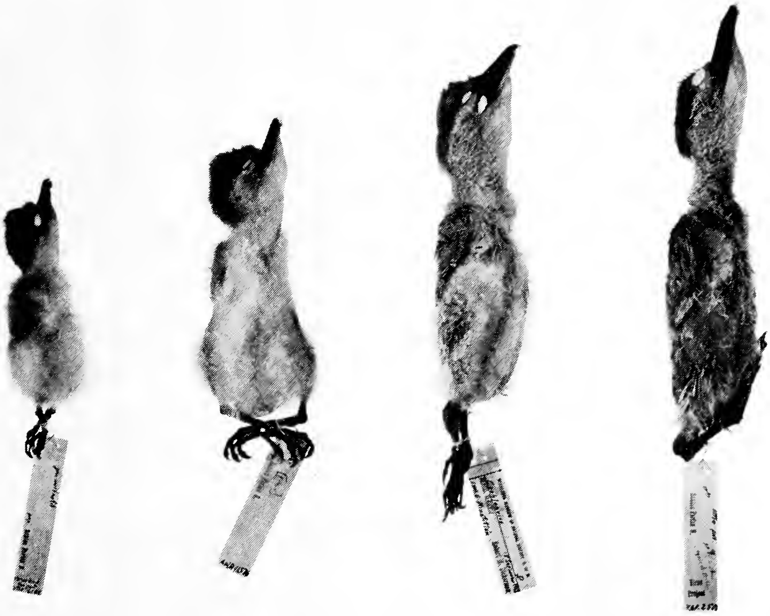

FIG. 8. Early stages of plumage development of Boat-billed Herons (representing ages, from left to right, newly-hatched, 4 days, 8 days, and 13–14 days).

are clearly demarked by developing pinfeathers. The major abdominal, rump, and sternal powder-down patches are barely discernible externally in two young 20–23 days of age, but are well developed in others of the same age.

Feathers of the ventral tracts, the scapular region, primaries and primary coverts begin to break from their sheaths when the young reach two weeks of age and by three weeks some young are well feathered (Fig. 9). As mentioned earlier there is great disparity in growth rates between birds of the same age in different nests. The young on the left in Figure 9 is 23 days old, only 2 days younger than the one next to it, but is similar in appearance to young about two weeks younger. The two young in Figure 10 are 30 days of age (larger; oldest young of nest 30) and 32–35 days of age (smaller: fourth young in nest 12). The tail feathers begin to show color at about 25 days. The pecten of the middle toe nail is visible in one of the young 20–23 days of age and in all young 25 days or older when development was not obviously retarded.

The following description of the juvenal plumage is based on one young 52 days of age (right-hand bird, Fig. 9) and two birds 40 days of age. The

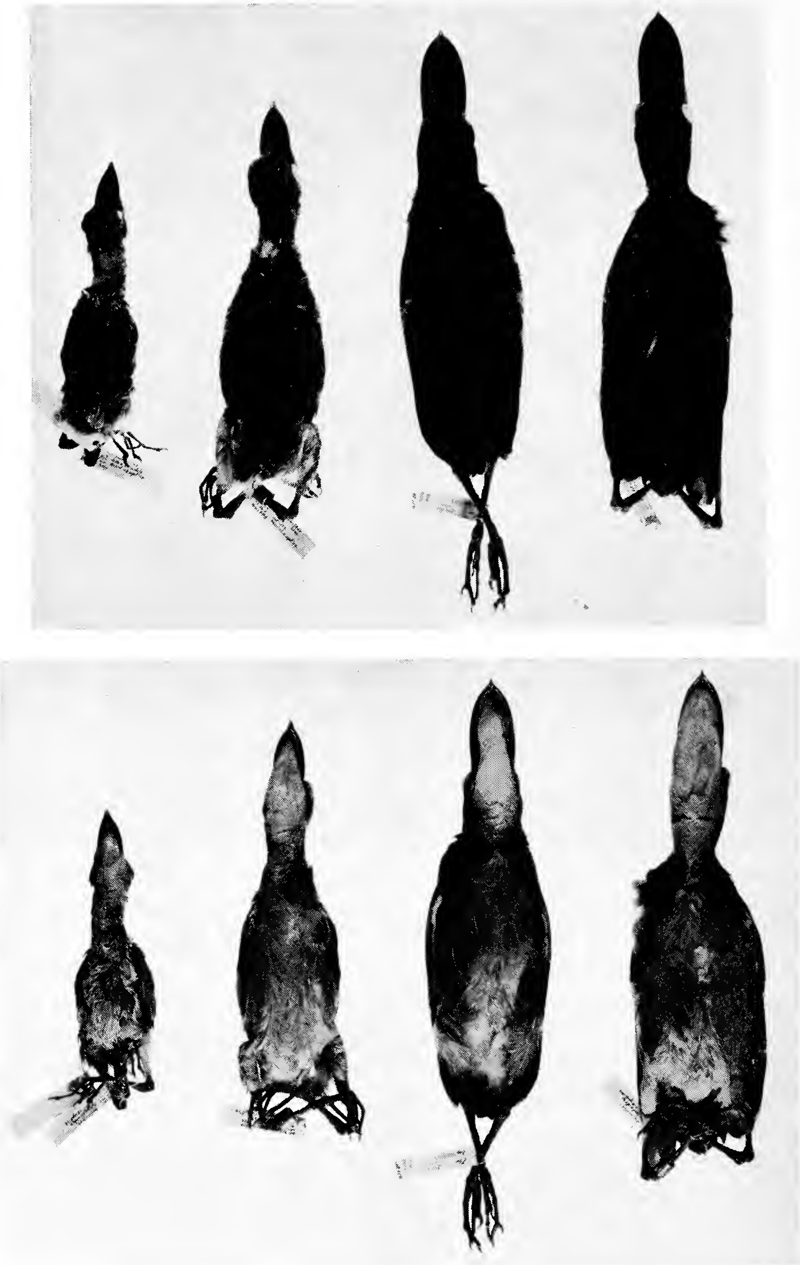

Fig. 9. Dorsal and ventral views of plumage development of Boat-billed Herons (representing ages from left to right, 23 days, 25 days, 30 days, and 32 days).

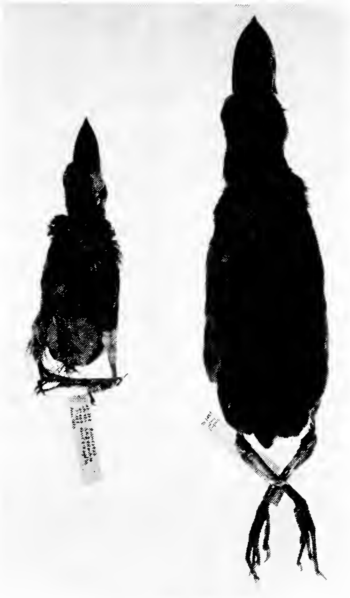

Fig. 10. Young Boat-billed Herons 30 days of age (larger) and 32–35 days of age (smaller) demonstrating disparity in growth rates occasionally observed among nestlings.

forehead, malar area, auriculars and sides are rich medium brown, darker in the subloral area. The crown is black, with the feathers of the nape elongated to 45 mm. The interscapular area and the lesser and middle wing coverts are rich brown, with some individuals showing a vinaceous cast. Remiges, rectrices, and rump area medium gray. The greater wing coverts are medium gray, edged with the brown of the interscapular area. The outermost primary and the feathers of the alula are paler than the other remiges and are tipped and edged with buff. All remiges and rectrices are still sheathed at 52 days.

Ventrally the overall appearance is pale grayish brown to buffy brown, paling to whitish on the belly. The breast is nearly uniform but feathers may be lightly mottled or, especially medially, tipped with dusky gray. The flank feathers are weakly streaked. They have a medial white area, varying in width between individuals from 1.5 to 3.5 mm, that is bordered by medium gray streaks; and the feathers are edged with buffy brown.

SUMMARY

Nestling development of the Boat-billed Heron was studied at San Blas, Nayarit, Mexico August–October 1964. Daily measurements were made on marked young, including weight and length of culmen from nostril and from the tear duct, width of the bill at base, tarsus and primaries 3 and 8. Sexual dimorphism is minimal in all measurements, except length

of the tarsus and culmen where it is about 8 per cent in adults, but did not constitute a significant variable in the measurements of nestlings.

Weights of nestlings were exceedingly variable due in part to prolonged hatching period within clutch and to irregular regurgitation of food. Minimal adult measurements were not obtained by any structure studied by 28–30 days of age at which time the young could no longer be caught. Maximal tarsus measurement, for example, was 63 mm compared to minimal length of 71 for 27 adults from the same region. Variations within an age group were so great that measurements of even a combination of structure would be of little use in determining age of nestlings.

The development of the final basic plumage is described.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bell, J. 1966. Boat-bills in our zoo's "Treetops." Animal Kingdom, 69:251–252.

Carpenter, J. A. 1971. Notes on the biology and behavior of captive Boat-billed Herons, *Cochlearius cochlearius*. Southwestern Naturalist, 16:31–41.

Dickerman, R. W., and G. Gavino T. 1969. Studies of a nesting colony of the Green Heron (*Butorides virescens*) at San Blas, Nayarit, Mexico. Living Bird, 8:95–111.

Dickerman, R. W., and C. Juarez L. 1971. Nesting studies of the Boat-billed Heron (*Cochlearius cochlearius*) at San Blas, Nayarit, Mexico. Ardea, 59:1–16.

Gavino T., G., and R. W. Dickerman. 1972. Nestling development of Green Herons at San Blas, Nayarit, Mexico. Condor, 74:72–79.

Gross, A. O. 1923. The Black-crowned Night Heron (*Nycticorax nycticorax naevius*) of Sandy Neck. Auk, 40:191–214.

Juarez L., C. 1967. Observaciones acerca de la biologia, nidificacion y crianzo de la garza pico de cochuron mexicana, *Cochlearius cochlearius*, en San Blas Nayarit. Thesis Professional, Univ. Nacional Autonoma de Mexico.

McClure, H. E., M. Yoshii, Y. Okada, and W. F. Scherer. 1959. A method for determining age of nestling herons in Japan. Condor, 61:30–37.

Palmer, R. S. 1962. Handbook of North American Birds. Yale Univ. Press, New Haven. Vol. 1, p. 474.

Wetmore, A. 1965. The birds of the Republic of Panama. I. Tinamidae (Tinamous) to the Rhynchopidae (Skimmers). Smithsonian Misc. Coll., 150.

Wolford, J. W., and D. A. Boag. 1971. Distribution and biology of Black-crowned Night Herons in Alberta. Canadian Field-Naturalist, 85:13–19.

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EGGSHELL THICKNESS AND ITS VARIATION IN THE CEDAR WAXWING

Stephen I. Rothstein

Much recent literature has dealt with the interrelations of certain chlorinated hydrocarbons to reproductive failure and declining populations in various birds. Ratcliffe (1970) has summarized these interrelations which are mediated largely through changes in eggshell thickness. Despite the importance of eggshell thickness, general analyses of the factors other than certain pesticides that might affect it are scarce, save in the chicken (*Gallus gallus*) where economic considerations have prompted many studies (see Romanoff and Romanoff, 1949). Furthermore, data on eggshell thickness in songbirds are almost totally lacking, even though the latter constitute the majority of living bird species. This study analyzes the various factors which might reasonably be thought to be related to the eggshell thickness of a bird in nature. I have utilized eggs of the Cedar Waxwing (*Bombycilla cedrorum*), an abundant Nearctic passerine.

METHODS

Eggs were collected in 1968 and 1969 in Cheboygan and Emmet Counties, Michigan and one randomly chosen egg was measured from each nest. Shell thickness, with the membranes, was measured one-third of the way down from the blunt end of each egg, using a specially adapted Starrett No. 1010 M micrometer. Although this micrometer is graduated in units of 0.01 mm, readings were estimated to 0.001 mm. Blus (1970) and Kreitzer (1971) apparently also followed this procedure. Accordingly, all statistical tests were performed with readings in 0.001 mm. However, all of these statistical tests have also been performed with the data rounded off to 0.01 mm and the results are only slightly changed from those reported in this paper. (Comparison 2 of Table 1 provides the only statistical test which is no longer significant when the readings are rounded off to 0.01 mm.)

RESULTS AND DISCUSSION

Natural variation.—The data were divided on the basis of factors which might relate to shell thickness. Mean eggshell thickness was 4.2 per cent greater in eggs from three-egg clutches than in eggs from four- and five-egg clutches, with the difference significant at $P < 0.05$ (comparison 1, Table 1). A possible inference of this result is that the availability of material for eggshell formation may act as a limiting factor for clutch size. Although Lack (1968) made a comprehensive review of the relations of ecological factors to egg characteristics, the possible limiting role of material for shell formation was not considered. Another, although not necessarily mutually exclusive, explanation of shell thickness dependent on clutch size rests on work with

TABLE 1

FACTORS RELATED TO EGGSHELL THICKNESS IN THE CEDAR WAXWING

	Entire sample	All eggs with no development	Clutches of less than four eggs		Four and five egg clutches	
			Eggs with no development	Eggs with development	Eggs with no development	Eggs with development
Recent eggs (1968–69)						
Median (mm)	0.091	0.092**	0.093*†	0.087†	0.091*‡	0.086‡
(N)	(68)	(52)	(15)	(2)	(35)	(14)
Mean (mm)	0.091	0.092	0.095	0.087	0.091	0.087
Old eggs (1871–1912)						
Median (mm)	0.095**					
(N)	(22)					
Mean (mm)	0.095					

All the vital data could not be acquired for a few eggs. This explains the small changes in certain sample sizes when tabulated under different headings or in Table 1 versus Table 2.

* 1. Probability for difference between these two samples is <0.05 (two-tailed Mann-Whitney U Test; Siegel, 1956).

† 2. $P < 0.01$ (Randomization test for two independent samples; Siegel, 1956).

‡ 3. $P < 0.02$ (Mann-Whitney U Test).

** 4. $0.05 < P < 0.06$ (Mann-Whitney U Test).

the chicken. Within a set of eggs, shell thickness generally decreases with each successive egg, except for the last one (and the penultimate one as well in sets of six or more) (Romanoff and Romanoff, 1949; Wilhelm, 1940; Berg, 1945). The first and last eggs usually have similar shell thicknesses. A similar trend has been found in the Japanese Quail (*Coturnix coturnix*) (Bitman et al., 1969). If this type of trend occurs in songbirds, it could explain the observed relation between clutch size and shell thickness reported here for the Cedar Waxwing. Sixty-seven per cent of the eggs in clutches of three would have thick shells, but the comparable percentages for clutches of four and five would be only 50 and 40 respectively. The occurrence of this trend in songbirds would necessitate the use of nonparametric statistics, the type applied in this paper, because the frequency distributions for shell thicknesses of eggs from different-sized clutches would have different shapes.

Eggs with embryos had significantly thinner shells than ones with no development, as is shown by two independent tests (comparisons 2 and 3, Table 1). To determine whether shell thinning occurs throughout much or all of incubation, the ideal measure of incubation stage would be the number of days each egg was incubated before it was collected. However, this is difficult to determine, especially for species like the Cedar Waxwing which

TABLE 2

EGGSHELL THICKNESS AND DEGREE OF DEVELOPMENT OF EMBRYO (AS INDICATED BY ITS EYE DIAMETER) IN CLUTCHES OF FOUR AND FIVE EGGS

Diameter of embryo's eye, mm	Eggshell thickness, mm
1.6	0.087
1.9	0.090
2.2	0.089
3.0	0.084
3.0	0.103
3.6	0.091
4.1	0.090
4.2	0.081
4.3	0.095
5.0	0.082
5.1	0.073
5.4	0.080
5.5	0.079

Probability for above association is <0.025 (Kendall rank correlation, $\tau = -0.416$; Siegel, 1956).

normally begin incubating before the clutch is completed (Putnam, 1949; pers. obs.). Thus, it was decided that some easily measured attribute of the embryo, such as eye diameter, provides the most reliable measure of the amount of incubation and development. There is a significant association ($P < 0.025$) between the degree of embryonic development (as indicated by eye diameter) and shell thickness (Table 2), suggesting that thinning occurs throughout much or all of incubation. The thinning was probably due to withdrawal of calcium from the shell by the embryos. About 80 per cent of the calcium in the hatching chick of the domestic fowl is derived from the shell (Simkiss, 1961) and this withdrawn calcium amounts to about 5 per cent of the total shell calcium (Simkiss, 1967).

Seven eggs from the four- and five-egg clutches with no development (Table 1) had undergone incubation as indicated by their contents which consisted of slightly to strongly malodorous yolk and albumen. The average shell thickness of these eggs was close to that for the remaining 28 eggs in the subsample (0.092 mm and 0.091 mm, respectively), thus substantiating the interpretation that the shell thinning during incubation is due to the metabolism of the embryo and not to some ageing or deterioration process in the egg. Previous studies of birds in nature have not shown a definite relationship between shell thickness and embryonic development, although such a relationship is suggested by data for the Brown Pelican (*Pelecanus occidentalis*) (Anderson and Hickey, 1970). However, Vanderstoep and Richards (1970) have shown that shell thickness in the chicken decreases significantly between the tenth and eighteenth days of incubation.

Additional analyses done on the 1968–69 sample of waxwing eggs failed to detect correlations between shell thickness and the following: egg length, width, or volume and date or year of laying. Although longer eggs tended to have thinner shells, the association was not statistically significant ($P > 0.05$) with the Kendall rank correlation coefficient; Siegel, 1956).

It is apparent from the above analyses that the determinants of eggshell thickness in nature may be quite complex, with little studied ecological and physiological factors playing significant roles. Indeed, under laboratory conditions many factors have been found to affect shell thickness in the domestic fowl (Romanoff and Romanoff, 1949). The possibility exists that some factors could bias results in studies intended to deal primarily with the relation of shell thickness to certain pesticides. A problem of this type occurred in this study. Waxwing eggs from orchards on farms had a significantly greater incidence of sterility and/or embryonic death than eggs layed away from farms (Rothstein, in press). Direct proof was lacking, but the difference seemed to be most likely due to pesticides, and statistical analysis demonstrated that the farm eggs had significantly thinner shells. Further analysis, however, showed the farm sample to have a disproportionate number of incubated eggs (because collecting was done later on the farms than in the other study areas). Eggs with no development from each habitat type were then found to have almost identical shell thicknesses.

Possible "unnatural" variation.—Several nonpasserines and two large passerines have undergone statistically significant shell thinning since the use of DDT began (Ratcliffe, 1970), but this aspect has not been investigated in what are perhaps the most ecologically important of all birds, moderate or small-sized passerines. To determine whether the shells of Cedar Waxwing eggs have also become thinner, a series of pre-1920 eggs was measured. These eggs are in the U.S. National Museum and were collected in various parts of the waxwing's range. The data (comparison 4, Table 1) strongly suggest that current waxwing eggs have thinner shells than older ones. The degree of thinning (3.2 per cent) is probably not severe enough to have a significant effect on the population size of the Cedar Waxwing. But, incomplete records made it impossible to determine the incubation status of all of the old eggs, and some heavily incubated eggs may be included in the sample. Thus, the shell thicknesses of the old eggs may be biased by being too low whereas in the sample for the recent eggs, all the eggs with development have been excluded (comparison 4, Table 1). Therefore, the degree of thinning may be greater than is indicated by the comparison in Table 1. Furthermore, even a slight degree of thinning may have a deleterious effect on individual reproductive output, since the shell thickness previously extant was presumably better adapted than the possibly unnaturally thinned one reported here.

Based on the available evidence it would be merely speculative to suggest a causal relationship between chlorinated hydrocarbons and the probable shell thinning in waxwing eggs reported here. However, given the widespread nature of this type of causal relationship there is a possibility of its existence in the waxwing and in moderate or small-sized passerines in general and additional studies of eggshell thickness in such birds would be highly desirable.

SUMMARY

Eggshell thickness in the Cedar Waxwing was analyzed in relation to various factors and the existence of important natural variation was demonstrated. Eggs from small clutches have thicker shells than eggs from large clutches. Embryonic development results in a thinning of the shell. Five other factors failed to significantly correlate with shell thickness. Recent waxwing eggs appear to have slightly (3.2 per cent) thinner shells than eggs collected before 1920. The possible significance of these findings to clutch size determination and other factors as well as to pesticide studies is discussed.

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LITERATURE CITED

Anderson, D. W., and J. J. Hickey. 1970. Oological data on egg and breeding characteristics of Brown Pelicans. Wilson Bull., 82:14–28.

Berg, L. R. 1945. The relationship of clutch position and time interval between eggs to eggshell quality. Poultry Sci., 24:555–563.

Bitman, J., H. C. Cecil, S. J. Harris, and G. F. Fries. 1969. DDT induces a decrease in eggshell calcium. Nature, 224:44–46.

Blus, L. J. 1970. Measurements of Brown Pelican eggshells from Florida and South Carolina. BioScience, 20:867–869.

Kreitzer, J. F. 1971. Eggshell thickness in Mourning Dove populations. J. Wildl. Mgmt., 35:563–564.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. Ltd., London.

Putnam, L. S. 1949. The life history of the Cedar Waxwing. Wilson Bull., 61:141–182.

Ratcliffe, D. A. 1970. Changes attributable to pesticides in egg breakage frequency and eggshell thickness in some British birds. J. Appl. Ecol., 7:67–115.

Romanoff, A. L., and A. J. Romanoff. 1949. The avian egg. John Wiley and Sons, New York.

Rothstein, S. I. Variation in the incidence of hatching failure in the Cedar Waxwing and other species. Condor, in press.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

SIMKISS, K. 1961. Calcium metabolism and avian reproduction. Biol. Rev., 36:321–367.

SIMKISS, K. 1967. Calcium in reproductive physiology. Reinhold, New York.

VANDERSTOEP, J., AND J. F. RICHARDS. 1970. The changes in eggshell strength during incubation. Poultry Sci., 49:276–285.

WILHELM, L. A. 1940. Some factors affecting variations in eggshell quality. Poultry Sci., 19:246–253.

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NEW LIFE MEMBER

Mr. Henry Bell, 3rd has recently become a Life Member of The Wilson Ornithological Society. Mr. Bell lives in Chevy Chase, Maryland and is a geologist with the U.S. Geological Survey. He holds a degree from the University of South Carolina and has also attended the University of Pennsylvania, Pennsylvania State University, and the University of North Carolina. His interests in birds are of long standing. He is a Fellow of the Geological Society of America and a member of the AOU and the Maryland Ornithological Society. Along with bird study he counts woodworking and boating as his hobbies. Mr. Bell is married with no children.

VERNAL TESTES DEVELOPMENT IN TROPICAL-WINTERING DICKCISSELS

JOHN L. ZIMMERMAN AND JAMES V. MORRISON

SINCE 12-hour daylengths experienced by tropical-wintering species are stimulatory to the hypothalamic—hypophyseal—gonad axis of temperate-wintering species (Burger, 1953; Dolnik, 1963; Farner, 1961; Wolfson, 1960), the question of why these migrants do not complete gametogenesis during the several months' stay on their contranuptial area has been of interest (Marshall, 1960; Wolfson, 1959*a*). It can be assumed that different tropical migrants could adapt the regulation of their annual cycles in a number of different ways or by a combination of different mechanisms in order to be successful in their specific environments.

One possibility was suggested by Wolfson (1959*b*) who hypothesized that these migrants might respond to 12-hour daylengths at a slower rate than temperate species so that gametogenesis cannot be completed until they are exposed to the longer daylengths of their temperate breeding grounds. This hypothesis is indirectly supported from work done on temperate species which has shown that the rate of testes growth is proportional to the length of the photoperiod (Lofts, Follett, and Murton, 1970) and hence birds wintering at tropical photoperiods might be expected to have even a slower rate of testes development. Another possibility could be that the refractory period of tropical-wintering species is longer than that of temperate species and thus they cannot begin to respond to photostimulation until just prior to the northward journey (Marshall, 1959). Both these hypotheses receive indirect support from the observation that gonad growth begins for tropical migrants on the winter range, but it does not appear to progress very far (Rowan and Batrawi, 1939; Marshall and Williams, 1959).

Lofts and Murton (1968:350) stated that "birds that are photosensitive to medium northern daylengths have had to evolve adaptations if they migrate to near or across the equator, in particular they require to have long refractory periods and a slow response to stimulatory daylengths once they are out of the refractory phase." As far as we know, however, this generalization based on the hypotheses of Wolfson and Marshall has not been supported by any direct evidence.

The Dickcissel (*Spiza americana*) breeds in temperate North America and winters in the Neotropics north of Amazonia. Although we have not shown that there is a relationship between this species' natural photoperiod experience and the regulation of its annual gonadal cycle, Morrison (1971) has demonstrated in post-breeding adults that after approximately 8 weeks exposure to a 12-hour photoperiod (around mid-November), precocial gonadal development can be stimulated by the 15-hour photoperiod that they would experience on the breeding grounds. These results show that a 12L-12D photoperiod regime will terminate photorefractoriness in the Dickcissel and that the length of its refractory period is similar to that of many Temperate Zone species (Farner, 1959; Shank, 1959; Wolfson, 1958). It seems, therefore, that a prolonged refractory period is not the mechanism this species uses to prevent the development of the reproductive state while on the wintering grounds.

The following data on the rate of testes growth and the magnitude of the response in wild birds living under their naturally-occurring photoperiod are presented to test the slower rate of response hypothesis.

METHODS

Male Dickcissels were collected from wild populations on the wintering grounds in Panama and the Canal Zone (9° N) from 19 January through 2 May 1961, and the length of each testis was measured in millimeters. The daylengths during this period of collection ranged from 11 hours, 40 minutes to 12 hours, 28 minutes. Similar data were obtained on the breeding grounds in Illinois (40° N) from birds collected during May, June, July, and August in 1961 and 1962.

In order to convert testis length into weight, Morrison in the course of his work on the refractory period measured the length of the testis and then after treatment according to the methods used by Wilson (1968), obtained their weight in milligrams. He calculated the following relationship:

$$\log \text{testis wt. (mg)} = -0.5845 + 3.0696 \log \text{testis length (mm)}.$$

In the quantification of the gonad growth rate from data collected by photostimulation of receptive birds under laboratory conditions, the time axis is calibrated according to days since the beginning of exposure to the stimulatory photoperiod. This, of course, is not possible with a free-living population, since day zero is not known. In order to calculate k, the logarithmic testicular growth-rate constant (= slope of the time × log weight regression), the logarithm of the combined weight of both testes was plotted against the date of collection. Then the linear portion of the curve was identified by inspection, and 28 February was selected as day 1. A linear regression of the logarithm of the combined testes weight as a function of time was computed through 2 May as day 64. The natural photoperiod during this period ranged from 11 hours, 56 minutes on day 1 to 12 hours, 28 minutes on day 64, averaging 12 hours, 13 minutes.

RESULTS

Figure 1 is a semi-log plot of the combined testes weights according to the date of collection. Even though Dickcissels will respond under experimental exposure to 15 hours of light in mid-November, under the natural photoperiod conditions of their wintering grounds the testes are still small in January.

This figure also includes the linear regression calculated for the period from 28 February through 2 May, which is expressed by the following equation:

$$\log \text{wt.} = 0.2757 + 0.03114\, t,$$

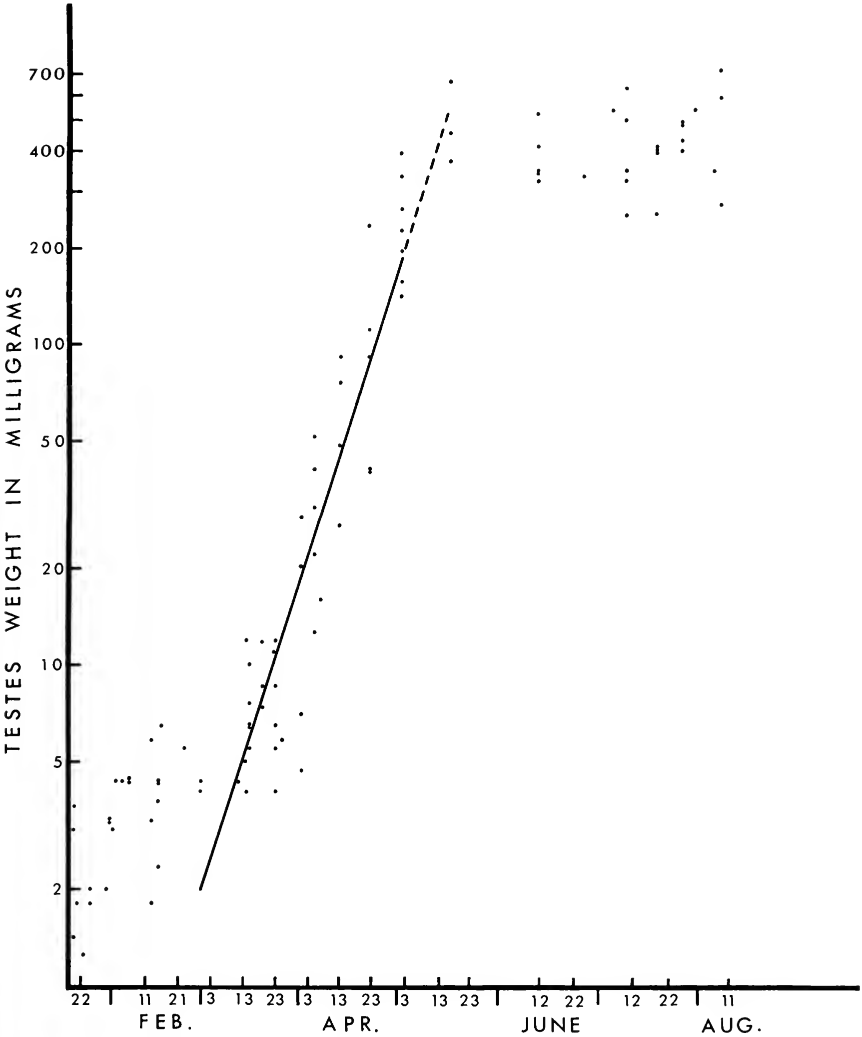

FIG. 1. Combined testes' weights of wild Dickcissels collected on both the winter and summer ranges.

in which "wt" is the combined testes weight in milligrams and "t" is in days, beginning with 28 February equal to day 1. The logarithmic testicular growth-rate constant, k, is thus equal to 0.03114 day^{-1}. It is also apparent that a growth rate of this magnitude will lead to testes of breeding size by the time the population migrates to and becomes territorial on its breeding range in mid-May (dashed extension of linear regression in Figure 1).

The average weight of the combined testes in Illinois is 439.23 ± 21.77 mg (SE, n = 28). Birds collected in June and July had swollen seminal vescicles, indicative of the production of spermatozoa. Even the bird collected on 19 July whose combined testes weight was only 256 mg was producing sperm. Finding functional breeding testes of such a wide range in size apparently is not unusual (Dolnik, 1963).

DISCUSSION

The temperate-wintering White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) has a *k* value for adult males on a 12-hour photoperiod equal to 0.0225 (Farner and Wilson, 1957). If the same ratio between growth rates of first year birds and adults that occurs in the White-crowned Sparrow (*k* of first year males = 1.16 k of adults) is valid for adult Chaffinches (*Fringilla coelebs*) then the *k* of first year males which equals 0.0213 in this temperate species has a value of only 0.0184 in adults at a 12-hour photoperiod (Dolnik, 1963). Both these values are less than the 0.03114 computed for the logarithmic testicular growth-rate constant in the Dickcissel at a 12-hour photoperiod, and therefore the slower growth rate hypothesis is rejected for this tropical-wintering species.

Hamner and Stocking (1970) have similarly rejected both the prolonged refractory period hypothesis and the slow growth rate hypothesis for a trans-equatorial migrant, the Bobolink (*Dolichonyx oryzivorus*).

The question therefore still remains open as to why the testes do not begin to develop earlier than they do. The energy resources of the environment do not appear to be the main limiting factor. Although the prenuptial molt is typically completed prior to the onset of gonadal growth, the development of the testes is coincident with fat deposition and migratory behavior (Zimmerman, 1965).

Hamner (1968) presents the following observations from his studies of the photoperiod control of the gonadal cycle in the House Finch (*Carpodacus mexicanus*): 1) the termination of photorefractoriness can be accomplished by daylengths as long as 14 hours or as short as 6 hours and in all cases the termination is completed in the same time interval, 2 months; 2) wild birds that *are* photosensitive in the autumn experience a daylength of 12 hours but show no gonadal growth while the same daylength does induce rapid gametogenesis in the spring; 3) the renewal of photosensitivity is a gradual process in that the long-day effect on birds in the fall is not as great as the same long daylength in the winter; and 4) using an interrupted night technique on photosensitive birds, there was a change in circadian sensitivity from October to January in that this period of photosensitivity shifted from 20 hours after dawn in the October birds to 12 hours after dawn in the January birds.

Hamner hypothesized that there are two components in the House Finch's refractory period. The first phase, the "absolute refractory period," follows immediately after breeding and is a period during which even continuous light treatment is non-stimulatory and whose duration is independent of the photoperiodic environment. The absolute refractory period is then followed by a period of "relative refractoriness" during which the bird initially is insensitive to daylengths equal to or shorter than those to which it had been previously exposed but this insensitivity is affected by the photoperiod regime it is experiencing so that as daylengths decrease in the fall there is a shifting of a threshold for stimulation until finally this threshold reaches a daylength less than that of the actual environment at that time and light again becomes stimulatory on the system.

On the basis of Hamner's (1968) suggested mechanism, we hypothesize that Dickcissels escape absolute refractoriness soon after their arrival on the winter range, but still remain in a state of relative refractoriness to the tropical photoperiod. Some time in February, as a result of the continued lowering of the photoperiodic threshold, Dickcissels are released from relative refractoriness and gonad growth begins.

Since we have not been able to illustrate in the tropical-wintering Dickcissel that there is a refractory period longer than that of temperate species or a slower rate of testes growth in response to the naturally-occurring photoperiod in the spring than has been shown for temperate species, we suggest that there is no special adaptation for the regulation of its gonadal cycle because of its wintering at a latitude where it seldom experiences days of less than 12 hours duration. It, like temperate species (Wolfson, 1960), is simply specifically adapted to the photoperiodic environment it experiences as a result of its migratory behavior.

SUMMARY

Sizes of testes obtained from wild populations of the Dickcissel on its wintering range in Panama and the Canal Zone were used to compute a logarithmic testicular growth-rate constant, *k*, equal to 0.03114 day^{-1}. Since this value is not less than that of temperate-wintering species exposed to 12-hour photoperiods, the slower growth rate hypothesis is rejected for the Dickcissel.

Furthermore, this *k* value is great enough to lead to the development of breeding-size testes.

Since previously completed work by Morrison led to the rejection of the prolonged refractory period hypothesis, the question of why gonads of wintering Dickcissels do not begin their development earlier is still not answered. A mechanism based on the notions of Hamner (1968) is suggested as a hypothesis yet to be tested.

ACKNOWLEDGMENTS

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LITERATURE CITED

Burger, J. W. 1953. The effect of photic and psychic stimuli on the reproductive cycle of the male Starling, *Sturnus vulgaris*. J. Exp. Zool., 124:227–240.

Dolnik, V. R. 1963. Quantitative study of vernal testicular growth in several species of finches (Fringillidae). Dokl. Akad. Nauk SSR, 149:191–193. (In Russian, translation by F. K. Plous, Jr., courtesy of S. C. Kendeigh.)

Farner, D. S. 1959. Photoperiodic control of annual gonadal cycles in birds. *In* Photoperiodism and related phenomena in plants and animals, R. B. Withrow, Ed. Amer. Assoc. Advance. Sci., Washington, D.C., pp. 717–750.

Farner, D. S. 1961. Comparative physiology: Photoperiodicity. Ann. Rev. Physiol., 23:71–96.

Farner, D. S., and A. C. Wilson. 1957. A quantitative examination of testicular growth in the White-crowned Sparrow. Biol. Bull., 113:254–267.

Hamner, W. M. 1968. The photorefractory period of the House Finch. Ecology, 49: 211–227.

Hamner, W. M., and J. Stocking. 1970. Why don't Bobolinks breed in Brazil? Ecology, 51:743–751.

Lofts, B., B. K. Follett, and R. K. Murton. 1970. Temporal changes in the pituitary-gonadal axis. Mem. Soc. Endocrinol., 18:545–575.

Lofts, B., and R. K. Murton. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. J. Zool., 155:327–394.

Marshall, A. J. 1959. Internal and external control of breeding. Ibis, 101:456–478.

Marshall, A. J. 1960. Annual periodicity in the migration and reproduction of birds. Cold Spring Harbor Symp. Quant. Biol., 25:499–505.

Marshall, A. J., and M. C. Williams 1959. The prenuptial migration of the Yellow Wagtail (*Motacilla flava*) from latitude 0.04′ N. Proc. Zool. Soc. London, 132:313–320.

Morrison, J. V. 1971. Evidence for a refractory period in the Dickcissel (*Spiza americana*). Unpubl. M.S. Thesis, Kansas State University.

Shank, M. C. 1959. The natural termination of the refractory period in the Slate-colored Junco and in the White-throated Sparrow. Auk, 76:44–54.

Rowan, W., and A. M. Batrawi. 1939. Comments on the gonads of some European migrants collected in East Africa immediately before their spring departure. Ibis, (ser. 14) 3:58–65.

Wilson, F. E. 1968. Testicular growth in the Harris' Sparrow. Auk, 85:410–415.

Wolfson, A. 1958. Regulation of refractory period in the photoperiodic responses of the White-throated Sparrow. J. Exp. Zool., 139:349–379.

Wolfson, A. 1959*a*. Ecologic and physiologic factors in the regulation of spring migration and reproductive cycles in birds. *In* Comparative endocrinology, A. Gorbman, Ed. John Wiley and Sons, Inc., New York, pp. 38–70.

Wolfson, A. 1959*b*. Role of light and darkness in regulation of refractory period in gonadal and fat cycles of migratory birds. Physiol. Zool., 32:160–176.

WOLFSON, A. 1960. Regulation of annual periodicity in the migration and reproduction of birds. Cold Spring Harbor Symp. Quant. Biol., 25:507–514.

ZIMMERMAN, J. L. 1965. Carcass analysis of wild and thermal-stressed Dickcissels. Wilson Bull., 77:55–70.

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NEW LIFE MEMBER

A new addition to the list of Life Members of the Wilson Ornithological Society is Dr. David F. Parmelee, one of the recognized authorities on bird life of the high Arctic. Dr. Parmelee is currently Professor of Biology and Chairman of the Field Biology Program at the University of Minnesota. He has made numerous expeditions to the Arctic and published approximately 50 papers on his observations there as well as two small books. Our picture shows him (with friend?) on one of these trips. Dr. Parmelee holds degrees from Lawrence College, and the University of Oklahoma. He is a member of the Cooper Society, the state ornithological Societies of Kansas, Oklahoma, and Minnesota, and an Elective Member of the AOU. Besides his scientific work he is also a skilled bird photographer and painter. Dr. Parmelee is married and has one daughter.

GENERAL NOTES

Tool-using by a Double-crested Cormorant.—In a recent review of tool-using in vertebrates, van Lawick-Goodall (Tool-using in primates and other vertebrates, *In* Adv. Study Behavior, Lehrman et al., eds., vol. 3, 1970) defines a tool-using performance ". . . as the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal." She adds that "This goal may be related to the obtaining of food, care of the body, or repulsion of a predator, intruder, etc." Later, van Lawick-Goodall describes tool-using performances by a variety of birds, but she does not give examples of birds using tools in relation to care of the body.

My purpose here is to describe an act of tool-using by a Double-crested Cormorant (*Phalacrocorax auritus*) in relation to care of the body. Additionally, the observation is unusual in that the bird made use of one of its own bodily products as a tool.

On 13 February 1970, I was seated on the edge of Florida Bay in the town of Layton, Long Key, in the Florida Keys. About 50 feet from my position a long finger of debris, stones, and sand extended out into the bay. This man-made finger was a regular resting place for numerous cormorants, pelicans, gulls, and herons. On this particular day I was watching the behavior of foraging herons as they waded in the shallows between my position and the finger of solid fill. After the herons left I turned my attention to a group of five adult cormorants resting on the fill. Two of the cormorants were dozing while the remainder were preening and head-scratching.

As I watched one of the preening adults it would stretch its head and bill, in what seemed like an awkward manner to me, back towards its uropygial gland, squeeze the gland then apply the secretion to its wing feathers with broad sweeps or dabs of the anointed bill. Suddenly, as the cormorant postured with its wings widespread, one of its secondary feathers, loosened by the molting process, blew away from the extended wing and landed about a foot in front of the cormorant. The bird turned and stared at the feather for several moments, then it picked up the feather and held it crosswise in its bill. It held this pose for several moments, then adjusted its grip on the feather's shaft so that the object was held almost parallel with the bill. The cormorant then deftly applied the tip of the feather to the preen gland by simply turning its head and extending the feather towards the gland. Next, the cormorant used the feather as a brush by applying the preen gland secretion to its extended right wing, doing so by making side to side sweeps with its head, the bill still holding the shaft of the feather. The sweeping brush-like motions were made smoothly and unhurriedly.

The bird continued this behavior, making three sets of such sweeping motions over its extended wings, once on the right wing, twice on the left, each sweep preceded by an application of the secondary feather tip to the preen gland. The gland was not manipulated by the bill after the feather had been grasped the first time. At no time did the cormorant modify the tool so as to render the "brush" a more efficient tool.

A passing motorboat startled the cormorants and the tool-using bird opened its bill slightly; a light easterly breeze wafted the secondary feather from the bird's bill to a place about a foot to the cormorant's left. The bird stared at the feather for a few moments, reached out and picked it up and manipulated it for a few moments more. Then the bird released the feather and the breeze carried it out over the bay to a point about 20 feet from the tool-user. The bird made no effort to retrieve its tool, and further observation of the tool-user and the other cormorants failed to reveal any further tool-using.

This example of tool-using is not only unusual in the startling nature of such an act by a non-mammalian vertebrate, but it is of further interest in that the bird made use of one of its own bodily products, a feather, to attain a goal in what seemed to me to be an easier performance than its typical preening and oiling behavior. Furthermore, this observation adds another facet to the use of tools by birds and other vertebrates—use of a tool to care for the surface of the body by means of a brush.—ANDREW J. MEYERRIECKS, *Department of Biology, University of South Florida, Tampa, Florida 33620, 11 February 1972.*

Cold hardiness and the development of homeothermy in young Black-bellied Tree Ducks.—The Black-bellied Tree Duck (*Dendrocygna autumnalis*) is a southern species and dump nesting is extensive in Texas (Bolen, 1962 and 1967). Dump nests are the results of several females laying eggs in the same nest. Large broods with as many as 43 ducklings have been recorded and are a direct result of these dump nests (Cain, 1970).

Koskimies and Lahti (1964) have shown that surface ducks (Mallard, *Anas platyrhynchos*, and Common Teal, *A. crecca*) could not maintain combined broods because the ducklings were not cold hardy. Combined broods are common however in most genera of diving ducks, such as *Aythya* and *Melanitta* (Hochbaum, 1944) and *Bucephala* and *Mergus* (Mendall, 1958).

This study was conducted to determine the cold-hardiness and ontogeny of thermoregulation in the Black-bellied Tree Duck young and relate this to possible success of large brood that result from dump nests.

METHODS

Forty ducklings hatched in forced-air incubators were kept for 3 days at 42° C and then placed at 32° C. Another 40 ducklings were placed in outdoor pens at one day of age without a brooder.

The fate of 22 ducklings found abandoned in nests were recorded for comparative purposes.

During the temperature regulating experiment ducklings were placed in a perforated paper box in a dark cabinet held at 0° C. At 5-minute intervals a quick-registering thermister was inserted into the duckling's mouth to a depth of 40 mm. This core temperature was then recorded on a Yellow Springs Inc. telethermometer. Cotton gloves were worn to reduce heat transfer to the ducklings.

The ducklings were removed from the cold when they were unable to stand up, or after 30 minutes, and returned to their initial room temperature. Maintenance of the ducklings followed the procedure used by Cain (op. cit.).

RESULTS AND DISCUSSION

Temperature regulation.—Ducklings of this species apparently are unable to maintain a constant body temperature for several days after hatching (Fig. 1) when exposed to a low ambient temperature. The body temperature dropped rapidly (1.26° C per minute) for ducklings 1 day old and slowed as the age increased (0.50° C per minute for 6 day old ducklings). At 12 days of age the rate of cooling was 0.35° C per minute for 20 minutes and then the ducklings maintained a steady temperature of 32° C.

The slower rate of cooling for older ducklings may be due partly to an increase in metabolism (Cain, in prep.), a decreased surface to volume ratio as the duckling increased in weight, and the increased insulation afforded by the development of the juvenal down between 10–12 days of age (Cain, 1970). A similar cooling trend for nestling House Wrens

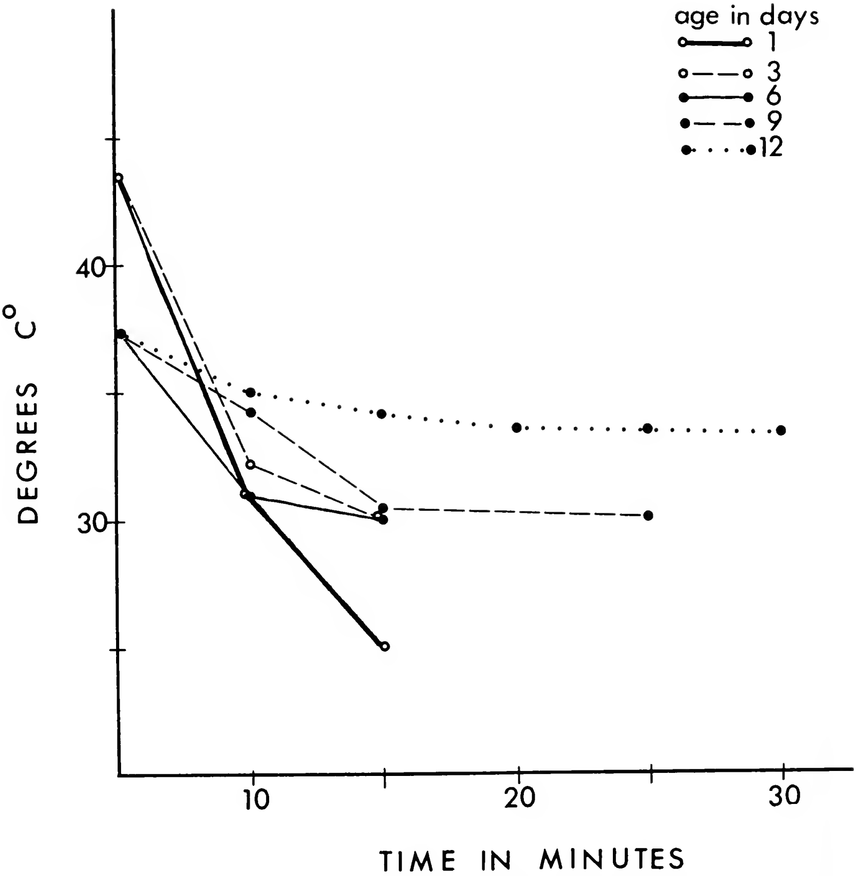

FIG. 1. The relationship between body temperature and time exposed to the ambient temperature (0° C) as a function of age.

(*Troglodytes aedon*) was reported by Kendeigh and Baldwin (1928) and for nestling Cactus Wrens (*Campylorhynchus brunneicapillus*) as reported by Ricklefs and Hainsworth (1968).

Cold-hardiness.—Both parents stay with the brood in this species even after the young have attained flight (pers. observ.) and it is assumed that both adults contribute to the brooding in the early stages. The importance of brooding may be seen in Table 1. Ducklings not brooded died before 7 days of age and their body weight at death was significantly lower than ducklings of the same age that were brooded.

This low degree of cold-hardiness, before thermoregulation develops, should restrict the independence of the young Black-bellied Tree Ducks and increase the adult's burden of supplying energy. This may be a considerable amount for the parents of large broods and this attentiveness may lead to the strong family bonds in this species.

I suggest then that large broods resulting from dump nests in south Texas may enjoy

TABLE 1

COMPARISON OF DUCKLINGS BROODED ARTIFICALLY AND THOSE NOT BROODED

The average body weight is for 7-day-old ducklings or as indicated.

Ducklings considered	Number hatched	Number survived	Per cent survival	Body weight (in grams)
Artificially incubated				
Unbrooded	40	0	0	22.0[1]
Brooded	40	30	75	31.5
Wild caught				
Unbrooded	10	0	0	21.5[1]
Brooded	12	6	50	32.0

[1] Average body weight at death.

a high success if adverse weather conditions do not occur during the first 10 days after hatching. This high degree of success would be a function of the low energetic stress upon the young themselves and the increased frequency of brooding because of both parents being present.

ACKNOWLEDGMENTS

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LITERATURE CITED

BOLEN, E. G. 1962. Nesting of Black-bellied Tree Ducks in Texas. Audubon Field Notes, 16:482–485.

BOLEN, E. G. 1967. The ecology of the Black-bellied Tree Duck in southern Texas. Unpubl. Ph.D. thesis, Utah State Univ., Logan.

CAIN, B. W. 1970. Growth and plumage development of the Black-bellied Tree Duck, *Dendrocygna autumnalis* (Linnaeus). Texas A&I Univ. Studies, 3:25–48.

HOCHBAUM, A. 1944. The Canvasback on a prairie marsh. Amer. Wildl. Inst., Washington.

KENDEIGH, S. C., AND S. P. BALDWIN. 1928. Development of temperature control in nestling House Wrens. Amer. Naturalist, 62:249–278.

KOSKIMIES, J., AND L. LAHTI. 1964. Cold-hardiness of the newly hatched young in relation to ecology and distribution of ten species of European ducks. Auk, 81:281–307.

MENDALL, H. L. 1958. The Ring-necked Duck in the northeast. Univ. Maine Studies, 2nd ser., 73:1–320.

RICKLEFS, R. E., AND F. R. HAINSWORTH. 1968. Temperature regulation in nestling Cactus Wrens: Development of homeothermy. Condor, 70:121–127.

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Ruddy Ducks colliding with wires.—Cornwell and Hochbaum (Wilson Bull., 83: 305–306, 1971) remarked that anatid strikes on wires (fence, communications, and power) occur commonly on the northern prairie breeding grounds, but go largely unnoticed and unreported. The following observations, made near Minnedosa, Manitoba, during May–August 1971 are offered in response to comments made by Cornwell and Hochbaum.

Incidental to carrying out weekly surveys of waterfowl breeding on potholes along roads regularly used as a transect route, I recorded all dead birds encountered while walking around ponds and while travelling by car. I noted the state of freshness of the carcasses and their locations, before gathering them up for removal. I covered the same 250 km of road every week; some 50 km of road served as a route for overhead lines.

Ten weekly three-day censuses were carried out, and freshly dead waterfowl were observed during the course of seven of these. I recorded a total of 16 dead birds; eight Ruddy Ducks (*Oxyura jamaicensis*); four Am. Coot (*Fulica americana*); two Blue-winged Teal (*Anas discors*); one Mallard (*Anas platyrhynchos*); and one Pintail (*Anas acuta*). Apart from the Pintail, the carcasses were located on the ground within 75 meters of the nearest pond edge and within 30 meters (mean of 10 meters) of overhead wires. The Pintail (an adult male) was found impaled on the top strand of a barbed wire fence standing in water 30 cm deep.

Three Ruddy Ducks were found between 15 May and 15 June, and five were found after 15 June. The Mallard and Pintail were found in mid-May, and the two Blue-winged Teal in the first week of June. The Coots were found in June. Apart from the Coots, which were aged but not sexed, all of the dead birds were adult males. Since the surveys were terminated before the end of August, the absence of juvenile birds is not so surprising.

Of a total of 50 adult Ruddy Ducks (24 females, 26 males) collected during my study two males with defective wings were taken, and three crippled females were taken in May. The crippled birds' injuries were consistent with the type expected as a result of colliding with wires. The birds were located on ponds close to overhead wires.

Stout (The nature and pattern of non-hunting mortality in fledged North American waterfowl. Unpubl. M.S. thesis, Virginia Polytech. Inst., 1967) used information from questionnaires and band recoveries to suggest that dabbling ducks are most often involved in wire strikes and that males may be more vulnerable than females; perhaps because of the "reckless" nature of pursuit flights. A comparison of absolute densities of all anatids on ponds near overhead wires and generally in the study area, showed the Ruddy Duck to be second to the Blue-winged Teal (Siegfried, unpubl.). However, the ratios favoring the Ruddy Duck were nowhere near as high as the 67 per cent (Coot excluded) for relative mortality as recorded here. While Stout (op. cit.) suggested that dabbling ducks are most often involved in wire strikes, he does state, too, that next to the Mallard the Ruddy Duck is most susceptible to mortality caused by striking overhead wires. Apparently, then, a factor other than mere relative abundance of species is involved. Further, since the Ruddy Duck does not perform pursuit flights, or any other kind of aerial courtship, this behavior cannot be evoked as contributing to the disproportionate mortality.

A time and motion study of the Ruddy Duck's daily behavior showed that, once on the breeding grounds, the birds very seldom flew by day and that aerial movement was virtually restricted to late evening twilight, starting just before darkness. During late May, June, and July these flights were observed to involve only males, flying at low altitude from one pond to another. In the study-area generally, there were more males than females, but the sex ratio was too close to parity to account for the disproportionate kill of males.

Apparently, females are most often involved in wire strikes early in the season during and shortly after arrival on the breeding grounds. Males, on the other hand, suffer collisions throughout the season, apparently because they move around much more. The fact that Ruddy Ducks normally fly only during and after dusk, and that they do not climb steeply after taking wing, but rather perform one or two low and wide circles while gaining altitude, adds to their risk of striking wires.

I am grateful to Dr. H. A. Hochbaum for commenting on the manuscript. For financial support in North America, I am indebted to: Delta Waterfowl Research Station; Chapman Memorial Fund of the American Museum of Natural History; South African Council for Scientific and Industrial Research; University of Cape Town. The Canadian Wildlife Service gave permission for the taking of specimens.—W. Roy Siegfried, *Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, Cape Province, South Africa, 9 February 1972.*

A note on Golden Eagle talon wounds.—The recent slaughter of Golden Eagles (*Aquila chrysaetos*) in Wyoming has again focused attention on the subject of eagle–livestock relationships. The problem has been variously studied in many parts of the world including the United States (Spofford, 1965, 1969; McGahan, 1968; Mollhagen et al., 1972), Scotland (Brown and Watson, 1964), and Australia (Leopold and Wolfe, 1970). An important aspect of these and related studies is the determination of whether the eagle foods—especially lambs—have indeed been freshly killed (i.e. outright predation) or secondarily secured as carrion.

Hence, emphasis has been placed on the field identification of wounds and other features present on carcasses alledgedly killed by eagles. In Australia, Rowley (1970) thoroughly examined the damage inflicted by Wedge-tailed Eagles (*Aquila audax*) and other carnivores on lambs whereas a similar but less exhaustive study was also undertaken in the southwestern United States where Golden Eagles nest and overwinter (Wiley and Bolen, 1971; Boeker and Bolen, 1972).

Talon punctures, coincident with extensive subcutaneous hemorrhages, are a priori indications of eagle predation despite the contrary opinion of some stockmen that talon wounds are more often absent on eagle-killed lambs (and hence, in their view, that the frequent absence of talon punctures on dead lambs does not preclude assigning the cause of death to eagles). Lambs are instead killed, according to some stockmen, by the impact of an eagle attacking with its feet closed in a "fist" or in some other way that does not involve the use of their talons.

We wish to cite an instance where deep talon punctures were indeed made by a Golden Eagle attacking decoys set at Muleshoe National Wildlife Refuge in Bailey County, Texas, on 23 January 1971. The decoy attacked was one of 24 female Pintail decoys set at Paul's Lake immediately within the refuge's eastern boundary. The attack occurred at 10:15 when the eagle flew across the lake and approached the decoys at an altitude of about 15 yards; the bird suddenly dropped onto the back of the decoy. The impact of the attack, even without the advantage of a long stoop, drove the eagle's talons deeply into the back and side of the plastic-bodied decoy leaving ample—and obvious!—evidence of puncture (Fig. 1). Later in the day, after the decoys had been left untended for several hours, another decoy was discovered with a fouled anchor cord; examination of this decoy showed that it, too, had deep punctures similar to the earlier "wounds" inflicted by the Golden Eagle. Sperry (1957) also described the attack of a Golden Eagle ". . . with distended talons" on a male Pintail decoy, although the eagle in this instance approached the decoy by wading.

Fig. 1. Golden Eagle talon damage inflicted on a plastic Pintail decoy at Muleshoe National Wildlife Refuge, Texas. Upper picture shows overall view of the damage; in the lower photo, the depth of the punctures are visible at two points on the decoy's back.

Talon wounds are equally present on ducks and geese attacked by Golden Eagles. Duck carcasses (listed only as *Anas* spp.) taken from a Golden Eagle nest showed ". . . talon marks on the shoulders and neck" (Arnold, 1954). Tener (1954) found several talon punctures along the back of a Canada Goose (*Branta canadensis*) attacked by a Golden Eagle whereas Wallace (1937) reported that an eagle ". . . buried its talons" into a domestic goose (*Anser* sp.). Recently, Kelleher and O'Malia (1971) watched a Golden Eagle snatch a drake Mallard in mid-air and hold it in its talons. Federal Game Management Agent Don Krieble reports that he has seen Golden Eagles at Muleshoe National Wildlife Refuge make mid-air attacks on waterfowl suffering from avian cholera; talons were used prominently in these strikes.

We thus cite our observation, with these others, as evidence that eagles indeed follow the expected course of action when striking at prey. Specifically, eagles use their formidable talons which, of course, are important adaptations to their mode of feeding. Contentions that carcasses of eagle prey are free of talon punctures would thus seem to be largely without merit.

LITERATURE CITED

Arnold, L. W. 1954. The Golden Eagle and its economic status. U.S. Fish and Wildl. Serv. Circ. 27, Washington, D.C.

Boeker, E. R., and E. G. Bolen. 1972. Winter Golden Eagle populations in the southwest. J. Wildl. Mgmt., 36:477–484.

Brown, L. H., and A. Watson. 1964. The Golden Eagle in relation to its food supply. Ibis, 106:78–100.

Kelleher, J. V., and W. F. O'Malia. 1971. Golden Eagle attacks a Mallard. Auk, 88: 186.

Leopold, A. S., and T. O. Wolfe. 1970. Food habits of nesting Wedge-tailed Eagles, *Aquila audax*, in south-eastern Australia. CSIRO Wildl. Res., 15:1–17.

McGahan, J. 1968. Ecology of the Golden Eagle. Auk, 85:1–12.

Mollhagen, T. R., R. W. Wiley, and R. L. Packard. 1972. Prey remains in Golden Eagle nests: Texas and New Mexico. J. Wildl. Mgmt., 36:784–792.

Rowley, I. 1970. Lamb predation in Australia: incidence, predisposing conditions, and the identification of wounds. CSIRO Wildl. Res., 15:79–123.

Sperry, C. C. 1957. Golden Eagle attacks decoy duck. Wilson Bull., 68:107–108.

Spofford, W. R. 1965. The Golden Eagle in the Trans-Pecos and Edwards Plateau of Texas. Audubon Conserv. Rept. No. 1, Natl. Audubon Soc., New York.

Spofford, W. R. 1969. Problems of the Golden Eagle in North America. *In* Peregrine Falcon populations (J. J. Hickey, Ed.), Univ. Wisconsin Press, Madison.

Tener, J. S. 1954. Three observations of predators attacking prey. Canadian Field Naturalist, 68:181–182.

Wallace, G. J. 1937. Notes from Vermont. Auk, 54:547.

Wiley, R. W., and E. G. Bolen. 1971. Eagle–livestock relationships: livestock carcass census and wound characteristics. Southwestern Naturalist, 16:151–169.

John R. Alford, III and Eric G. Bolen, *Department of Range and Wildlife Management, Texas Tech University, Lubbock, Texas 79409, 10 February 1972.*

Roadside raptor census in Colorado—Winter 1971–72.—From 11 November 1971 through 15 February 1972, 13 counts of wintering birds of prey were made in the grasslands and wheatlands east of Colorado Springs and Fort Collins, Colorado. Two routes

TABLE 1

FREQUENCIES OF RAPTORS ON PLAINS EAST OF COLORADO SPRINGS AND FORT COLLINS, WINTER 1971–72

Species	Total number observed	Miles traveled per individual
Rough-legged Hawk (*Buteo lagopus*)	107	10 (9)
Golden Eagle (*Aquila chrysaetos*)	57	18 (52)
Prairie Falcon (*Falco mexicanus*)	36	29 (27)
Sparrow Hawk (*Falco sparverius*)	34*	31 (52)
Marsh Hawk (*Circus cyaneus*)	24	44 (22)
Ferruginous Hawk (*Buteo regalis*)	20	52 (112)
Bald Eagle (*Haliaeetus leucocephalus*)	6	175 (186)
Red-tailed Hawk (*Buteo jamaicensis*)	4	262 (419)
Pigeon Hawk (*Falco columbarius*)	3	349 (186)

* Eleven of the total were observed on 11 November 1971.

were followed, the first, extending south and east from Colorado Springs, was approximately 150 miles long, involving a total observation area of approximately 48,000 acres (a linear strip 150 miles long and ½ mile wide). The second route, beginning 8 miles east of Fort Collins, was 54 miles long and involved 17,280 acres. A total of 1,048 miles was driven during the censuses (910 miles near Colorado Springs, and 138 miles near Fort Collins). Both routes were chosen because of the abundance of utility poles upon which raptors perch. Observations were generally made early in the morning, on days when the wind was light (0–8 mph), using binoculars and a spotting scope. Table 1 summarizes the frequencies of raptors observed. The data in parenthesis were collected in the same area by Enderson (Wilson Bull., 77:82–83, 1965) in the winters of 1962–63 and 1963–64.

A total of 306 raptors was seen (one every 3.4 miles), including 15 buteos not identified to species. Although the 11 Sparrow Hawks observed on 11 November 1971 were not identified with respect to sex, 17 of 21 identified to sex on the following counts were males. Of 20 Marsh Hawks identified with respect to sex, 16 were males. Three of four Bald Eagles identified with respect to age were adults.

Enderson (op. cit.) counted raptors along nearly identical routes about 10 years ago, traveling 1,675 miles. He recorded Marsh Hawks and Pigeon Hawks twice as often as we did. We recorded Sparrow Hawks 1.7 times more often, and Ferruginous Hawks 2.1 times more often than he did. For the latter species, these and nesting season observations tend to support our impression that Ferruginous Hawks are more abundant in the region in the last two years. We recorded more Red-tailed Hawks, but three of four were seen along a creek just outside of Enderson's route.

In this survey, Golden Eagles, second only to Rough-legged Hawks in abundance, were seen 2.9 times more frequently than a decade ago.—DAVID JOHNSON AND JAMES H. ENDERSON, *Department of Biology, Colorado College, Colorado Springs, Colorado 80903, 14 April 1972.*

Sparrow Hawk eats European corn borer.—Because insect prey of the Sparrow Hawk (*Falco sparverius*) are usually not identified to species, cases in which such determinations are made, especially when unlikely prey are consumed are of interest.

On 4 April 1970 a Sparrow Hawk was caught on a Balchatri trap near Newark, Licking County, Ohio. A few minutes after capture, the bird died of unknown causes. The specimen was a male with enlarged testes and weighed 113.7 g. The stomach contained 71 European corn borer (*Ostrinia nubilalis* Hübner) larvae of various sizes. This prey item comprised about 95 per cent of the stomach contents. Other contents were two small pellets composed wholly of fur of the meadow vole, *Microtus pennsylvanicus*. At this time of year in central Ohio, Sparrow Hawks subsist principally on small rodents, particularly the meadow vole.

Since during the early spring European corn borer larvae are dormant within the stalks of corn plants and emerge as adults in June, this insect would not be regularly incorporated into a Sparrow Hawk's diet. In a search of the literature, we found no records of Sparrow Hawks eating this insect, although Lepidopterans in general frequently comprise a substantial part of this falcon's diet. The significant aspect of this record is that these larvae were eaten so early in the season. In fact, it is surprising these insects were eaten at all. One may speculate on the source and manner in which the hawk obtained such a large number of larvae. Early spring plowing or disking of fields may have broken corn stalks exposing many larvae to predators.—Clive A. Petrovic, *F. T. Stone Laboratory, The Ohio State University, Columbus, Ohio 43210* and Gregory S. Mills, *Dept. of Zoology, The Ohio State University, Columbus, Ohio, 3 April 1972.*

Black Rails hit a television tower at Raleigh, North Carolina.—In 1969 and 1970 two Black Rails (*Laterallus jamaicensis*) collided with the WRAL television tower, nine miles southeast of Raleigh, North Carolina. This tower is 1,175 feet high, and its base is 190 feet above sea level.

The first bird, a female with unossified skull, died the night of 19–20 September 1969. Its weight was 32.9 g; fat class, 2; chord of wing, 78 mm; culmen from skull, 13.2 mm. The crop contained 14 quartz particles each measuring about 1 × 1 mm. The stomach contained no food. During the night of 19–20 September there was rain, wind of 7–12 mph from N to NNE, and the ceiling was 400 to 1,500 feet.

The second bird, a male with an unossified skull, died the night of 27–28 September 1970. It weighed 31.7 g; fat class, 3; weight of subcutaneous fat, 2.6 g; culmen from skull, 14 mm. The stomach was empty. During the night, there was rain, and the wind was 9–11 mph from the NE. The ceiling lowered to 100 to 1,200 feet.

These are the first records of the Black Rail in central North Carolina since 1902. In 1891, C. S. Brimley found Black Rails nesting in the present town of Raleigh (Ornithologist and Oologist, 16:26, 1891). However, it is unlikely that the tower killed birds were local birds, since local Black Rail habitat has long since disappeared. The two birds probably originated from a coastal area to the northeast. That such a flight is possible is indicated by the finding of a Seaside Sparrow (*Ammospiza maritima*) at this tower (Wilson Bulletin, 83:102, 1971). A Clapper Rail (*Rallus longirostris*) also has hit this tower (N. C. State Museum specimen No. 2671, picked up 28 September 1965).

Black Rails are rarely killed in collisions with man-made structures. There are only 10 recorded casualties, all from Florida (Bull. Tall Timbers Res. Sta. No. 8:51, 1967; Fla. Nat. 39:53, 1966; Am. Birds, 25:723, 1971). Since Black Rails are nocturnal birds and also have a limited distribution, it is no wonder they are rarely found colliding with man-made obstacles. However, it is more unusual that they should be found at an inland television tower. The nearest known present breeding site for Black Rails are the marshes of Chesapeake Bay, about 200 miles NE of Raleigh.—MICOU M. BROWNE AND WILLIAM POST, *Zoology Department, North Carolina State University, Raleigh, 27607. 3 February 1972.*

Eggshell removal in the Spotted Sandpiper.—Tinbergen and co-workers suggested that the latency of eggshell removal depends on two factors: the importance of cryptic coloration to protection of the eggs and young and the extent of predation on unguarded young (Tinbergen, Broekhagsen, Feekes, Houghton, Kruuk, and Szulc, Behaviour, 19: 74–117, 1962: Tinbergen, Nat. Hist., 72:28–35, 1963). Partially hatched and wet gull chicks are subject to heavy intraspecific predation (Tinbergen, 1963, op. cit.). Removal of conspicuous eggshells is often delayed until the chicks dry. The Ringed Plover (*Charadrius hiaticula*) and Oystercatcher (*Haematopus ostralegus*) are less subject to the intraspecific predation found in gulls, depend on cryptic coloration for escape, and remove their eggshells much sooner after hatching than do the gulls. But this is all the comparative evidence Tinbergen mustered in support of his hypothesis.

On 14 July 1970 I saw an adult Spotted Sandpiper (*Actitis macularia*) flying over a speckled alder thicket and holding an eggshell in its bill. The shell hung down, pointed end forward. The bird called loudly every 5 sec during its entire flight. It landed on a plank bridge and placed the eggshell on the bridge. It stood by the shell for a short time then flew through the alders in the general direction of its nest. It continued to call, a loud *peet-weet* whistle, while standing by the shell, but became silent upon departing.

The eggshell, the larger portion with the pointed end, the blunt end having been knocked out, was damp inside with the allantoic membranes still clinging to the inner surface. The shell was deposited about 40 m from the nest.

Four chicks were present in the nest which less than two hours earlier had contained only two chicks. There were no eggshells in the nest nor within 1 m of the nest. Two of the chicks were dry, one was damp, and the fourth was wet.

I had checked the nest two hours earlier, thus no more than two hours could have elapsed between hatching and eggshell removal. The wet membranes lining the eggshell and the chick's wet down would seem to indicate that only a few minutes had elapsed. The Spotted Sandpiper, a solitary-nesting species not subject to intraspecific predation on wet chicks, a species whose eggs and young are cryptically colored, appears to remove eggshells quickly as predicted by Tinbergen.

I made these observations while doing research supported by a grant from the Surdna Foundation to Bowdoin College.—EDWARD H. BURTT, JR., *Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, 14 February 1972.*

Stomach capacity in the Common Nighthawk.—Analyses of the stomach contents of the Common Nighthawk (*Chordeiles minor*) have occasionally revealed the presence of surprisingly large numbers of insects, particularly winged ants (Bent, U.S. Natl. Mus. Bull., 176:224–225, 1940). Two nighthawks collected from a migratory flock near Roanoke, Virginia, on 4 September 1971, contained such an impressive quantity of food material that I was prompted to make the following measurements.

The birds, both female, weighed 101.2 g and 99.7 g, and were extremely fat. Their stomachs were distended with queen ants (Formicinae), and the wet weights of the contents were 20.5 g and 19.7 g, respectively. This represents 25.4 per cent and 24.6 per cent of the food-free weight of each nighthawk. In comparison, Stevenson (Wilson Bull., 45:155–167, 1933) found the food in the stomachs of several species of passerine birds amounted to about 1.5 per cent of their body weight. The wing-loading of the Roanoke specimens (0.295 and 0.287 g/cm^2) is 36.6 per cent and 32.9 per cent greater than the value given by Poole (Auk, 55:511–517, 1938).

The food was freeze-dried and the caloric content measured in a Parr non-adiabatic bomb calorimeter. The average of three determinations was 7.434 ± 0.020 kcal/g dry weight. Total caloric values of the stomach contents were 78.9 kcal and 75.9 kcal, respectively. Using 70 per cent as a conservative estimate of the metabolic efficiency of this species, 55.2 kcal and 53.1 kcal would be available to the nighthawk from these meals. This is 3.7 to 3.8 times the daily standard metabolism of the nighthawk as calculated from the equation given by Lasiewski and Dawson (Condor, 66:477–490, 1964), and the average temperature of the collection site during September (20.6 C).

Since the time required for the passage of insect materials through an avian digestive tract may be as little as 1.5 hours (Stevenson, ibid.), the total calories collected by individual nighthawks from a generous source such as an ant mating swarm may be quite large. In the absence of a crop, a large stomach capacity is certainly adaptive in such feeding situations, although Bent (ibid.) intimates that one nighthawk met accidental death because of the handicap of carrying a large mass of food material.

I am indebted to C. F. Murray for assistance in collecting the nighthawks.—Charles R. Blem, *Virginia Commonwealth University, Department of Biology, Richmond, Virginia 23220, 10 February 1972.*

Retention of egg in a wild Downy Woodpecker.—The observations given below on egg-binding in a wild Downy Woodpecker (*Dendrocopos pubescens*) have appeared worth reporting from three points of view: first, the condition which can be severe or even lethal under aviary conditions (Boosey, E. J., Foreign bird keeping. Iliffe Books, Ltd., London, 1970) might be even more so in the wild where the bird would be a helpless victim to any passing predator. Secondly, if egg-binding is as prevalent in the wild as in the aviary, it could be a highly important and largely unrecognized mortality factor among adult breeding birds of many species; and thirdly the present report serves to document that egg-binding can occur in the wild and is thus not just an artifact of captivity. The circumstances attending the observations were as follows:

A pair of Downy Woodpeckers had excavated a nest hole in Lyme, New Hampshire and I had witnessed a total of seven copulations on 6, 7, and 8 May 1971, when at 06:30 on 9 May I noted the female clinging to the bark of a tree not far from the nest stub. She was in a drooping position as if about to fall asleep. After a few minutes she ascended to a cavity, the work of a Pileated Woodpecker (*Dryocopus pileatus*) to rest at the bottom of it with her bill tucked into her back feathers. Her mate disturbed her a half hour later but she returned. I could not locate her at 09:15 until the male, coming close to another cavity, caused her to show herself. She clung to the bark weakly as before. On my next glance she was clinging with white belly uppermost, then fell fluttering into swamp water below. Here she made feeble efforts to reach a tree trunk. With head held back and having difficulties in breathing, she would doubtless have drowned had I not picked her up. I took her home, a 10-minute walk, and my wife and I both felt a hard ovoid mass, the size of a large egg, distending her abdomen. The woodpecker appeared to be in spasm and made no efforts to resist. Forty minutes later she was stronger, attacking my finger for the first time. Her abdomen was no longer distended. There was no trace of her having laid an egg and I presumed that she had either laid one and eaten it or that it had broken inside. I now took her back to the swamp. She was barely able to flutter to a tree where she remained clinging to the bark without further efforts to move.

By afternoon a second female with different head markings (Kilham, Condor, 64:126, 1962) and habits, had arrived by the nest stub. She engaged the attentions of the male Downy Woodpecker on this and throughout the following day. On 11 May, the original female re-appeared. She was now in excellent condition and after further copulations she must have laid at least four eggs, for on 21 June I watched three fledglings fly from the nest, leaving a fourth one still looking out.—Lawrence Kilham, *Department of Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755, 1 March 1972.*

The use of sawdust piles by nesting Bank Swallows.—The Bank Swallow (*Riparia riparia*) generally digs its burrows in banks of sand, gravel, or clay along inland bodies of water and marine coastlines. Rarely, it employs such unusual man-made substrates as drain holes in concrete banks (Hollom, Auk, 60:270–271, 1943) or a pile of iron ore "tailings" (Van Deusen, Auk, 64:624–625, 1947). Sawdust heaps in abandoned mill yards are used also as colony sites by the Bank Swallow (Torrey, Auk, 20:436–437, 1903; Barrows, Michigan Bird Life, 1912; Norton, Bird-Lore, 29:117, 1927; Brewster in Griscom, Bull. Mus. Comp. Zool., 66:554, 1938; and Palmer and Taber, Auk, 63:299–314, 1946).

The colonies in sawdust heaps reported by the above authors occur in northern lumbering regions from Michigan to Maine. These occurrences, together with additional ones discovered by the present author in Maine and northern New York, suggest that the use of this substrate in the north may not be altogether unusual. Few of the above authors provided much more than a simple notice of the location of such a colony.

In this paper, I present information on two colonies of Bank Swallows in old sawdust piles along the Aroostook River near Ashland, Aroostook County, Maine. Both colonies (about 600 m apart) were discovered in 1962 shortly after the mill sites were abandoned. To my knowledge, there had not been any colonies in the immediate area before 1962, apparently because of the absence of suitable natural or man-made banks. Both colonies were still active in 1970 when one of them was bulldozed out of existence. In the late 1960's swallows established a few burrows in narrow veins of sand in a new gravel pit nearby.

Burrows in the sawdust piles.—Repeated visits to the colonies from 1962 to 1970 revealed that slumping, erosion, and perhaps human disturbance changed the total amount of bank surface available to the Bank Swallows as burrow sites from one year to the next. The size of the colonies varied accordingly from ca. 50 to 100 active burrows in each sawdust heap.

Some swallows apparently faced local slumping problems on the steep banks as they dug fresh burrows into the compact, weathered sawdust (Fig. 1). Partly excavated burrows with severe slumping around their entrance, forming large, irregular depressed areas in the side of the bank, were abandoned. Other burrows with only slightly or moderately enlarged entrances contained active nests. The entrances to still other burrows, especially those near the rim of the banks, retained a compact, elliptical shape. Norton (op. cit.) and Brewster (op. cit.) also reported compact, horizontally elliptical entrances to burrows in other sawdust piles in Maine.

FIG. 1. Bank Swallow colony in an old bank of sawdust at Ashland, Maine. See the text for comments. Photograph by Stanley H. Greenlaw.

The problems of slumping and wearing of the sawdust around the entrances to burrows is in part a function of age of the burrow and perhaps age of the bank (time since formed) as well. Entrances to active burrows which were compact early in the breeding cycle, often showed wear and sometimes moderate slumping later in the cycle. Also, most entrances in freshly formed vertical banks were compact but those in older banks (such as in Fig. 1) were more often enlarged and irregular in shape.

In old banks of sawdust, erosion and local slumping created variation in the angle of exposure of adjacent "faces" (Fig. 1). Some of the tunnels in one face converged and joined tunnels in an adjacent face situated at an oblique angle to the first. Thus an active burrow sometimes had two entrances. Other tunnels passed from one face to an adjacent one and were open at both ends. This was not a problem in the smooth, newly formed banks.

Burrows in low sawdust banks 1.5 to 3 m high were placed at all heights from top to the bottom. But in two apparently freshly formed banks 6 to 8 m high, one sparsely and the other moderately occupied by burrows, the burrows were concentrated near the rim. The texture and compactness of the sawdust in all faces seemed to vary little from top to bottom. Evidently there is a behavioral tendency for Bank Swallows to dig their burrows as high as bank conditions permit. Burrows excavated early tend to be situated high on the bank and those dug later perforce must be lower as the higher sites are occupied (cf. Peterson, Wilson Bull., 67:246, 1955).

Tunnel orientation relative to the horizontal was variable. Some tunnels slanted upward then leveled off at the nest. Other tunnels dipped downwards to the nest or were horizontal. A few even slanted upwards then downwards. Such variability in tunnel orientation, though perhaps not this extreme, has been noted in natural substrates elsewhere (Stoner, Roosevelt Wild Life Annals, 4:126–233, 1936; Beyer, Wilson Bull., 50: 122–137, 1938).

The length of completed burrows in the sawdust piles also varied, usually from 47 to 60 cm (ca. 18–24 inches). A few were up to 120 cm in depth. Thus, burrow depths in the sawdust banks correspond in general to depths recorded for burrows in easily excavated natural substrates such as sand (Stoner, op. cit.; Gross *in* Bent, U.S. Natl. Mus. Bull., 179:405, 1942).

Importance of sawdust as a nesting substrate.—Forbush (Birds of Massachusetts and other New England States, Part III, p. 160, 1929) and Gross (*In* Bent, op. cit.:404) speculated that sawdust is likely to be an unsuitable if not precarious nesting substrate for Bank Swallows because of the problems of erosion and slumping. Contrary to this view, I am unable to conclude that the erosion and slumping faced by Bank Swallows in sawdust heaps within a given breeding season are substantially more severe or prevalent than in certain natural substrates, especially in sand banks exposed to wave and current action, and spring flooding, along streams (cf. Stoner, op. cit.; Beyer, op. cit.). The large size of the colonies in the sawdust piles at Ashland (among the largest in northeastern Maine [unpubl. data]) suggests that over-all nesting was fairly successful. Burrows destroyed in the sawdust heaps are probably replaced by re-nesting attempts (Stoner, op. cit.).

The biggest disadvantage of the sawdust pile as a nesting substrate is its relatively short life. The old piles slowly wear down or are mined by local residents. Otherwise, within the short term, old sawdust heaps seem to offer both a suitable and perhaps an important local substrate for nesting Bank Swallows. Holes are readily dug in the compact sawdust. And the problems of slumping, wear, erosion, and even total bank destruction in natural substrates probably have provided important sources of selection in the evolution of ground-burrowing behavior in this species.

I gratefully acknowledge the help of S. H. Greenlaw, B. A. Greenlaw, and I. Currie in obtaining information on the colonies at Ashland.—Jon S. Greenlaw, *Biology Department, C. W. Post College, Greenvale, New York 11548, 12 April 1972.*

Additional vertebrate prey of the Loggerhead Shrike.—On 4 April 1970 Casto and Dr. R. W. Strandtmann observed an adult Loggerhead Shrike (*Lanius ludovicianus*) flying 20 to 30 feet above the ground carrying a snake in its bill. The pair startled the bird which immediately dropped the dead reptile and flew on to alight on a nearby wire. The snake, a desert massasauga rattlesnake (*Sistrurus catenatus*) measured 0.41 m in total length. After preservation in formalin for over a year, the snake weighed 33 g (probably less than the living weight due to tissue dehydration by the preservative). This would represent a considerable burden for a bird that weighs a maximum of 49 g (Miller, Univ. Calif. Publ. Zool., 38:11–242, 1931). The ability of Loggerhead Shrikes to fly while carrying heavy prey has also been documented by Vaiden (*In* Bent, U.S. Natl. Mus. Bull., 197:142, 1950).

Later examination of the snake demonstrated a puncture wound in the neck and damage to the region behind the postocular scales. Thielcke (Z. Tierpsychol., 13:272–277, 1956) noted that the Northern Shrike (*Lanius excubitor*) always kills its prey with a bite, or series of bites behind the head. The Loggerhead Shrike also punctures prey in the neck region by striking the prey repeatedly with the point of the bill (Wemmer, Z. Tierpsychol., 26:208–224, 1970).

The incident reported herein represents apparently the only record of a shrike killing a poisonous reptile of any species. The snake, collected two miles west of Milnesand, Roosevelt County, New Mexico is deposited in the Herpetology Collection (Specimen 5401), The Museum, Texas Tech University.

A pair of Loggerhead Shrikes removed three Merriam's pocket mice (*Perognathus merriami*), a green treefrog (*Hyla cinera*), and a spring peeper (*H. crucifer*) from a study area one mile south of Riviera, Kleberg County, Texas in August 1966. Pocket mice are nocturnal but are occasionally taken by diurnal predators at dawn or dusk (Beal and McAtee, U.S. Dept. Agr. Farmers' Bull., 506:1–35, 1912). Although Northern Shrikes have captured a similar sized pocket mouse, *P. parvus* (Scheffer, U.S. Dept. Agr. Tech. Bull., 608:1–15, 1938), this is the first record of pocket mice being taken by Loggerhead Shrikes.

The frogs were impaled on a barbed wire fence near a stock tank. Desiccation lessened the food value of the frogs within 2 days, but the shrikes visited and pecked the mummified carcasses for eight months. It is not known how long that shrikes will visit impaled prey (Bent, loc. cit.). *Hyla* has been previously reported in the diet of *L. ludovicianus* but the species was not identified (Miller, 1931).

The observations at Riviera, Texas were made while the senior author was supported by a National Science Foundation grant GY 369 administered by Dr. R. L. Packard, Texas Tech University.—Brian R. Chapman and Stanley D. Casto, *Department of Biology, Texas Tech University, Lubbock, Texas 79409, 13 March 1972.*

Cowbird parasitism of Western Kingbird and Baltimore Oriole nests.—On 9 June 1971, in a farm woodlot in York County, Nebraska, I examined a Western Kingbird (*Tyrannus verticalis*) nest that contained three kingbird eggs and one Brown-headed Cowbird (*Molothrus ater*) egg. The nest was in a Siberian elm (*Ulmus pumila*) approximately 20 feet above ground. The eggs were being incubated.

Subsequent examinations at two day intervals indicated that all of the eggs hatched on approximately 18 June. Examination of the nest was conducted at irregular intervals after 19 June. However, I observed feeding of the young daily until 1 July when the nest was empty. Throughout the entire period the ground in the vicinity below the nest was searched daily. On 19 June a few bits of kingbird egg shell were found. A dead young kingbird was found on 23 June and another on 26 June. It appears that the cowbird and one kingbird were fledged from the nest.

Cowbird parasitism of Western Kingbirds appears to be rare. Friedmann (U.S. Natl. Mus. Bull., 233:49–50, 1963) notes one other instance of its occurrence and that one without precise data.

On 20 June at the same location, I observed a female Baltimore Oriole (*Icterus galbula*) enter her nest which was approximately 25 feet from the ground in a Siberian elm. I was standing a short distance away from immediately under the nest. My attention was directed elsewhere until I heard a soft "plop" on the ground under the nest. Examination showed the source of the noise to be a fresh cowbird egg that was broken. The female oriole was then observed on a twig next to the nest preening. It appears that the oriole removed the cowbird egg from the nest. This might explain the lack of records of cowbird parasitism of Baltimore Orioles as Friedmann (op. cit.:133) suggests.—Thomas S. Smith, *Department of Natural Resources, Nelson Hall, University of Wisconsin, Stevens Point, Wisconsin 54481, 26 March 1972.*

Observations of birds at *Cecropia* trees in Puerto Rico.—The fruits of *Cecropia* trees are a favored food of many tropical birds (Eisenmann, Auk, 78:636–637, 1961), and in fact the seeds of these fruits show an enhanced viability after passing through the alimentary canal of birds (Olson and Blum, Ecology, 49:565–566, 1968). Observations on the avian exploitation of *Cecropia* have been conducted throughout second-growth areas of Central and South America, but there have been no studies from the West Indies. In this note I summarize sightings at *Cecropia* trees in Puerto Rico to compare with my work at mainland trees and to add another perspective of the impact of North American migrants in the Caribbean.

Observations were made in January (17–27) 1970, and January (15–26) 1971, in eastern Puerto Rico at Luquillo National Forest. The ecology of this wet montane area, with almost 200 inches of rain annually, has been extensively reviewed by Odum (A tropical rain forest, 1970). I worked between 2,300 feet elevation near the base of El Yunque to 1,500 feet elevation at the La Mina Visitor's Center. Large *Cecropia peltata* trees were common along cleared areas in the forest, and many individuals were fruiting in both years. A 1971 census in the study area showed 45 in flower, 27 fruiting, and six non-reproducing.

Species account of birds at *Cecropia* trees.—An asterisk is used to identify species actually seen feeding on *Cecropia* fruits.

* Canary-winged Parakeet (*Brotogeris versicolorus*).—This parakeet is an escaped species that is becoming established in the lowlands of Puerto Rico, and recently (1971) expanding in Luquillo Forest. It was relatively tame while feeding on fruits.

Puerto Rican Parrot (*Amazona vittata*).—This endangered endemic regularly perched in *Cecropia* trees, but was never actually observed feeding.

Puerto Rican Lizard Cuckoo (*Saurothera vieilloti*).—A few individuals fed on large insects on the branches. They probably take the common tree lizards (*Anolis* sp.) as well.

Puerto Rican Emerald (*Chlorostilbon maugaeus*).—Several took insects from the underside of leaves.

* Puerto Rican Woodpecker (*Melanerpes portoricensis*).—Woodpeckers fed on fruits, and would sunbathe on the exposed limbs (this is the first report of sunbathing in a tropical woodpecker—Kennedy, Brit. Birds, 62:249–258, 1969).

* Pearly-eyed Thrasher (*Margarops fuscatus*).—Thrashers regularly took fruits and sang from *Cecropia*.

* Red-legged Thrushes (*Mimocichla plumbea*).—The crepuscular thrushes were infrequently observed feeding at the fruits.

* Bananaquit (*Coereba flaveola*).—Bananaquits were abundant at *Cecropia* and frequently fed on fruit and insects.

Black-and-white Warbler (*Mniotilta varia*).—This species was an infrequent insect feeder at the trees.

* Parula Warbler (*Parula americana*).—The Parula was common at *Cecropia* where it fed on fruit and insects.

* Cape May Warbler (*Dendroica tigrina*).—This species was also common and fed on both fruit and insects at the trees. One individual was permanently territorial at a *Cecropia* where it would supplant and chase Bananaquits and Black-throated Blue Warblers (*away* from this tree the Cape May Warbler was subordinate to the Bananaquit and of equal dominance with the other warbler).

* Black-throated Blue Warbler (*Dendroica caerulescens*).—This species was an uncommon fruit feeder at *Cecropia*, and scarce throughout the forest.

* Chestnut-sided Warbler (*Dendroica pensylvanica*).—This rare migrant regularly fed at the catkin fruits. The species has not been previously reported from the Luquillo Forest (Bond, Fifteenth supplement to the check-list of birds of the West Indies, 1956).

* American Redstart (*Setophaga ruticilla*).—The redstart was generally an uncommon fruit feeder at *Cecropia.*

Blue-hooded Euphonia (*Euphonia musica*).—Euphonias were regular about *Cecropia* but I have no definite feeding records. However it is quite probable that they take the fruits like other euphonias in Central America (e.g. *E. fulvicrissa*).

* Stripe-headed Tanager (*Spindalis zena*).—This tanager uses *Cecropia* for exposed song perches and eats quantities of fruit.

* Puerto Rican Tanager (*Neospingus speculiferus*).—This endemic arrives at the trees in small flocks to feed on fruits.

* Puerto Rican Bullfinch (*Loxigilla portoricensis*).—The bullfinch only feed infrequently at the fruits.

* Black-faced Grassquit (*Tiaris bicolor*).—Grassquits rarely fed on fruits, at short trees near clearings.

Diet Summary.—Of the 20 species of birds utilizing *Cecropia* at Luquillo Forest, 14 definitely came for fruit feeding. Three of these frugivores and three additional species were recorded taking insects from the trees. Similar avian exploitation is noted in Central America. At Barro Colorado Island in the Canal Zone I recorded 41 species at *Cecropia* (13 taking fruits, four insectivores, and 24 incidental visitors), over several months (Leck, The seasonal ecology of fruit and nectar eating birds in lower Middle America, Unpubl. Ph.D. thesis, Cornell, 1970). At *Cecropia* trees in Costa Rica, H. Hespenheide (in litt.) and others recorded 21 species of frugivores, one insectivore, and four visitor species.

Birds exploiting the Puerto Rican *Cecropia* included almost all of the common species in Luquillo Forest, while the trees in Central America were visited by only a small part of the total local avifauna. This difference reflects the large number of rare species on the mainland and the more specialized feeding niches of mainland birds, with many species strictly limited to non-fruit diets (e.g. antbirds).

North American Migrants.—Six of the 20 species recorded at Luquillo trees were North American migrants. This is a considerably higher migrant percentage (30 per cent) than noted at the trees in Panama (22 per cent) or in Costa Rica (15 per cent). Such a shift in the proportion of migrants is predictable from a comparison of selected avifaunal lists from the neotropics—the percentage of an area's avifauna that is non-resident dramatically increases in insular situations and with decreasing island size. Percentages of non-residents from sample areas will demonstrate this gradient: Mexico 22 per cent, Canal Zone 26 per cent, Hispaniola 41 per cent, Puerto Rico 44 per cent, Jamaica 48 per cent, St. Croix 48 per cent and San Andres 80 per cent. This change in the percentage of migrants is of course produced by a rapid decline in the number of resident species in insular situations, while there are relatively similar numbers of migrant species throughout. Of considerable interest then is an evaluation of the impact of the migrants at food resources in the West Indies—are they a more important competitive element on islands than on the mainland? I made a comparison of migrant vs. resident exploitation by recording all feeding visits to *Cecropia* in six hours (Table 1). The migrants were responsible for more than 60 per cent of both the insect and the fruit-feeding visits. At fruit trees in Panama migrants accounted for only about 10 per cent of the feeding visits in the lowland and up to 46 per cent in the highlands (Leck, Auk, 89:842–850, 1972). Thus, in Puerto Rico the migrants, again associated with higher eleva-

TABLE 1

COMPARISON OF RESIDENT AND MIGRANT EXPLOITATION OF *CECROPIA* TREES IN LUQUILLO NATIONAL FOREST

(Six hours—January 1971).

	Insect-feeding Visits	Fruit-feeding Visits
Residents		
Canary-winged Parakeet		2 (9%)
Puerto Rican Emerald	1 (6%)	
Puerto Rican Woodpecker		1 (5%)
Bananaquit	5 (30%)	3 (13%)
Puerto Rican Tanager		1 (5%)
Puerto Rican Bullfinch		1 (5%)
Resident Subtotals	6 (36%)	8 (37%)
Migrants		
Parula Warbler	4 (23%)	4 (18%)
Cape May Warbler	7 (41%)	7 (31%)
Black-throated Blue Warbler		1 (5%)
Chestnut-sided Warbler		2 (9%)
Migrant Subtotals	11 (64%)	14 (63%)

tions, are obviously of greater impact than on the mainland. Over 10 years ago Bond (*In*: The warblers of America, 1957) suspected the competitive importance of migrant warblers in the Greater Antilles, but almost no field data were available.

Cecropia *resources.*—In both Central America and the West Indies human activities have greatly increased *Cecropia* populations through the disruption of forested areas. *Cecropia* rapidly invades such disturbed areas and has thus become ubiquitous in most of the neotropics. As an "insect-resource" *Cecropia* are fair on islands, but poor on the mainland where symbiotic ants constantly remove other insects and epiphytes (Janzen, Ecology, 50:147–153, 1969). As a fruit-resource *Cecropia* are important to at least several hundred bird species in the New World, and they are a significant resource for many opportunistic migrants.

During both recent visits to Luquillo Forest I enjoyed the kind hospitality of Drs. Cameron and Kay Kepler, U.S. Forest Service. Their suggestions and added sightings at *Cecropias* were most helpful.—CHARLES F. LECK, *Department of Zoology, Rutgers University, New Brunswick, New Jersey 08903, 7 February 1972.*

ORNITHOLOGICAL NEWS

Your attention is directed to the "Preliminary Call for Papers" for the 1973 meeting appearing on the back cover of this issue. It is absolutely imperative that all applications for a position on the program be in the hands of the Chairman, Dr. Andrew Berger, Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822, before 1 March. Because of Dr. Berger's location it is essential that all correspondence with him be carried out by (domestic) air mail.

The final number of another volume is once again the place to show appreciation to the large number of ornithologists who have aided in the preparation of this volume by refereeing papers, by offering advice, and in countless other ways. Special thanks are due to Treasurer William Klamm for his preparation of the Membership List that accompanied the September issue, and to Emma J. Messerly and John F. Messerly who prepared the index to this volume.

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists. 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 contribution to ornithological knowledge. Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the editor of the *Bulletin* for consideration.

Most of the statements applicable to the Fuertes Awards are also applicable to the Nice Award. However, the Nice Award is limited to amateurs, i.e., those whose research is not associated with their livelihood and is not being done in pursuit of an academic degree.

In some years two Fuertes Awards have been made, in some years one. Amounts have been between $200 and $100. One Nice Award is made annually, in the amount of $100.

Interested persons may write to Val Nolan, Jr., Department of Zoology, Indiana University, Bloomington, Indiana 47401. Completed applications must be received by 15 April 1973. Final decisions will be made by the Council at the annual meeting of the Society, 17–20 May 1973.

RED CROSSBILLS

Little has been done to implement Griscom's suggestion (Proc. Boston Soc. Nat. Hist., 1937) that specimens of Red Crossbill (*Loxia curvirostra*) be preserved from every major flight; but a new study of this unpredictable bird emphasizes this necessity. Any material, including road, net, and window casualties, will be welcome. If whole skins cannot be saved, the heads alone (with bills closed in their natural form, if possible) will be useful—especially if sewed, not too tightly, to the same individual's wing(s) and preferably tail as well. Even skeletons of birds long dead may be very helpful. Please be sure to tag each with the standard data: collector; locality (if this is some distance from the nearest conifers, please so state); date; if found dead, an estimate (from the bird's condition) of how long it had been dead; and its weight, in grams, if fresh.

Kindly submit material for study to the undersigned. It will be returned later, after identification of the subspecies, if you so request. Shipments from outside the United

States should be marked "Scientific specimens. No commercial value." Please give your return address, in all cases.

I would especially prize records of movements of banded crossbills, or measurements of birds banded, accompanied by a sketch of how the measurements were taken, and weights.—ALLAN R. PHILLIPS, *Delaware Museum of Natural History, P.O. Box 3937, Greenville, Delaware 19807.*

Dr. George M. Sutton has been honored by the President of Iceland by the award of the Knight Cross of the Icelandic Order of the Falcon.

On 21 October 1972 the Cornell Laboratory of Ornithology awarded the sixth Arthur A. Allen Award to Allan D. Cruickshank.

Hoyes Lloyd is the latest addition to the roster of 50-year members of the Wilson Society.

Members who know students that are interested in ornithology 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.

The Laboratory of Ornithology at Cornell University is offering a college-level course in ornithology to be undertaken at home. In nine seminars the course gives a substantial background in readable style for the appreciation and enjoyment of birds.

Each seminar has been prepared by one or more eminent ornithologists and profusely illustrated by well-known bird artists and photographers. The course is offered sequentially, with each seminar mailed to the participant for his study and completion before progressing to the next one. Upon his completion of the course, the participant will receive an appropriate certificate.

For further details including the procedures and costs of enrollment, write to the Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850.

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

Request for Specimens. The University of California at Santa Barbara conducts a large scale program in the natural history of terrestrial vertebrates. However, our small collection of specimens severely limits the program. We would like to acquire additional specimens, especially of western North American forms but other forms, even foreign ones, would be desirable. We would welcome the donation of specimens no matter how small the collection and could probably use the specimens more valuably than institutions maintaining large collections. Stephen I. Rothstein, Department of Biological Sciences, University of California, Santa Barbara, California 93106.

ORNITHOLOGICAL LITERATURE

High Arctic, An Expedition to the Unspoiled North. By George Miksch Sutton. Paul S. Eriksson, Inc., New York, N.Y. 1971: 11 × 8½ in., xiv + 119 pp., 11 col. + 17 bl. and wh. pls., $12.95.

In 1969 Dr. Sutton was invited by S. D. MacDonald and David F. Parmelee to accompany a Canadian National Museum expedition to the northern Canadian Arctic Archipelago. This book is the author's very personal account of his part in that expedition illustrated by several of his paintings and sketches, and also by black and white photographs contributed by other members of the party.

The expedition spent most of June on Bathurst Island, and then made a brief tour by chartered aircraft of Western Ellesmere and Meighen islands in an unsuccessful attempt to locate nesting Ivory Gulls. Ironically after the long flight searching for them, Ivory Gulls which proved to be breeding, were observed at Resolute Bay, Cornwallis Island, while the group was waiting for a commercial airline flight back south.

This was Dr. Sutton's 15th trip to arctic regions, but his first to the high arctic, and the experience seems to have inspired him. The eleven color plates in the book include some of the finest work by Sutton that I have seen. He has used water color with lovely effect to capture the feel of wet snow, melt water pools, misty fog, and the mood of night-long twilight, grey skies and sun-saturated fog. The arctic landscape dominates many of the paintings reducing the animal subjects to focal points on the scene. This approach conveys the overwhelming impact that the large openness of high arctic landscapes has on an observer and dramatizes the larger-than-life conspicuousness of any living creature on the northern tundra barrens. Particularly successful are the three King Eiders flying under a band of drizzly grey fog, and above the green of wet fresh sea ice; or the four distant muskoxen casting long shadows across wet snow as they walk; and the seven Black Brant flying along a valley under a luminous grey sky, below the tops of hills where bare patches of earth are just beginning to show. These paintings and several others beautifully capture the feeling of the high arctic tundra in spring and are well worth the price of the book.

I do have a cavil with one painting, however, even allowing for the artist's impressionistic style in these works—the back of a Long-tailed Jaeger is slate gray and not sepia toned.

The text recounts the author's daily experiences and impressions, as well as his observations of birds and mammals. Anecdotes about muskoxen, wolves, arctic hare, and Sanderling are particularly interesting. The style is episodic and reads as if the author has expanded his field notes for presentation. This approach has the advantage of retaining the author's immediate impressions but it has the disadvantage that continuity is poor and that mood and feeling are not created for the reader. This is an instance where less matter and more art would have helped.

Some of the scenes are too short and contribute so little that I wonder why they were included. The account of the Buff-breasted Sandpiper (p. 48–49) is an example. Some of the author's conclusions, i.e. that sparring male Rock Ptarmigan partly open their wings to keep themselves upright (p. 57), are questionable. Another statement, that prostrate arctic willows possibly live for a century (p. 10) is incorrect.

The format of the book is spacious and well designed. The text is confined to part of each page and a few small black-and-white sketches and photographs are tastefully inserted. The photographs are on-the-whole interesting and contribute greatly to the overall impression of the work.

Despite my criticisms I enjoyed this book, and recommend it to anyone wanting a sensitive impression of the far north. The paintings are certainly its outstanding feature and the publisher has, in fact, printed them in a separate portfolio available at $14.95.—William J. Maher.

Birds of the Antarctic and Subantarctic. By G. E. Watson, J. P. Angle, P. C. Harper, M. A. Bridge, R. P. Schlatter, W. L. N. Tickell, J. C. Boyd, and M. M. Boyd. Antarctic Map Folio Series, Folio 14, American Geographical Society, New York, 1971: 11 × 17¼ in., 15 pls. bearing many maps and photos. $10.00. Obtainable from: American Geographical Society, Broadway at 156th St., New York City.

This elaborate and useful atlas is a milestone along the road of antarctic and subantarctic ornithology. George E. Watson, of the United States National Museum, and seven collaborators have explored an enormous oceanic area by personal field observation, as well as by searching the formidable mass of pertinent scientific literature, dating from 1838 to 1968. The authors cite about 125 references to texts covering the relatively narrow scope of their interests, and 713 additional books, journals, and manuscript sources of the data that they record in their tables and charts. An adequately labelled map, keyed to the list of geographic localities, concludes the text of the introductory section. Then follow 14 large charts in south polar projection on which the nesting places of fifty or more taxa of Panantarctic birds are indicated. The final or 15th plate shows photographs of the birds themselves, pictured at breeding sites or in flight in various parts of the "Roaring Forties."

The charts present a clearly organized plan of bird distribution throughout a wide circumpolar belt. The list of breeding places includes every island and all parts of the Antarctic Continent for which information is available, and the latter is related by number to the bibliographic sources. On the charts, moreover, the seas are peppered with symbols that tell whether the record of a species was established by the collection of a specimen or rests on an observation. Complicated clusters of islands, such as those that fringe the Antarctic Peninsula, are commonly enlarged in insert maps near the borders of the circumpolar charts so that islands and symbols can appear in ampler scale. The score or more of isolated insular groups throughout the Panantarctic ocean are not named on the charts, but can readily be identified from the locality map. At any rate, they rapidly become familiar by position alone to anyone who has an interest in their avifauna.

Dr. Watson is responsible for the ten pages of introductory information that precedes the charts. This is accompanied by an ingenious table of distribution of the species of birds and by colored maps of the biotic zones, provinces, and districts that the author recognizes. Other maps show the great divergence, the inner and outer pack ice, and the subantarctic and subtropical convergences that divide the successive surfaces of the ocean between the Antarctic Continent and the surrounding tropical world ocean. The Continent itself embraces 13 million square kilometers, of which less than five per cent is free of permanent ice cover. Furthermore, much of the exposed land is too remote from the sea, the sole source of food, to offer breeding stations for birds which, therefore, are obliged to nest in favorable coastal areas or on the more or less distant antarctic and subantarctic islands.

Of the birds included in this study, 7 are penguins, 7 albatrosses, 27 petrels, 2 cormorants, 2 skuas, 1 gull, and 3 terns (one of which is the Arctic Tern!). The only non-webfooted species are the two sheathbills and the pipit of South Georgia, which is the southernmost native land bird in the world. Watson groups the prions (*Pachyptila*) with the gadfly petrels, whereas this reviewer would include them in the fulmarine section of the Procellariiformes. He errs in inferring that *Daption*, the name of the far-famed Cape Pigeon, should be classed as a Greek neuter. On the contrary, it is a nonsense word, an anagram of the Spanish adjective "pintado," and the name still stands as *Daption capensis.*

Instances of how rapidly knowledge of antarctic birds is being amassed at present show up occasionally in this publication. The recent (1971) appearance of "Marion and Prince Edward Islands" (A. A. Balkema, Cape Town), representing an expedition under South African auspices, is a case in point. In this hefty volume, Professor van Zinderen Bakker, Jr. reports that the South Georgian diving petrel breeds abundantly on both islands, and to higher altitudes (700 m) than any other birds there. Again, Ian Strange has recently reported (Ibis, 110:358, 1968) *Pachyptila turtur* as a resident of Beauchêne Island in the Falklands, but my examination of Strange's specimens shows that they represent, in reality, the first record of a different bird, the fulmar-billed prion (*Pachyptila crassirostris*).

Such matters have just barely escaped notice by the authors of this notable atlas, which summarizes so well the environment of the south polar region and the causes of the varying geographic influences on the distribution of birds. The authors, in their recognition of three special faunal "districts"—in the subantarctic Atlantic, the southern Indian Ocean, and the seas to southward of New Zealand and Australia—are abundantly supported by evidence from the flora and fauna of many groups other than birds. They have produced a major study that may be amended in numerous details but is likely to stand for a long while in its substantive structure.—ROBERT CUSHMAN MURPHY.

BIRDS OF NORTH AMERICA. By Austin L. Rand. Doubleday and Co., Inc., New York, 1971: 6¼ × 9 in., 256 pp., 46 col. photos, 35 bl. and wh. photos, by various photographers. $9.95.

This is a volume in the "Animal Life of North America" series, planned and produced by Chanticleer Press. Following an introduction in which the author presents very well a lot of information in a few succinct sentences on bird anatomy, evolution, migration, molt, etc., the families of North American birds are taken up one by one, with comments and short descriptions of the species in each family.

I am unable to ascertain, however, the niche this book is expected to fill. There is little new for the advanced birder or ornithologist, and it does not seem that it will aid the beginner in learning family characters, or in identifying birds or learning their habits. It is interesting reading, and has many personal touches by the author which I found charming. The section on warblers is handled particularly well. But I found myself wanting more specific details throughout. Even in species descriptions, or hints for identification, it often seems that a key character is lacking. In fact the treatment of species in general is shallow—a reader wanting a little more on breeding habits or description or range than is in the field guides will not find it here. Admittedly this may not be the purpose of the book, but what is the purpose? It is called a "survey in pictures and text of 600 birds."

The color reproduction and quality of the illustrations is very good, with few exceptions. In my copy, at least, the American Goldfinch on page 240 is fuzzy. I have seen the original photograph and it is sharp. The Bald Eagle picture is of a captive, rather disheveled bird. This reviewer always objects to having to hunt for the name of a particular photographer; in this volume all photographic credits are lumped on the last page.

It seems regrettable that in a book of general interest the author makes little or no mention of recent well-documented declines in several species, and avoids all mention of the role played by pesticides and by human interference of various kinds in such declines. It is implied that the Peregrine Falcon still nests throughout the east, and "sometimes even nests on the ledges of skyscrapers." There is no mention of the decline of the Brown Pelican as a nesting bird in part of its range, and the present sharp decrease of the Eastern Bluebird is lightly dismissed as being temporary and due to weather and competition with other hole-nesters—factors which contribute but are not the whole answer.

There are a number of typographical errors, and a few minor errors of fact. "On spring migration the birds (thrushes) are silent; their songs are reserved for their breeding grounds." Certainly Gray-cheeked and Swainson's Thrushes frequently sing in migration. The Yellow Warbler arrives throughout the northeast in early May, not mid- to late May as stated by the author. "The Trumpeter Swan differs from the Whistling Swan in having a black bill. . . ." Both have black bills. On page 10: "within each species range the bird lives only in certain habitats" while on page 59 mention is made of "the great seasonal changes in (diets and) habitats made by a great many migrating birds." Vultures are listed as using large tree roosts—but certainly in the southwest cliff roosts are more common. In other parts of the text, insertion of the word "usually" or "generally" would have made for greater accuracy.

This is an interesting book, an easily-read book, and contains many solid bits of information and charming personal observations, even if it does not add much to ornithological information. It will be read and enjoyed, but probably not often used as a reference. —SALLY HOYT SPOFFORD.

CLASSIFICATION OF THE OVENBIRDS (FURNARIIDAE). By Charles Vaurie. H. F. and G. Witherby Ltd., London, 1971: 8¾ × 5½ in., 46 pp., hard cover. Price not given.

Few bird families are more in need of thorough study, or more difficult for the taxonomist, than the ovenbirds, one of the two large families of the New World antbird-ovenbird assemblage. Members of the Furnariidae fill many niches occupied by oscines in other parts of the world; as predators on non-flying arthropods, they are variously convergent on thrushes, warblers, creepers, nuthatches, and titmice. Past revisers, the most recent of whom were Hellmayr (1927) and Peters (1951), evidently relied on bill shape and general body plan in subdividing the family, defining genera, and creating a linear sequence.

Vaurie now provides a new classification, the result of many months of study, involving thousands of skins. It differs strongly from those of Hellmayr and Peters, especially in the number of genera. Hellmayr recognized 53 furnariid genera and Peters recognized 58; Vaurie has reduced these to 34. There has been little change in the total number of species, however, the respective figures being 209, 221, and 218.

The brief (half-page) introduction notes that the classification was written originally for a few colleagues, and subsequently published in order to make it more widely available and to establish a base of reference for future work. These remarks are followed immediately by the classification (pp. 9–15) which divides the family into subfamilies, genera (with some subgenera), and species. The classification is followed by 35 numbered notes (pp. 16–45) that are apparently intended to explain major changes from previous classifications and to account for missing species. To some extent, the notes do fulfill these functions, but many of Vaurie's mergers and separations must be accepted largely on faith. Note 9 (p. 20), for instance, states in its entirety: "*Synallaxis azarae* and *S. elegantior*, which are currently considered to be conspecific, are apparently two separate polytypic species." Presumably the data supporting this conclusion are to be presented in a subsequent paper. (Or have they already been published? The reader is not told.) Two species seem to have vanished without a trace. One of these, *Xenoctistes mirandae* Snethlage, 1928 (placed in *Syndactyla* by Peters) is probably considered by Vaurie to be a form of *Philydor dimidiatus*, following Hellmayr (in Meise, Proc. Eighth Internatl. Ornithol. Congr.: 150, 1934); the other, *Cranioleuca baroni* Salvin, 1895, has probably been lumped into *Certhiaxis albicapilla*, if Vaurie agrees with the footnote in Hellmayr (1927, p. 117). This agreement is no means certain, for there are many other instances in which Vaurie disagrees with Hellmayr and/or Peters on the affinities of species. The genera *Cranioleuca* and *Certhiaxis* are not considered separable, and the author devotes nearly four pages to a discussion of nesting behavior, pigmentation (the presence of yellow), and number of rectrices, the characters which he feels unite the 19 species.

In reading this work, one cannot avoid the feeling that there must be more to come, that what is left unsaid will be covered in an in-depth review of the family. I have no doubt that this will be the case. In the meantime, evaluation of many of Vaurie's taxonomic conclusions will probably be withheld until they are supported by data and by a discussion of taxonomic characters for this group. One can only guess what Vaurie considers to be good taxonomic characters at the generic and specific levels. He states emphatically that bill shape is of no use, and that the number of rectrices cannot be used to define genera but may be useful in separating species. Although he does not say so directly, Vaurie clearly considers that nest type (sometimes restricted to details of construction) is a good generic character in ovenbirds. Unfortunately, the nests of only a fraction of the species have been described in detail.

It is regrettable that this short, but important work, which must rank as one of the slimmest hard-cover "books" on the ornithological shelf, was not published in a journal or museum bulletin. With only 250 copies printed, it will hardly attain the wide availability that it deserves. We can only hope that it will soon be followed by a more detailed treatment, in which we are provided greater insight into the author's research on this diverse family.—PETER L. AMES.

BIRDS OF THE AFRICAN RAIN FORESTS. Sounds of Nature No. 9. Two 33⅓ rpm records. Recorded by Stuart Keith. Produced by S. Keith and William W. H. Gunn. Federation of Ontario Naturalists (1262 Don Mills Rd., Ontario, Canada) and the American Museum of Natural History. $12.75.

Guaranteed to instill nostalgia in ornithologists who have worked in Africa's great forests, this well-produced pair of records provides a splendid supplement to earlier discs on African birds. This set is perhaps the most useful of those available; it is limited to a single habitat, one in which bird voices are particularly important in field identification. Additionally, these records stress the passerines and certain small non-passerines which are most numerous and which provide most of the voice recognition problems.

A much appreciated feature is the absence of superfluous narration. There are no spoken words except for the announcement by Mr. Keith of each bird's English name (following Mackworth-Praed and Grant). Introduction and comments are properly confined to the jacket, allowing maximum record space for the recordings.

The jacket itself, attractively decorated by a photograph of a Cinnamon-chested Bee-eater by C. Hilary Fry, consists of five sides of "text" (marred only by two or three typographical errors). There is also a map depicting the numerous forest areas given, along with dates of each cut, in the notes pertaining to every recording. Identification of significant background sounds is universal. Comment is brief and informal but interesting and instructive, often drawing attention to such things as possible taxonomic implications of the vocalizations. The records cover 92 bird species, plus 20 more distinguished in the backgrounds of these. Another, not identified, is the Uganda Woodland Warbler (*Seicercus budongoensis*) which gives one readily recognizable song in the Joyful Greenbul recording. Of the main 92 species, eight are duplicated on Myles North's and Donald McChesney's "More Voices of African Birds" records. Some listeners might criticize this overlap but the species involved are typical sylvan birds whose absence from a forest bird production would be inappropriate. (Together with the two Cornell University Laboratory of Ornithology African albums, the present set brings the total of African bird songs available on American records to about 237 species.)

Anyone who has spent time learning tropical forest bird voices will appreciate the effort and time that went into the recordings. Hearing the wierd moan of the Buff-spotted Crake (*Sarothrura elegans*) recalled my first stay in Kenya's Kakamega Forest where this perplexing sound defied identification for so many evenings—as did the song of the Honeyguide Greenbul (*Baeopogon indicator*) which issued from the canopy for days before I could trace it to its author. It is great to have available vocalizations of these and of such rarities as the Green Ibis (*Bostrychia olivacea*) and Green-breasted Pitta (*Pitta reichenowi*).

Of taxonomic interest are the recordings of the coastal and interior forms of *Nicator.* I share Keith's opinion that these two are not conspecific. The voice of *Macrosphenus kretschmeri*—identified from Keith's tapes by the late R. E. Moreau—does indeed suggest that this Longbill is not a pycnonotid. Those who have never heard Archer's Robin-chat will be surprised at the great difference between its voice and that of other *Cossypha* species. A major contribution is presentation of vocalizations from 12 species of greenbuls (*Pycnonotidae*). Of particular value are the songs of three shy forest babblers: *Malacocincla fulvescens*, *M. albipectus*, and *M. pyrrhoptera.* Unfortunately, no recording of *M. rufipennis* is available. In places this bird is sympatric with *fulvescens* and *albipectus* and apparently no one has yet been able to distinguish its song from that of the latter. Both are almost equally numerous in the Kakamega Forest where these recordings were made.

Technically the records certainly are up to modern standards. Nearly all of the individual recordings are very good. Only one (Charinda Apalis) do I consider to be of inferior quality and it is not bad. There is considerable background sound but as Keith states, this adds more "flavor" to records of this type. An African forest should not sound like a recording studio. It is often a noisy place and a visitor's auditory impressions are more vivid than his visual ones. I would enjoy these songs and calls much less if the extraneous sounds had been filtered out.

Along with the decided utilitarian value of these records is considerable aesthetic appeal. Several of the bird species presented here possess exceptional voices—among them the Mountain Yellow Warbler (*Chloropeta similis*), Wattle-eye Flycatcher (*Platysteira cyanea*) and certain of the thrushes. The African Wood Owl recording is, to me, pure auditory delight. Almost all of the vocalizations are pleasing as well as educational. The final band of the second disc reveals a few impressive mammalian voices. Some purists may object to these occupying space that could have been devoted to another four or five birds, but I, at least, have always considered the calls of black-and-white colobus monkeys and wild chimpanzees to be among Africa's most thrilling sounds; I was delighted to find these on the records. Furthermore, the visitor to an African forest surely will want to know what animals are responsible for such noises. (The peculiar bird-like chirping of the copper-tailed monkey, *Cercopithecus nictitans*, would have made an interesting inclusion along with the calls of the other primates.)

Messrs. Keith and Gunn have produced a pair of high quality records which I hope will be the forerunner of more to come. Perhaps eventually we can expect positively identified recordings of *all* the forest greenbul species, or some of the other "problem" groups. The African forests hold much promise for continued work of this sort.—DALE A. ZIMMERMAN.

THE WAYS OF WILDFOWL. REPRODUCTIONS OF ETCHINGS AND PAINTINGS BY RICHARD E. BISHOP. Text by Russ Williams. Edited by Thomas C. Jones. J. G. Ferguson Publishing Co., Chicago, 1971: 10½ × 13½ in., 260 pp., 38 etchings and 64 col. paintings by Bishop, more than 50 marginal sketches by Bob Hines. $24.95.

For many years Bishop paintings have appeared on calendars—each a mixture of marshes or woodlands in fall colors and close-ups of waterfowl, pheasants, and other gamebirds in dramatic action. "Prairie Wings," published in 1947, included many Bishop sketches interpreting flight of ducks, a major contribution from joint studies by author Qweeny and artist Bishop. Their "action shots" revealed many details of flight that are too complicated for the human eye to catch. In his paintings, Bishop has tried to show birds in motion, in take-off and in landing—and he has been fairly successful.

Readers of this book will enjoy many of the color plates, although it is a pity that cropping has left partial birds in some of the pictures. To me, among the most accurate and pleasing paintings are those of Mallards on pages 129 and 136, and those of Pintails on pages 135, 157, and 158. Numerous other pictures, however, show poor action and proportion, as in the Wood Duck hen on page 132, with its too-small tail feathers and most unnatural bend of the body. A similar distortion appears in the four nearest Pintails on page 153. Bishop's upland gamebirds also tend to have too-heavy shoulders. It is unforgivable to label a drake Gadwall as a "Redhead" (p. 48), even though this particular painting is far from good of the Gadwall.

The etchings vary greatly in quality and interest; some have suffered, I suspect, from cropping to fit the page, while offering large images.

Usually the text supports the pictures in a publication of this sort, but alas there is not a word to explain the flight action nor to identify the earlier works from more recent ones. Thus, in fairness to the artist, I venture to say that this collection does not represent the best of his paintings; I doubt that it can be taken as a gallery showing.

A word as to the marginal sketches by Bob Hines: some are fair but many are poor renderings. On page 59, a pair of Ring-necked Ducks are shown with far too skinny necks and a misleading white wingpatch. In the mergansers on page 89, the female has the head and neck pattern of a Common Merganser instead of a Red-breasted. Also, it is confusing to use unlabelled sketches of Mallards alongside text about eiders on pages 82 and 89.

In the introduction, Mr. Williams states that his contribution is "not a scientific work or textbook." He has given popular accounts of the species of waterfowl and certain upland game and marsh species, and to a degree has discussed their "ways." But for his stories he has drawn heavily, and at times not too critically, on other authors. Accounts of species, flyways, etc. were so well presented in "Waterfowl Tomorrow" (U.S. Dept. of Interior, 1964) that an abstract such as this is far less useful. Also, I regret the repetition of numerous myths or assumptions now disproved by competent biologists, such as that "all swans mate for life" or that "when pitching into the water, swans do not usually extend their feet in front as the geese and ducks do. With feet retracted, they glide easily into the water with a belly landing—so gracefully and lightly they barely make a splash." Loons, grebes, and at times of exercise or play, all waterfowl may "skip" on the water, but as a rule swans "skate" on the surface when alighting.

The chapter on attracting upland game and waterfowl greatly oversimplifies this subject. The author forgets aesthetics and beauty in nature when he suggests artificial structures such as "old tractor tires, washtubs, oil drums" to improve nesting conditions! It is especially regrettable that the text fails to explain Bishop's contributions to the understanding of bird flight. Nevertheless all of us can sharpen our knowledge of wildfowl if we really study both text and illustrations.—MILES D. PIRNIE.

THE FORESTS AND WETLANDS OF NEW YORK CITY. By Elizabeth Barlow. Little, Brown & Co., Boston, 1971: 7¼ × 10 in., xxiv + 160 pp., maps, many photos. $8.95.

This book purports to discuss the woodlands and marshy areas of the great metropolis. Although there are chapters on Staten Island, the Jamaica Bay Refuge, and Pelham Bay and Inwood Hill parks, nothing is said about Bronx or Van Cortlandt parks in the Bronx, nor about Alley Pond or Forest parks in Queens. These last four are most certainly well worth treating in detail, and their omission is serious, indeed.

On the other hand, we are given the bizarre history of the lunatic asylum and its inmates on what was once known as Blackwell's Island, now called Welfare Island. Whatever this has to do with "Forests and Wetlands" completely escapes this reviewer. Nor can I visualize the chapter on "The Foundations"—a history of the geological formations of New York City—as having any connection with either the swamps or sylvan tracts of the five boroughs, except in a very indirect way.

The opening chapter, "The Green Breast," is a rambling, historical account of Manhattan Island, chiefly in the Dutch colonial period, and does manage to touch lightly on its green belt of former times. The portions on the four forest and wetland locations are informative and well written, if somewhat chatty.

Many of the black-and-white photographs are good to excellent. The avid birder will recognize the names of Howard Cleaves and Arthur Swoger as well-known wildlife photographers. The maps are adequate, if not outstanding. Altogether, this reviewer found the book light, entertaining reading, but a great disappointment by reason of its incompleteness.—JOHN BULL.

A MANUAL OF WILDLIFE CONSERVATION. Edited by Richard D. Teague. The Wildlife Society, Suite S-176, 3900 Wisconsin Ave., N.W., Washington, D.C., 1971: 8½ × 11 in., x + 206 pp., photos, many drawings by Francis L. Jaques, Ralph Oberg, and Charles W. Schwartz. $5.50.

This is the text of a "Short Course in Game and Fish Management" conducted annually since 1965 at the Colorado State University. As a reviewer, I can happily present an accolade to the editor, to the Wildlife Conservation Manual Committee, chaired by Dwight R. Smith, and to The Wildlife Society.

There has always been a gap between scientists and administrators in our natural resources society. Lack of understanding and lack of appreciation of the one for the other is the rule, and is responsible in part for our dying environment.

This book is a series of about 50 brief articles directed to the administrator, and designed to provide him with the essentials of policy, state and federal objectives, sociology and public values, wildlife and fisheries management techniques, wildlife law, and research. It is an administrator's handbook, but it is a fine adjunct to any course in wildlife management.

There has not been a wiser book on conservation published in the last quarter century. —Oliver H. Hewitt.

PUBLICATION NOTES AND NOTICES

Annual Bird Report for Southern Vancouver Island, 1970. Prepared by the Ornithological Records Committee for Southern Vancouver Island, edited by J. B. Tatum. Victoria Natural History Society, Victoria, B.C., Canada, no date: 5½ × 8¼ in., paperbound, 72 pp., photos, sketches, and map. $1.90. Order from Dr. J. B. Tatum, 416-3187 Shelbourne Street, Victoria, B.C., Canada.

An annotated summary of the records of 235 species seen during 1970 in southeastern Vancouver Island and the adjacent Gulf Islands. The records have been scrutinized by a local experienced committee. Hopefully future reports will be more concise.—P. S.

Birds of Moose Mountain, Saskatchewan. By Robert W. Nero and M. Ross Lein. Special Publication No. 7, Saskatchewan Natural History Society, Regina, Sask., 1971: 5½ × 8½ in., 55 pp., 8 photos, 2 maps, paperbound. $2.00. Order from Saskatchewan Natural History Society, Box 1121, Regina, Sask., Canada.

Moose Mountain is situated in extreme southeastern Saskatchewan. Its avifauna—173 known species—consists of species characteristic of grassland, deciduous forest-edge, deciduous forest, and boreal forest. This well-prepared booklet presents a description of the area, a brief discussion of the avifauna, and species accounts.—P. S.

Catalog of Bird Specimens Southwestern Museum of Natural History. By David M. Niles. New Mexico Ornithological Society, 1963: 6 × 9 in., 36 pp., paperbound. Revised supplement published in mimeographed form, 1968: 8½ × 11 in., 33 pp.

Bird-Finding Localities in Southwestern New Mexico and Southeastern Arizona. By Dale A. Zimmerman. New Mexico Ornithological Society, 1966: 6 × 9 in., 12 pp., 3 maps by Bruce J. Hayward and Mary Huey, paperbound.

Bird-Finding Localities in the Vicinity of Roswell, New Mexico. By Vester A. Montgomery. New Mexico Ornithological Society, 1969: 6 × 9 in., 10 pp., 2 maps by Mary Huey, paperbound.

These publications are available (price not given) from the New Mexico Ornithological Society, P.O. Box 277, Cedar Crest, New Mexico 87008.—P. S.

ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS. Volume 2. Edited by Richard F. Johnston, Peter W. Frank, and Charles D. Michener. Annual Reviews Inc., Palo Alto, Calif., 1971: 6¼ × 9 in., ix + 510 pp. $10.00.

The limits of ecology and systematics spread widely as interpreted by the editors of this volume. Papers deal with economics and human evolution as well as many subjects in the natural sciences. Douglass H. Morse presents a theoretical discussion of The Insectivorous Bird as an Adaptive Strategy and Daniel H. Janzen reviews Seed Predation by Animals.—P.S.

BIRD STUDY. By Andrew J. Berger. Dover Publications, New York, 1971: 5½ × 8½ in., xi + 389 pp., many drawings and photographs, paperbound. $3.95.

An unabridged republication of the work first published in 1961 and reviewed in The Wilson Bulletin, 75:222, 1963.—P. S.

BIRDS OF MARICOPA COUNTY, ARIZONA. ANNOTATED FIELD LIST. Compiled by Salome R. Demaree, Eleanor L. Radke, and Janet L. Witzeman. Maricopa Audubon Society (4619 East Arcadia Lane, Phoenix, Arizona 85018), 1972: 5 × 8 in., 64 pp., one map. $2.95 + $0.25 postage and handling.

A FIELD LIST OF THE BIRDS OF THE DELAWARE VALLEY REGION. By Alan Brady, W. Ronald Logan, John C. Miller, George B. Reynard, and Robert H. Sehl. Delaware Valley Ornithological Club, Academy of Natural Sciences, Philadelphia. 1972: 4 × 7 in.. 39 pp., two maps. No price given.

Regional lists giving the familiar bar graphs indicating dates of occurrence and abundance of the species together with minimal annotations. Both include brief descriptions of good birding areas.—G. A. H.

SUGGESTIONS TO AUTHORS

Manuscripts.—Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced (*especially tables and "literature cited"*), with at least one-inch margins all around, and on one side of good quality white paper. Ribbon copies are preferred but xerographic copies will be accepted if in readable condition. The review process may be hastened if a duplicate copy (carbon or xerographic) is submitted. All pages should be numbered.

Tables.—Tables are expensive to print and authors should consider carefully whether or not a table is really necessary or adds to the paper. Tables should be designed so as to be narrow and deep rather than wide and shallow. Double space all entries in tables, including titles. Do not use vertical rules. Tabulate only such data as are important to the point at hand. Tables should be typed on separate sheets and placed at the end of the MS.

Figures.—All illustrations should be prepared (particularly insofar as the lettering goes) so as to be readable when reduced in size. The final size will usually be 4.5 inches wide. Illustrations larger than 8½ × 11 will not be accepted, and these should be reduced photographically before submitting. Legends for all figures should be typed on a separate sheet. Photographs should be clear, of good contrast, and on glossy paper. Drawings should be in India ink on good drawing board, drafting paper, or blue-lined graph paper. All lettering on drawings should be done with a lettering instrument or the equivalent. Designate the top of each illustration and identify (on the back in soft pencil) with author's name, and figure number. Submit a duplicate or readable xerographic copy of each figure for the use of the reviewer.

Style and Format.—For general matters of style in preparing a scientific article authors should consult the "CBE Style Manual," 3rd Ed., Am. Inst. Biol. Sci., Washington, D.C. 1972. All MSS should be submitted in the general format used in recent issues of the *Bulletin.* Avoid footnotes, and avoid more than two levels of subject subheadings. Except in rare circumstances lead papers should be followed by a summary, not to exceed 10 percent of the length of the paper. Summaries should be informative when standing by themselves. Most units should be given in the metric system, and compound units should be given in one-line form (i.e. cm-sec^{-2}). The continental system of dating (21 March 1972) and the twenty-four hour clock (09:00 and 22:00) should be used.

References.—If more than five papers are cited these should be included in a terminal "Literature Cited" section. Include only such references as are actually cited, and include only material that is available in the open literature ("In-house" technical reports and the like should not be cited). The style of citation can be obtained from recent issues of the *Bulletin.* For abbreviations of periodical names use the list given in "Biological Abstracts List of Serials," Bioscience Information Service, Philadelphia, Pa., 1968. If in doubt, do not abbreviate serial names. All references in "General Notes" and in long papers containing less than five references should be cited internally e.g. (James, Wilson Bull., 83:215–236, 1971) or James (Wilson Bull., 83:215–236, 1971).

Nomenclature.—Common names and technical names of birds should be those given in the 1957 A.O.U. Check-list (and such supplements as may appear) unless justification is given for departing from this list. For bird species in Middle and South America the *Bulletin* uses the common names appearing in Eisenmann, "Species of Middle American Birds," 1955 and Meyer de Schauensee "The Species of Birds of South America," 1966. Common names of birds should be capitalized.

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INDEX TO VOLUME 84, 1972

By Emma J. Messerly and John F. Messerly

This index includes in addition to the names of genera, species, and authors, references to the following topics: aggression, anatomy, banding, behavior, breeding, care of young, communication, conservation, copulation, courtship, clutch size, density, display, distribution, ecology, eggs, food and food habits, genetics, growth and development, habitat, hatching, incubation, measurements, migration, molts and plumages, mortality, nest site, nesting, nesting success, nests, parasitism, pesticides, physiology, populations, predation, recognition, roosting, seasonal distribution, taxonomy, territory, voice and vocalizations, weather, and weights. Also included are references of biological significance to reptiles and mammals. Forms described as new in this volume are given in **boldface.**

This issue of *The Wilson Bulletin* was published on 29 December 1972.

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 84:513, 1972 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, with at least one inch margins, and on one side only of good quality white paper. Tables should be typed on separate sheets, and should be designed to fit the normal page width, i.e., narrow and deep rather than wide and shallow. Before preparing these, carefully consider whether the material is best presented in tabular form. 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 "CBE Style Manual" (1972, 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. Extensive alterations in copy after the type has been set must be charged to the author.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, William A. Klamm, 2140 Lewis Drive, Lakewood, Ohio 44107. He will notify the printer.

The permanent mailing address of the Wilson Ornithological Society is: c/o The MUSEUM of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

PLAN TO ATTEND THE 1973 ANNUAL MEETING

The 1973 meeting of the Wilson Ornithological Society will be held jointly with the Carolina Bird Club on the campus of the oldest state university, The University of North Carolina in Chapel Hill, from Thursday, 17 May through Sunday, 20 May. Chapel Hill is a small university town, with trees along much of the main street. The downtown area, with its many small shops, boutiques, and a variety of restaurants, borders the University. The campus contains many historic buildings, gardens, an art museum, and the finest planetarium in the nation. The nearby county seat, Hillsborough, was founded in 1754, and has a number of homes and public buildings that were built before the Revolution. Duke University, less than ten miles away, has a beautiful chapel and extensive formal gardens. Tours of these and other attractions are being arranged.

Chapel Hill is served by the Raleigh-Durham airport and four airlines provide frequent service from a variety of cities, including direct flights to points as distant as Los Angeles. Passenger trains still run to Raleigh, and Chapel Hill can be reached by bus. Rooms in dormitories and the University-owned hotel will be available for housing.

Chapel Hill lies in the Piedmont, near the edge of the Coastal Plain. The Brown-headed Nuthatch, Blue-gray Gnatcatcher, White-eyed Vireo, Prothonotary, Yellow-throated, Prairie, Kentucky, and Hooded Warblers and other typical southern birds are found in the vicinity. Red-cockaded Woodpeckers nest nearby. A field trip is being planned to the coast where one can expect to see resident two species of ibises, ten species of herons, six species of terns, Black Skimmers, Brown Pelicans, Willets, Wilson's and Piping Plovers, Avocets, stilts, and many other birds. We expect to find considerable numbers of migrating shorebirds, and pelagic species, such as shearwaters, are not unlikely.

The chairman of the local committee is Dr. Helmut C. Mueller, Department of Zoology, Wilson Hall, University of North Carolina, Chapel Hill, N. C. 27514. Detailed information concerning accommodations, transportation, field trips, and tours will be sent to members with advance registration forms.

PRELIMINARY CALL FOR PAPERS

The program chairman is Dr. Andrew J. Berger, Department of Zoology, University of Hawaii, Honolulu, Hawaii 96822. Members who wish to present papers should send the following to the program chairman: (1) title of paper; (2) name and address (institutional affiliation, if any) of author; (3) three copies of an abstract, typed, double-spaced, not to exceed 250 words; (4) amount of time desired; (5) special facilities needed (a blackboard, 2 × 2 (35 mm) and 3¼ × 4 slide projectors will be available for all sessions). **Applications for a place on the program must be in the Program Chairman's hands before 1 March. All correspondence with Dr. Berger should be by (domestic) air mail.**

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