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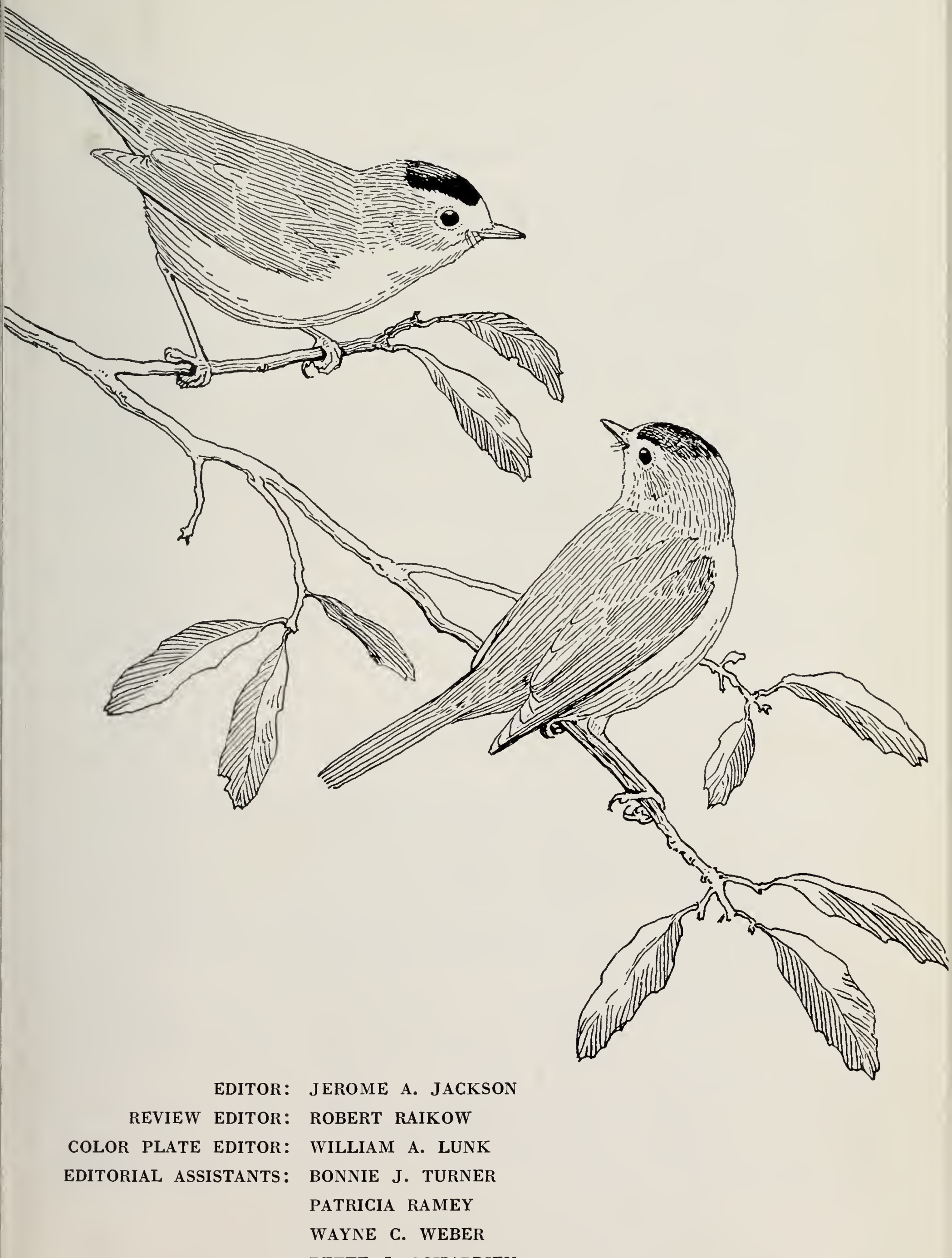

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Monkey-eating Eagle *(Pithecophaga jefferyi)* at Tudaya Falls,
Mt. Apo National Park, Mindanao, Philippines. Painting by John P. O'Neill.

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NOTES ON THE BIOLOGY AND POPULATION STATUS OF THE MONKEY-EATING EAGLE OF THE PHILIPPINES

Robert S. Kennedy

The Monkey-eating Eagle (*Pithecophaga jefferyi*, see Frontispiece) is a huge forest raptor endemic to the Philippines. After its discovery in 1896 on the island of Samar (Ogilvie Grant 1897b), it was considered so rare that nearly every specimen obtained before 1940 prompted a published account. Gonzales (1968) provided the first life history data in his 10-month study of a nesting pair in the province of Davao del Sur, on the island of Mindanao.

Field censuses of this endangered species in 1969 on Mindanao, where the species is most abundant, produced estimates of 40 (Alvarez 1970) and 36 (Gonzales 1971). Rabor (1971) estimated the numbers in 1970 at 50 to 60 birds.

During a study of this species on Mindanao from August 1972 to April 1973, I assisted the Philippine Research, Parks, Range, and Wildlife Division of the Bureau of Forest Development in efforts to conserve this eagle. I collected data on the behavior of wild eagles and on their numbers and distribution. Here I report on my findings and include a summary of the former and present status of the species on other islands where it has been recorded.

STUDY AREA AND METHODS

I studied activities of a pair of Monkey-eating Eagles at Tudaya Falls in Mt. Apo National Park on Mindanao. The area is dissected by a series of deep ravines carved by swift mountain rivers. Elevation ranges from 700 to 1200 m. Because of the close proximity to the equator, the time for sunrise and sunset varied little over the year. A canyon below Tudaya Falls was the primary study area. It was ca. 400 m wide, 100 to 200 m deep, and 2 km long (Fig. 1). On the ridges surrounding the canyon, Bagobo natives have cleared some of the virgin forest (see Fig. 2). I spent 8 full days and 14 one-half days from September to March (153 hours of observation) at 3 lookouts overlooking the canyon, the choice of which depended on the location of the eagles at the time.

With personnel from the Philippine Parks stationed in Davao City and Zamboanga City, I traveled to 10 provinces of Mindanao: Lanao del Norte, Missamis Occidental, Zamboanga del Norte, Zamboanga del Sur, Davao City, Davao del Norte, Davao Oriental,

FIG. 1. View of canyon in the Tudaya Falls study area. Photo taken from Lookout #1 facing the southeast.

Davao del Sur, North Cotabato, and South Cotabato. Coverage was greatest in the last 6 provinces. Records of eagles killed, sighted, or captured since 1970 were collected from local residents and were accepted or rejected on the basis of the information provided. Personnel from logging companies and natives provided the most reports.

Aerial surveys over 12 of the 17 provinces of Mindanao facilitated plotting the distribution of Monkey-eating Eagle habitat on Joint Operation Graphic (AIR) Maps, Series 1501 AIR, 1:250,000, current through 1969. Observations from the ground contributed additional data for habitat plotting. Provinces surveyed by air in their entirety were Davao City, Davao del Sur, Lanao del Sur, and Missamis Occidental. Partially surveyed were Bukidnon, Davao del Norte, Davao Oriental, Lanao del Norte, North Cotabato, South Cotabato, Zamboanga del Norte, and Zamboanga del Sur. For other areas, the extent of the habitat was estimated from the topography and the density of human habitations, as printed on the air maps. Areas of questionable human density were plotted with the 3000 foot contour line as the perimeter of the eagle's habitat. By use of squared graph paper, the area of potential eagle habitat was determined from the air maps. The method does not account for the increase in surface area due to variation in altitude.

BEHAVIOR OF WILD EAGLES

Hunting techniques.—Monkey-eating Eagles hunt both singly and in pairs. I did not see a pair of eagles hunt together, but several natives and loggers

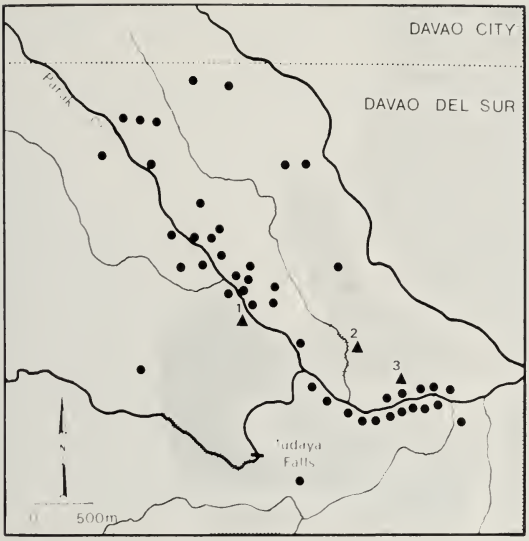

Fig. 2. Map of Tudaya Falls showing the distribution of cleared land (shaded area), forests (unshaded area), sightings of eagles (dots), and lookouts (triangles).

reported that pairs of eagles course through the forest looking for groups of monkeys. An engineer with the Misamis Lumber Co., stated that one eagle would distract the monkey, which would then be captured from behind by the other bird. He reported that, after the kill, the eagle covered the prey with its wings and then gutted and skinned the animal. Gonzales (1968) suggests that eagles are more successful when hunting in pairs than when hunting alone, because of the wariness of monkeys and the defense of the family unit by a lead male.

Thirty of 38 observations at Tudaya Falls, and several elsewhere on Mindanao, were of eagles on the hunt. Though I never observed a complete hunting sequence, because of the bird's sudden appearance and disappearance in the forest, a general 3 part hunting pattern can be reconstructed as follows (Fig. 3):

Part 1—Preparatory Period: On 28 September I watched an eagle perched on the lower branch of a tree above the near-vertical cliffs across the canyon from Lookout #3 (Fig. 2). There it called from 13:00 to 13:30. It then became increasingly alert to the sounds and movements in the canyon below. The usual position of a perched Monkey-eating Eagle is vertical, and, from a distance, the white breast and belly of a bird in this stance closely resemble the light-colored bark of the trunks and main branches of many Philippine

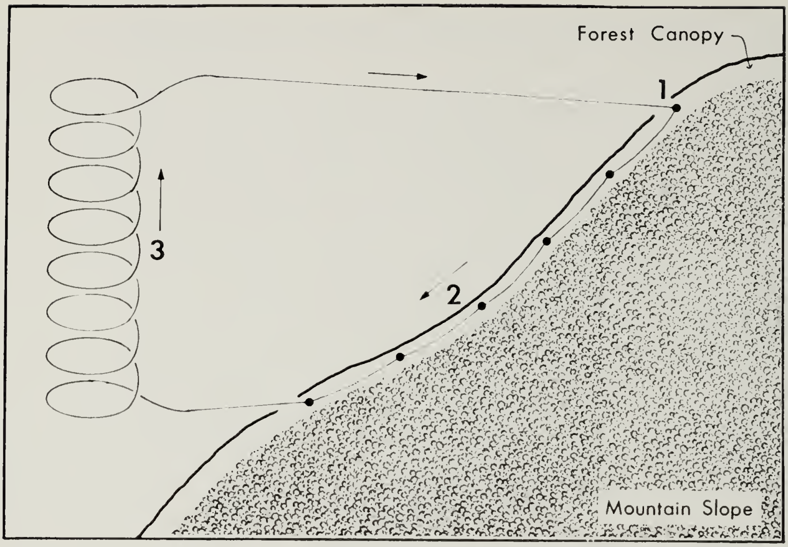

Fig. 3. Schematic representation of a hunting sequence, consisting of three parts: Part 1—a preparatory period; Part 2—the act of hunting within the forest canopy; Part 3—return to a starting point.

trees. This may be a form of cryptic coloration. Because I observed the preparatory period only once, I do not know if the calling activity is characteristic of all hunting sequences.

Part 2—The Act of Hunting: At 13:35, the eagle dropped from its perch and without flapping, glided about 75 m at a downward diagonal, along the canyon wall, to a resting place in a small tree growing out of the canyon wall. Because of the minimal vegetation growth, I could see the bird clearly. It remained there for 5 min surveying the surrounding trees. When the eagle seemingly perceived movements, it would shift its head to the right and left of the body axis, frequently twisting its head upside down. It made 6 more short flights before it disappeared at 14:35. In flights ranging from 75 to 125 m, the bird moved toward the floor of the canyon. The short direct flights from one perch to another usually within the forest canopy (Fig. 3) are the most common hunting technique used by the eagles when they work down a mountain slope or along a heavily forested ridge. I noted one variation from the pattern: on steep slopes, instead of gliding directly to a perch, the eagle would frequently drift out of the forest canopy away from the slope, circle one or more times, and then return to another perch. During these flights, the birds searched the forest around them, apparently for prey or for a suitable perch. J. Hamlet (pers. comm.) described the eagle in pursuit of prey as having direct, flapping flight.

Part 3—Return to a Starting Point: If the eagle failed to capture prey, it would return to a higher elevation to initiate a new hunt. From Lookout #2, on 13 February 1973, I saw a Monkey-eating Eagle perched on the lower branch of a large tree at the forest edge, 400 m west of my position. At 09:45, it left the perch and glided parallel to the canyon, heading south for approximately 500 m, with minimal loss of altitude. Then it began to circle slowly, gaining altitude. When it attained a height of 300 to 450 m above its initial elevation, the eagle glided directly north for 2 to 3 km, disappearing into the forest higher up the mountain at 10:05. This same eagle (which had 2 left primaries missing) reappeared at the forest edge at 13:45 and repeated a similar sequence. I saw 3 eagles elsewhere on Mindanao performing this part of the hunting technique with little deviation from the pattern. Elevations attained varied from 150 to 700 m above the start of the spiral, and the distance glided varied from 400 m to 3 km. Part 1 lasted 35 min, Part 2, 60 min, and Part 3, 20 min.

If one assumes that the eagle used to exemplify Part 3 did not engage in any other activities besides hunting from the time it was first seen at 09:45 to the time it reappeared at 13:45, then this hunting cycle lasted 4 h. In another case, the cycle lasted 2 h 55 min. The times for the 3 hunts average 2 h 56 min.

Figure 4 indicates 2 peak periods in the day when eagles are likely to be seen. During these periods, the birds often emerge from the forest and fly to another location on the mountain, as described earlier. For the morning peak, 8 of 11 and 7 of 8 sightings made at 09:00 and 10:00, respectively, were of eagles ostensibly hunting. In the afternoon, the sightings at 13:00 and 14:00 were of eagles hunting. The peaks for calling (Fig. 4) suggest that vocalizations occur in Part 1 of the hunting cycle.

I observed the result of a successful hunt at Tudaya on the morning of 16 February 1973. While at Lookout #1, I heard an eagle calling at 08:20 from the side of the canyon. It was apparently perched in a tree, and I did not see it until 15 min later, when it stopped calling, flew over the canyon, circled once, then glided 150 m west up Parak Creek and landed in a small tree. I noticed a monkey in the eagle's talons when the bird flew past me. At the perch, the eagle resumed calling but did not mantle the prey or attempt to eat it. At 08:45, the eagle left its perch, glided west about 500 m, and disappeared into the forest. The manner in which it traveled from one resting place to another was similar to Part 2 of the hunting cycle.

Flight.—Brown and Amadon (1968) state that Monkey-eating Eagles "sometimes, but rather rarely, soar over the forest . . . ," and Grossman

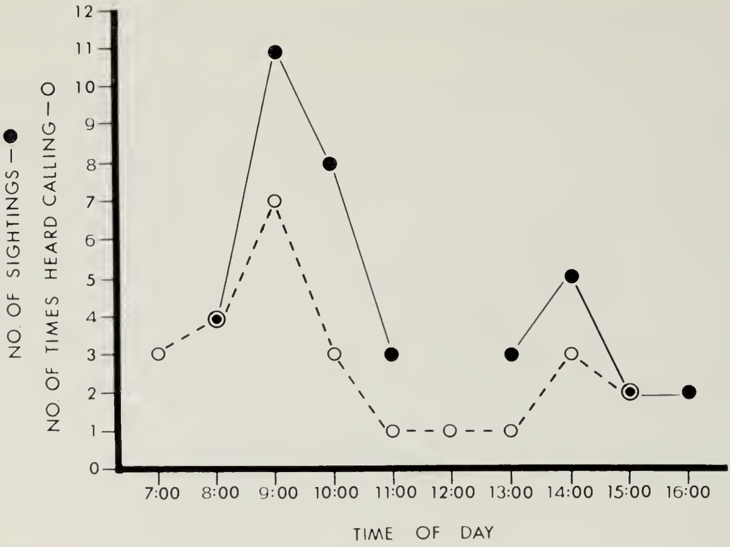

FIG. 4. Plot of time of day when eagles were sighted or were heard calling at the Tudaya Falls study area.

and Hamlet (1964) claim that these eagles have "flapping flight with little soaring." With but 2 exceptions, I never saw eagles flap their wings, and I frequently saw birds soaring, though not for extended periods. In traversing an area, they would either glide in a straight line from a higher to a lower elevation or drift over a mountain slope or canyon, riding thermals and mountain updrafts. The most typical glide occurred when the eagles were hunting, and during it the wings were usually fully extended. Sometimes, when greater speed was required, the wings were folded partially or completely. A gliding or soaring Monkey-eating Eagle holds the wings horizontally.

When riding updrafts, the eagles usually circle, but they occasionally tack back and forth just above a ridge or glide in a straight line at high altitudes. In these situations, the birds usually either maintain or gain altitude. Circling flight exhibits at least 3 forms. During Part 2 of the hunting cycle, when the bird leaves the forest canopy, it may circle one or more times. During these circles, it maintains its altitude but drifts horizontally as it turns. It reenters the forest at about the same elevation as the exit point. Circling also occurs during Part 3 of the hunting cycle (Fig. 3) when the bird gains altitude. Here the eagle leaves the forest and, finding an appropriate updraft, circles slowly without flapping, gaining height all the time. The diameter of the circles I observed varied from 25 to 40 m. At the highest point, the birds either glide directly toward a mountain slope, usually without loss in altitude and always without flapping, or begin a series of short glides and large sweeping circles. This third form is frequently initiated in instances where a bird has gained altitude. Sometimes, a bird drifts from the forest at a higher elevation and glides over the lower slopes, where it begins soaring. The duration of this third type of circling averaged 5 min. Gonzales (1968) once noted 3 eagles soaring together. I saw only 1 or 2 birds at a time, though I received a report (Engineer Rizardo, pers. comm.) that as many as 7 eagles were seen soaring together.

The Monkey-eating Eagle is relatively short-winged and long-tailed. This structural pattern, which has been termed the Goshawk silhouette by Brown and Amadon (1968), is an adaptation of forest-hunting species which require maneuverability and quick bursts of speed to overtake their prey. Birds with this silhouette usually have flapping flight and seldom soar without flapping. Though the eagle is a forest-hunting bird and is capable of quick flapping flight in pursuit of prey, it is also a bird that frequently soars. This soaring ability is, energetically, clearly an adaptive advantage for this species which has a rather large territory.

Vocalizations.—Gonzales (1968), Seth-Smith (1910), and Whitehead (1899), have described the calls of the Monkey-eating Eagle. Whitehead (1899) rendered the call phonetically as "*w-aū waū*," and Gonzales noted it as a long, mellow whistle ending sometimes with a downward inflection but usually with an upward inflection. He stated that the latter call was the one more frequently given by the breeding pair he was studying. When I heard eagles call, the downward inflection was most frequent. A series of 3 to 9 whistles was repeated at intervals ranging from 45 sec to 5 min. The individual whistles lasted 0.5 to 1.5 sec and were uttered at 1 to 2 sec intervals. The number of series varied from 1 to 15.

A possible juvenile bird at Tudaya gave a different call. Calling began in the morning with the typical downward inflection; but as the day progressed, the call changed to a more plaintive whine-whistle, as if the bird was distressed. Each whine-whistle lasted about 2 sec, and a series of these calls was repeated every 45 sec for up to 0.5 h. This type of vocalization resembled that of an eaglet calling after long periods without food as described by Gonzales (1968).

At Tudaya, adult eagles called (1) during Part 1 of the hunting cycle, (2) just after the capture of a prey, and (3) during and immediately after being pursued by Rufous Hornbills (*Buceros hydrocorax*). In the first 2 cases, the call had the typical downward inflection. In the third case, the call consisted of a single whine-whistle repeated every 10 sec. This was unlike the call

Gonzales (1968) described as "short, intense, high-pitched notes" during attacks on eagles by avian enemies.

Interspecific encounters.—The presence of a Monkey-eating Eagle in an area is often revealed by the noisy mobbing of the bird by groups of up to 20 Rufous Hornbills whose raucous call can be heard as much as 2 km away. The eagle tries to avoid the hornbills by flying from perch to perch within the forest. If unsuccessful, it leaves the canopy and begins circling slowly, gaining altitude as in Part 3 of the hunting cycle. The hornbills follow for awhile, but eventually are outdistanced and retire to the forest. I saw such mobbing on 5 occasions. On the average, the incidents lasted 2 to 3 min, but the duration varied from less than 30 sec to just over 15 min. Though I never observed contact, Gonzales (1968) reported that Rufous Hornbills actually strike the eagle's head. He also noted that Writhed-billed Hornbills (*Aceros leucocephalus*) and Large-billed Crows (*Corvus macrorhynchos*) mob eagles. Both these species were numerous at Tudaya, but I saw no interactions between them and eagles. I watched an Oriental Hobby (*Falco severus*) attack a Monkey-eating Eagle as the larger bird flew slowly at about 60 m above a ridge. Three times the falcon stooped, nearly grazing the eagle's head. During the harassment the eagle continued flying normally, but it landed shortly afterwards.

HABITAT AND HOME RANGE

Habitat.—The original habitat of the Monkey-eating Eagle on Mindanao was undoubtedly dipterocarp forest, which comprised 75% of the virgin forest in the Philippines (Whitford 1911). Dipterocarp forests are characteristic of moist plains and extend up mountain slopes to 800 m (Brown and Mathews 1914). Today eagles are mainly confined to the larger mountain masses (Rabor 1971), but at one time they occupied lowland forest down to sea level. A specimen taken in 1954 in Cotabato City at an elevation of ca. 15 m provided evidence for eagles using lowland forests. The highest elevation at which eagles occur is about 2000 m, where their preferred prey becomes scarce. At Tudaya, I saw eagles enter the forest to begin a hunt at about 1700 m.

As land has been cleared for agriculture and for lumber, the lower edges of the forests inhabited by the eagles have been retreating up the sides of mountains. The birds have partially adapted to this change by hunting over cleared land and living in second growth forest. This adaptive ability was first indicated by Whitehead (1899), who stated, "He [the eagle] is well known to the natives as a robber of their poultry and small pigs . . . ," thereby implying that the birds forage near clearings. Gonzales (1968) described the habitat of the pair he studied as follows: "Some of the hills are still clothed with original dipterocarp forest, but others are either naked . . . or covered with coarse cogan grass mixed with shrubs and small trees. The forested hills, however, have not remained virgin for they too have been invaded by the natives as well as logging concessionaires."

At Tudaya, the eagles' territory included cleared farmland, various stages of secondary growth, and virgin forest. The birds mainly confined their activity to virgin forest or advanced secondary growth (Fig. 2). Of the 11 eagles I sighted on Mindanao, 10 were in areas of virgin forest or in mixed virgin and advanced secondary forest.

Occasionally eagles were reported in areas where no typical habitat existed. Most of the reports probably resulted from misidentifications, but one confiscated eagle (LSUMZ 73747) was shot in a cornfield about 10 km from the closest forest. The abnormal occurrence of the bird at this location is possibly attributable to destruction of habitat in its former territory.

Apparently suitable Monkey-eating Eagle habitat on Mindanao in 1973 (Fig. 5a) comprised 29,000 km^2 (without allowing for increased area resulting from elevational differences) or about 30% of the 95,587 km^2 of land area of the island. The alarming rate of forest destruction was reported by Gonzales (1971), quoting the Philippine Free Press for 7 June 1969, which stated that the rate of deforestation in the Philippines at that time was 1 ha every 3 min. This problem is not new, however, for Whitehead (1899) stated: "The forests that are left in Samar are still very vast, especially on the Pacific Coast, but for miles inland those of the western coast have been destroyed, leaving ranges of low undulating clay hills chiefly covered with lalang grass. When this country has been passed, the traveler finds himself at an elevation of nearly 1,000 feet and meets with the true virgin forest of Samar. This forest is becoming annually smaller owing to the cultivation of hemp . . . ."

Land clearing has confined suitable habitat on Mindanao to the mountain ranges, but even there the trees have been removed up to at least 500 m in most cases, and sometimes to as high as 1586 m (Gonzales 1971).

Nine eagles I sighted on Mindanao were associated with steep mountain slopes that formed the sides of deep ravines, canyons, or valleys. Data collected on the hunting and soaring behavior of the eagle indicate that it is well adapted to such topography, thus I believe that steep mountains are important in the eagle's habitat.

Home range.—Rabor (1968) believes that a pair of Monkey-eating Eagles have a home range comprising from 40 to 50 km^2. Gonzales (1968, 1971) says that the range can be as large as 100 km^2. Grossman and Hamlet report a smaller range, 31 to 34 km^2.

To determine the area used by the pair at Tudaya, I have drawn upon my own observations and those of Parks personnel as well as verbal reports by

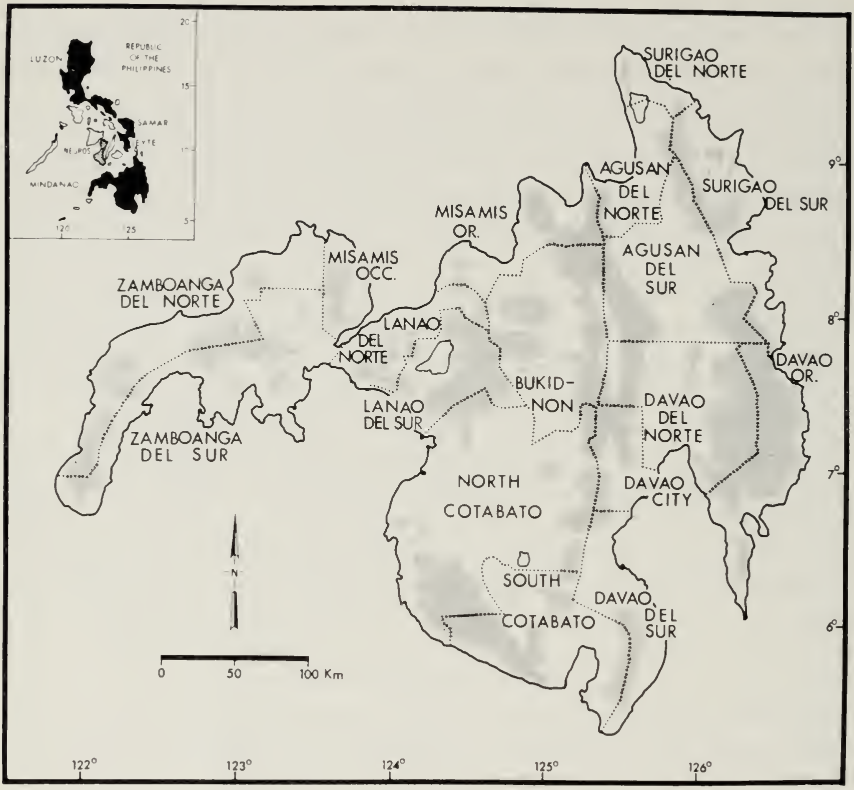

FIG. 5. a. Distribution of the remaining habitat for the Monkey-eating Eagle on Mindanao. b. (Insert) The Philippine Islands, showing the islands where the species has been positively recorded (colored black) and where it was believed present (shaded area).

the natives living there. Bagobo natives said that the eagles mainly confined their activities to the Tudaya canyon, Parak Creek, and the adjacent ridges and that they were rarely seen elsewhere in the area. Parks personnel first sighted the eagles at Tudaya on 8 April 1972. They found the birds to be restricted to the Tudaya Falls area also. My own observations (Fig. 2) confirm these reports. I saw eagles on 7 of 8 full days and 10 of 14 half days of surveillance. Clearly, the vicinity around Tudaya Falls has been a center of the eagles' activity for several years.

I calculated the area of the home range of this pair by 2 methods. Connecting the outermost points where eagles were sighted (shown in Fig. 2) forms a polygon with an area of 6.34 km^2, the minimum home range. A second method was to determine the range by measuring the greatest distance between sightings. If this length is considered the diameter of a circular home range, the area would be 12.5 km^2. Since the range was measured as horizontal surface area and does not account for the increased surface resulting from elevational differences, the total area would be greater, perhaps twice as much. The adjusted home range would then be 12.68 km^2 (polygon method) to 25.0 km^2 (circular method). These figures suggest that the area necessary to support a pair of eagles may not be as great as formerly believed.

DISTRIBUTION AND STATUS

The Monkey-eating Eagle is known from accounts in the literature to occur on 4 of the larger islands in the Philippines: Luzon, Samar, Leyte, and Mindanao (Fig. 5b). John Hamlet, while visiting the island of Negros in 1945–1946, received a photograph of a Monkey-eating Eagle allegedly captured on that island. He personally sighted 2 birds soaring over a small island in the Surigao Straits, just north of the province of Surigao del Norte on Mindanao. These reports of eagles from additional islands suggest that the species was probaby more widely distributed in the recent past. An account of the present and former status of the eagle on the islands from which specimens have been taken follows.

Luzon.—Earlier records of Monkey-eating Eagles from Luzon were frequently reported in the literature and chronologically follow: 1 killed near the Agus River in Rizal Province on 11 May 1907, the first specimen positively known from Luzon (McGregor 1907); 2 sighted near Montalban, Rizal Province on 13 August 1907 by W. P. Lowe (Seth-Smith 1910); 1 captured on Mt. Ballong, south of Imugan, Nueva Vizcaya Province in January 1917 (McGregor 1918); 1 captured near Pagbilao, Tayabas Province in July 1926 (McGregor 1927); 1 taken from Albay Province (Davidson 1934).

More recent data on the status of the eagle on Luzon were gathered by Rabor (1971) during collecting trips in 1959, 1960, and 1961. In the Cordillera and Ilocos mountain ranges in northwest Luzon, he received reports that eagles were last seen in the late 1930's. However, in the Sierra Madre Mountain Range in northeastern Luzon, including the provinces of Cagayan, Isabela, Nueva Vizcaya, and Quezon, the eagles were still being sighted by natives as late as 1960. A specimen captured by personnel from the Philippine Parks in the Isabela–Nueva Vizcaya territory in 1963 is the last known record from this island (Gonzales 1968).

Samar.—The type of the Monkey-eating Eagle was taken on this island by one of Whitehead's collectors in 1896 (Ogilvie Grant 1897a). Davidson (1934) cites one other record of the species on Samar; and Rabor (1971), on the basis of the absence of verbal reports in the 20 years prior to his collecting trip in the north central mountains in 1957, considers the bird extinct on Samar. There are no recent data to confirm or refute this supposition.

Leyte.—For a long time, the only indication that the Monkey-eating Eagle occurred on Leyte was provided by Ogilvie Grant (1897a), who mentioned that J. Whitehead had heard the call of the eagle on this island. Recently, personnel from the Philippine Parks learned of the following records in the province of Southern Leyte: eagles reported sighted in 1951, 1963, and 1968; nest site with young observed in 1969; and 2 eagles killed in 1965 (S. E. Macanas, Regional Director of the Parks. pers. comm.). Macanas and others sighted the bird in Southern Leyte on 21 November 1970, and he estimated the number remaining there to be 8 to 10.

Mindanao, early population data.—There are many reports in the literature (Clemens 1907; Davidson 1934; McGregor 1907, 1921; Mearns 1905; Seth-Smith 1910) of specimens of the Monkey-eating Eagle acquired throughout Mindanao in the early part of this century, and apparently the first record came from 1 taken near Davao City on 3 September 1904 (Mearns 1905). Published population reports are lacking for the first 6 decades of its known existence on the island. However, Hamlet, who worked on Mindanao from 1945 to 1946, has informed me that the eagle was not uncommon there, since he located several active nests and knew of many other pairs.

In a recent report, Gonzales (1971) attempted to estimate the population of Monkey-eating Eagles on Mindanao in 1910, when the forests still covered 65% of the island. Assuming a home range of 100 km^2 and the use of all the available habitat, he calculated that at least 600 pairs existed on Mindanao in 1910.

Mindanao, recent population data.—According to the 3 surveys mentioned earlier, the population on Mindanao in 1969 and 1970 was between 36 and 60 birds. Careful examination of each report reveals discrepancies among the estimates. In 9 of 17 provinces, the authors agreed on the presence or absence of the eagles; and in 5 of the 9, the estimates were the same. However, Rabor (1971) reported the eagle in 4 provinces where neither of the other investigators did. Also, in 4 provinces, 2 of the authors were in agreement as to the eagle's presence, but the third considered it to be absent. A striking area of such disagreement is the province of North Cotabato. There, Alvarez (1970) recorded 11 birds, Rabor (1971) 8, and Gonzales (1971) none.

In Table 1, I have combined the population data of the 3 workers, and without duplicating records collected from specific locations, derived a population size of 70 birds. This number is 16.6% greater than the highest total and thus clearly shows their estimates to be low. Reasons for their low figures are that they counted only birds that they saw or that were reported to them,

TABLE 1

SUMMARY OF MONKEY-EATING EAGLE POPULATION DATA ON MINDANAO

	Published Population Accounts				Present Study January 1970–April 1973					
	1[a] 1969	2 1969	3 1970	1–3 Combined[b]	Habitat Remaining (km²)	No. of Breeding Pairs Calculated	No. Actually Sighted[c]	No. Reported Sighted	No. Known or Reported Shot	No. Known or Reported Captured
Agusan del Norte	–	–	–	–	900	9	–	–	–	–
Agusan del Sur	–	–	2	2	3200	32	–	–	(1)	–
Bukidnon	3	3	2	3	2900	29	–	2	1	–
Davao City	–	–	–	–	900	9	(1)	(3)	–	–
Davao del Norte	2	2	–	2	2800	28	(4)	2(4)	(1)	(2)
								6		
Davao Oriental	2	–	2	4	2800	28	5(10)	9(15)	1(5)	1(3)
							12	24	6	4
Davao del Sur	9	3	4	11	800	8	3(5)	8(1)	1	(2)
							5	9		
North Cotabato	11	–	8	11	3700	37	3(6)	6	5(2)	3
							6		7	
South Cotabato	4	4	4	6	2100	21	–	6	1	2
Lanao del Norte	2	2	2	2	700	7	–	2	–	–
Lanao del Sur	–	–	6	6	1800	18	–	–	–	–
Misamis Occidental	2	2	8	8	400	4	–	6	–	2
Misamis Oriental	–	–	2	2	900	9	–	–	–	–

TABLE 1—*Continued*

	Published Population Accounts				Present Study January 1970–April 1973					
	1[a] 1969	2 1969	3 1970	1–3 Combined[b]	Habitat Remaining (km²)	No. of Breeding Pairs Calculated	No. Actually Sighted[c]	No. Reported Sighted	No. Known or Reported Shot	No. Known or Reported Captured
Surigao del Norte	–	–	–	–	300	3	–	–	–	–
Surigao del Sur	3	–	2	3	1600	16	–	–	–	–
Zamboanga del Norte	–	–	2	2	1800	18	–	8	1	1
Zamboanga del Sur	2	2	6	8	1400	14	(1)	2	–	–
Total	40	18 36[d]	50	70	29000	290	11(27) 29	51(23) 74	10(9) 19	9(7) 16

[a] Published population accounts by 1, Alvarez (1970); 2, Gonzales (1971); 3, Rabor (1971).

[b] Nonrepetitive combined data.

[c] First numbers are data I collected. Numbers in parentheses are data collected by personnel from the Philippine Research, Parks, Range, and Wildlife Division of the Bureau of Forest Development. These unpublished data are subject to revision. Underscored numbers equal the combined total.

[d] Gonzales (1971) considered the population size to be twice the total records he collected; thus 2 × 18 = 36.

they did not survey all the habitat available to the eagles, and they did not extrapolate their findings to include all the habitat.

Mindanao, present population data.—To determine a reasonably accurate population estimate of the Monkey-eating Eagle on Mindanao during the period January 1970 to April 1973, I used 3 censusing methods. Though each method differed slightly, all used the following formula to derive the total population size:

$$\hat{T} = (N/n)\, t$$

where $\hat{T}$ = total population size; t = sample total; N = area of total habitat remaining on Mindanao; and n = area of habitat censused.

Similar to the one Gonzales (1971) used to estimate population size for 1910, the first method involved determination of the extent of the eagle's habitat remaining on Mindanao. The amount remaining (N_1) was found to be approximately 29,000 km^2 (see Fig. 5a and Table 1). Using the maximum home range size of 100 km^2 (n_1) for one pair ($t_1 = 2$), the total population estimate ($\hat{T}_1$) equals 580 birds.

A second method involved sampling an area of known size. The Mt. Apo range, west of Davao City proper, was chosen as the site for this study. The amount of suitable habitat in this area was found to be approximately 640 km^2 (n_2). Nine eagles were sighted in this area (t_2), but as it was physically impossible to cover the whole mountain range, there were probably more. Since the area of total habitat remains the same, $N_1 = N_2 = 29{,}000$ km^2, the total population estimate ($\hat{T}_2$) is 408 birds.

A third method entailed the visitation of as many areas as possible, collecting reports of eagles sighted, captured, or killed, and confirming as many reports as possible. The results of this method are shown in Table 1. The combined totals were: number actually sighted by official investigators, 29; number known or reported captured, 16; number known or reported shot, 19; and number of additional eagles reported to the investigators, 74. These data were obtained from 12 of the 17 provinces of Mindanao, but only 6 provinces (Davao City, Davao del Norte, Davao Oriental, Davao del Sur, North Cotabato, and South Cotabato) were visited regularly, but none was completely surveyed. A rough estimate of the area covered by this method would be 1/3 of the total habitat on the island; thus $n_3 = 1/3\ N_1$. Excluding the numbers shot or captured, the total known population in the wild on Mindanao (t_3) was 103 birds (number actually sighted plus number reported sighted) during the period of investigation. This gives a $\hat{T}_3$ of 309 birds.

Implicit in these censusing methods are the following assumptions: (1) all the habitat is used by eagles; (2) all the birds in areas sampled were known;

(3) each pair of birds occupies a fixed range; (4) results found in one area are applicable to other areas not sampled; (5) population is stable; (6) ranges did not overlap.

The degree of variance among the different methods results from not meeting these assumptions entirely, because of insufficient data and the difficulties of censusing. But these techniques do provide a reasonable range (309 to 580) in which the number of surviving eagles probably lies.

Mortality should be considered in connection with these estimates since evidence indicates that the population is decreasing. No data are available regarding natural causes of mortality, such as disease and predation, but something is known about 2 unnatural factors. These are: (1) loss of habitat (discussed earlier in this paper); and (2) the shooting and capturing of wild birds.

During the course of this study, 35 eagles were known to have been taken from the wild either by being captured or shot (see Table 1). Since the duration of the entire study was 40 months, the average number of birds known to have been lost from the population was 0.87 birds per month or 10.4 birds per year. As previously mentioned, these data were collected from about 1/3 of the available habitat. Thus, the estimated number removed from the population is an average of 31.2 per year. This calculation introduces still another assumption, that each eagle, regardless of the degree of its isolation, has an equal chance of being captured or shot.

The importance of this unnatural mortality depends greatly upon the size and annual recruitment rate of the population. If the population does lie within the limits suggested by the census methods above, i.e., 309 to 580 birds, then the mortality rate would be from 10.1 to 5.4%.

With high reproductive success and a great percentage of young surviving to adulthood, the 5.4% and possibly the 10.1% mortality could be absorbed on an annual basis. However, few data are available concerning the reproductive biology of these birds. Grossman and Hamlet (1964) summarized what was known in 1964. "Although as a rule only one eaglet seems to survive in each nest, there may be two eggs, and occasionally (in at least one known instance) two young birds. The adults at several nest sites have produced young every year." Gonzales (1968) found that the pair he studied produced 1 egg and that 1 eaglet per nesting reached fledging age for 2 consecutive attempts. Rabor (1968) also feels that the eagles breed every year. We do not know the age at which these eagles attain sexual maturity nor do we know the proportion of fledglings that survive to that age.

The age of the individuals captured or killed also influences the importance of the unnatural mortality. If all were birds successfully breeding for the first time, the loss would be extremely damaging, as at the 10.1% level it would nearly eliminate this, the most valuable age class. Since the ages of the birds that were captured or shot are not known in all cases, the effect of their loss from the population cannot be determined.

Population ecologists generally agree that a pair of a species requires and usually defends a certain semi-fixed area or territory. From this premise, it follows that the number of individuals a system can support is directly proportional to the available habitat. On Mindanao, the habitat is being destroyed by logging and other land clearing practices to such a degree that many birds are forced to leave their former range and search out new suitable habitat. I believe that a good percentage of the individuals that are captured or shot are birds whose habitat has been destroyed and that have become "surplus." Thus, presumably, even if they had not been captured or shot, they would not have contributed significantly again to the continuation of the species, unless they were able to establish a new territory in an unoccupied area.

The population surveys conducted have, in the main, shown that the eagles are rather evenly distributed over Mindanao. In some cases, especially parts of Davao del Norte, Davao Oriental, and North Cotabato, the eagles were as common in 1973 in the remaining habitat as they probably had ever been.

CONCLUSIONS AND RECOMMENDATIONS

The total range of the Monkey-eating Eagle has been greatly reduced during the time in which the species has been known. The reduction has been caused by the loss of the eagle's habitat, and, since the population varies directly with the amount of habitat, it has suffered also. In this paper, I have brought up-to-date most of what is known concerning this species, knowledge that is still extremely patchy. Though the population is larger than formerly believed, the census techniques used are based on a modest amount of data, and thus the resulting figure should be considered only a rough estimate. Since the third census included data from about 1/3 of the remaining habitat and was the most extensive survey, I am inclined to regard it as the most accurate. However, no census technique is entirely dependable, especially one based on extrapolation. Taking everything into account, I feel that the population on Mindanao during the period of investigation was about 300 ± 100. The total number of individuals of the species is unknown, as little population work has been conducted on the other islands where it exists or could exist.

Alvarez (1970), Gonzales (1971), and Rabor (1968) have listed the following as the principal reasons for the eagles' decline: (1) the loss of the eagle's habitat by logging and agricultural practices; (2) shooting the eagles for trophies; and (3) capturing the eagles for private and public display. In addition, Gonzales (1971) and Rabor (1968, 1971) have presented excellent recommendations for the conservation of the eagle. Though all their recommendations are sound, the 2 that I feel most important are:

1. Educational programs on the conservation of the natural resources in the Philippines, including wildlife.
2. The establishment of Wildlife Sanctuaries and the protection of lands from illegal logging and agricultural practices.

Though shooting and capturing of the eagle certainly contribute to the population decrease, I feel that the primary reason for its decline is the loss of habitat, and therefore, base my recommendations for the conservation of the species on maintenance of its natural environment, as follows:

1. The establishment of preserves in mountain ranges where logging and agricultural practices are not economically feasible. The size of these preserves should be at least 200 km^2, in order to encompass enough land for several pairs of birds.
2. For areas used as commercial forests, I suggest that the minimum interval between selective logging be 30 years, to allow regeneration of the *native* forest.
3. When areas are reforested, I recommend that a diversity of *native*, Philippine species be planted, thereby recreating as closely as possible, the natural state of the forest.

The destruction of forests in the Philippines is the result of broad social-economic problems that need not be described here. However, if the above minimal recommendations are heeded, they should eventually prevent any further decline in this rare endemic.

SUMMARY

A study of the Monkey-eating Eagle was conducted on the island of Mindanao, Republic of Philippines, from August 1972 to April 1973, in conjunction with the Philippine Research, Parks, Range, and Wildlife Division of the Bureau of Forest Development. Information on the hunting techniques, flight, calls, interspecific encounters, territory size, habitat, and population status are presented.

Though the eagles at one time occupied mature forests from sea level to 2000 m, the forests have been destroyed at lower elevations and thus suitable habitat and the eagles are primarily confined to the mountains. The size of the home range of a pair may range from 12 to 100 km^2.

The eagles are known to have occurred on Luzon, Samar, possibly on Negros, on a small island in the Surigao Straits north of Mindanao, on Leyte, and on Mindanao. Except for Leyte and Mindanao, no recent population data are available. An eagle was sighted on Leyte in 1970 and an estimated 8 to 10 birds were thought present at that time on the southern half of that island. On Mindanao, the combined data collected by the author and by personnel from the Philippine Parks from June 1970 to April 1973 suggest that earlier population estimates of 36 to 60 for 1969 and 1970 were low, and that the population size for the period 1970 to 1973 was about 300 ± 100.

The species is declining annually because of destruction of its habitat. Recommendations to prevent further decline are presented.

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NEW LIFE MEMBER

Robert S. Kennedy is a new life member of the Wilson Ornithological Society. He is presently completing his doctoral work at Louisiana State University. His research interests include studies of several species of raptors, including the Monkey-eating Eagle of the Philippines. Other studies deal with avian population dynamics. Mr. Kennedy has had extensive field experience in the Philippines and in North and South America. In addition to his research interests, Mr. Kennedy enjoys traveling, and collecting and marketing wildlife art.

COWBIRD PARASITISM AND EGG RECOGNITION OF THE NORTHERN ORIOLE

Stephen I. Rothstein

Little information exists on host-parasite interactions between the Northern Oriole (*Icterus galbula*) and the parasitic Brown-headed Cowbird (*Molothrus ater*) (Friedmann 1963) even though both species are abundant and broadly sympatric. The small number of nests known to have been parasitized is not due to a scarcity of observations on oriole nests; e.g., parasitism was observed at only 8 (2.5%) of 318 oriole nests in Ontario (Peck 1974). Alternative explanations can account for the scarcity of observed parasitism: (1) Northern Orioles typically accept cowbird eggs but are rarely parasitized; or (2) Northern Orioles typically eject cowbird eggs causing a large proportion of cowbird eggs to disappear before observers see them. Under the first explanation, the frequency of observed parasitism would equal the frequency of actual parasitism. But under the second, incidences of observed parasitism would always be less than incidences of actual parasitism and orioles might be frequently parasitized even though parasitism is rarely seen.

If orioles typically eject cowbird eggs, the cases of natural parasitism most likely to be seen would be those rare ones in which parasitic eggs are accepted. Thus observations of natural parasitism do not give reliable data on the frequency with which birds eject cowbird eggs. Reliable data on ejection can be derived by experimentally placing cowbird eggs into nests because the experimenter can determine the fate of all the cowbird eggs within a sample. In 1968 I placed an artificial cowbird egg in a Northern Oriole nest. The egg was ejected within 24 h. This was one of a series of experiments on many species. These experiments demonstrated little intraspecific variation in response to experimental cowbird parasitism (Rothstein 1975a, 1975b). Thus species were easily divided into 2 discrete groups—accepters and rejecters. Based on the 1 experiment and on several reports of ejections of naturally deposited cowbird eggs (Friedmann 1963, Smith 1972), I tentatively designated the Northern Oriole as a rejecter species. New experiments on 27 additional nests reported here demonstrate that this designation was correct. Experiments on 2 nests also deal with behavioral mechanisms responsible for the oriole's egg recognition.

MATERIALS AND METHODS

Artificial eggs.—Artificial cowbird eggs (Fig. 1) made of plaster of Paris were used in most experiments. These eggs are identical to ones described elsewhere (Rothstein 1975a, 1975c) except that eggs used in nests whose number begins with "74-" or "75-"

FIG. 1. Egg Types Mentioned in Text. Top row: 2 cowbird eggs; an artificial cowbird egg; 2 artificial cowbird eggs damaged by orioles (The surface of the artificial egg on the left has been blackened so as to better reveal the peck marks. The most heavily damaged area of the egg on the right is within the black lines.). Bottom row: House Sparrow egg after being ejected from nest 75-81; 2 Northern Oriole eggs; Red-winged Blackbird egg; Loggerhead Shrike egg from same clutch as eggs placed in nest 74-86.

were coated with a clear acrylic polymer gloss medium, not with shellac. Controls performed on other species show birds do not reject these eggs because they are artificial (Rothstein 1975a, 1975c). I performed controls on orioles by experimentally parasitizing nests with a real cowbird egg or with real House Sparrow (*Passer domesticus*) eggs. The latter simulate cowbird eggs in color and size (Fig. 1, see data in Bent 1958).

Experimental procedures.—During a single visit to each nest, one "parasite" egg was added and one "host" (oriole) egg was removed. I experimentally parasitized most nests between 12:00 and 18:30. Elsewhere (Rothstein 1975a) I discussed differences between my procedures and those usually employed by cowbirds; but these differences have no detectable influence on the incidence of rejection. Experimentally parasitized nests were usually checked within 24 ± 2 h. If an experimental egg was not ejected I left it in the nest for at least 7 days except at nest 73-01 where nest checks ceased after 3 days.

Nest stage.—Most naturally parasitized nests receive cowbird eggs during the host's laying period (Friedmann 1963). The question of whether there is a correlation between host response and nest stage can be answered by parasitizing nests throughout the cycle. I divided nests into 3 stages. Those known to be parasitized on or before the day

TABLE 1

NORTHERN ORIOLE NESTS SUBJECTED TO EXPERIMENTS SIMULATING COWBIRD PARASITISM

Nest Number	Experimental Egg Type	Clutch Size[a]	Date Nest Parasitized	No. of Eggs Present When Parasitized	Nest Stage When Parasitized	Type of Rejection	Days For Rejection	Oriole Eggs Missing (M) or Damaged (D)
68-220	A	≥ 6	May 27	5	L	E	0–1	None
74-88	A	≥ 5	May 6	2	L	E	0–7	None
75-101	A	≥ 5	May 19	5	L	D	0–1	4M
75-112	A	≥ 4	May 22	2	L	D	0–1	None
75-123	A	≥ 3	May 29	2	L	D	0–1	None
73-33	A	≥ 5	May 10	5	L-I	D	0–1	4M
74-79	A	≥ 6	May 6	6	L-I	E	0–7	None
74-86	A	≥ 5	May 6	5	L-I	D	0–7	None
74-94	A	≥ 4	May 13	4	L-I	E	0–1	1M, 1D
75-105	A	4	May 20	4	L-I	D	0–1	3M
72-01	A	≥ 3	June 14	3	I	D	0–1	2M, 1D
74-81	A	6	May 6	6	I	D	0–7	2M
74-93	A	5	May 13	5	I	D	0–1	4D
74-96	A	5	May 13	5	I	D	0–1	3M
74-97	A	4	May 13	4	I	D	1–7	1D
75-107	A	≥ 2	May 21	2	I	D	0–1	1M
75-108	A	5	May 21	5	I	D	0–1	None
73-01	A	4	June 10	4	?	D	0–3	2D
75-81	HS	≥ 5	May 10	5	L-I	E	0–1	None
75-88	HS	5	May 11	5	L-I	E	0–1	None
75-84	HS	5	May 11	5	I	E	0–1	1M
75-103	HS	4	May 20	4	I	E	0–1	None
75-109	CB	5	May 21	5	L-I	E	0–1	None

Note: Prefixes of nest numbers equal year in which experiment was conducted. A = artificial cowbird egg; HS = House Sparrow egg; CB = real cowbird egg; E = egg ejected; D = egg damaged and left in nest.

[a] Additional eggs could have been laid in nests where "⩾" precedes clutch size. Uncertainties exist for various reasons, e.g. visits to one nest ceased before it was certain that egg laying was completed (68-220). At other nests parasitized during the laying stage, egg disappearance may have been impossible to detect because eggs lost could have been replaced by eggs laid between nest checks.

the last oriole egg was laid were in the laying stage, "L" in Table 1. Nests at which no additional oriole eggs appeared after parasitization were in the incubation stage, "I," if the oriole egg I removed contained an embryo. The third stage was intermediate, "L-I," and consisted of nests at which no additional eggs appeared but at which the removed oriole egg was fresh and lacked an embryo. I estimate nests in the L-I stage were parasitized between the day the last egg was laid and 2 or 3 days later.

Study areas.—Most nests were studied during May 1974 and May–June 1975 within 18 km of Shandon, San Luis Obispo Co., California. Nests studied in other areas are as follows: 68-220, Woodbridge, New Haven Co., Connecticut; 72-01, Delta, Manitoba; 73-33, Goleta, Santa Barbara Co., California; 73-01, Chaffey's Locks, Ontario, and 75-103, Tupman, Kern Co., California.

RESULTS OF EXPERIMENTS SIMULATING NATURAL COWBIRD PARASITISM

Responses to experimental parasitism.—Rejection occurred at all 5 nests where I added a real cowbird or cowbird-like egg (Table 1). In addition, Raleigh J. Robertson and Richard Norman (pers. comm.) added real cowbird eggs to 5 oriole nests at Delta, Manitoba. Each was rejected. As Robertson and Norman's techniques differed slightly from mine, I do not include their data in statistical tests that follow. Because rejection of real eggs occurred at 10 of 10 nests, I assume rejections of artificial cowbird eggs at 18 other nests (Table 1) were not in response to artificiality of the eggs. Thus, orioles rejected at each of 28 nests sampled. The 95% confidence interval for percent rejection in the total population is 86 to 100% (determined from Owen 1962). All the real eggs in my experiments were ejected whereas only 4 of 18 artificial eggs were ejected; the remainder were damaged and left in the nest. The incidence of ejection differs significantly for the 2 egg types ($P < 0.02$; Fisher exact test. Bailey 1959 and tables in Owen 1962. All subsequent probabilities also involve this test.). I searched for ejected eggs in an area 3 to 5 m around the point below each nest but failed to find them except in 1 case in which I watched the oriole eject (next section). Most of the damaged artificial eggs had numerous shallow peck marks (Fig. 1). To determine the total number of pecks I counted the peck marks in an area centered around the equator of the egg from nest 74-81. This egg had undergone moderate to heavy damage. I extrapolated this figure to the entire egg (using a formula in Romanoff and Romanoff 1949 for surface area). During the 7 days it was in the nest at least 196 pecks were inflicted, or half this number if each peck was with the bill open. Besides these shallow peck marks, most of which did not penetrate the paint to the underlying plaster, the eggs from 3 nests also had gouges up to 1 mm into the plaster indicating these birds concentrated pecks at specific sites.

Observations of rejection behavior.—After parasitizing a nest I usually left the area as quickly as possible, not returning until a subsequent day. I did watch 6 nests immediately after I inserted the experimental egg and at 2 other nests I returned within an hour: (1) At 18:30 I parasitized nest 75-81 (Table 1) with a House Sparrow egg while a female scolded. About 4 min after I left the nest the female landed on the nest rim, looked into the nest for several sec and then "up-ended," clinging to the inside of the nest wall with her body roughly perpendicular to the ground and her tail protruding from the nest. The motion of her tail indicated she began to peck immediately at the eggs. Pecking continued for about 75 sec; then she flew from the nest and fluttered within several m of it for about 30 sec. She then returned to the nest, immediately up-ended and began to peck. After about 40 sec she left the nest with the House Sparrow egg in her bill and flew to a branch about 10 m away. Upon landing she seemed to immediately wipe the egg across a twig and then dropped it. I retrieved the sparrow egg from the ground and found part of the shell at the pointed end missing (Fig. 1). The missing shell may have remained in the tree. At 18:57 I returned to the nest, and added an artificial cowbird egg. Until 19:04 the female fluttered within 5 m of the nest, frequently looking into it. She then flew to the nest, immediately up-ended as before and began to peck. She stayed in the nest about 2 min, frequently pecking in rapid series of 2–4 pecks. She then left the nest and fluttered nearby only to return at 19:10 again up-ending immediately and pecking until she left at 19:12. She had not returned to the nest when I ceased observations at 19:15. Pecks against the artificial cowbird egg were delivered with such force that they were audible about 6 m away. During these observations I did not see or hear a second oriole.

(2) At 10:53 a real House Sparrow egg was inserted into nest 75-84, while the female scolded. For the next 34 min the female fluttered within 3 to 10 m of the nest, vocalizing frequently. Several times she perched about 1 m over the nest, tilted her head and apparently inspected the nest contents. She was evidently reluctant to return to the nest, perhaps frightened by a rope we had tied to a nearby branch and by occasional disturbances from a nearby house. We removed the rope between 11:27 and 11:31. At 11:42 the female landed on the nest rim, stood there and began to frequently bend over and peck into the nest. She did not up-end as did the bird at 75-81, probably because this nest was not as deep. At 11:44 she flew from the nest, landed about 12 m away and began to bill wipe for several min. At 11:48 and 11:50 she again stood on the nest rim, pecked into the nest and then flew suddenly. In none of her 3 departures were we able to determine whether she carried an egg. At 11:55 we inspected the nest. The House Sparrow egg and one oriole egg were missing. Pieces of oriole eggshell were found beneath the branches the female flew to after her second and third pecking sessions. Perhaps the sparrow egg was removed after the first pecking session and the oriole egg

was broken while the bird tried to eject the sparrow egg. A second oriole was not detected.

(3) I added a real cowbird egg to 75-109 at 15:45 while 1 or 2 orioles scolded. At 15:47 a female landed on the nest, up-ended and began to peck. She flew after about 90 sec but I couldn't see if she carried an egg. This performance was repeated about 1 min later and again I couldn't detect whether an egg was carried away. At 15:50 the female went to the nest and began to incubate. At 16:02 I ceased my observations, chasing the female from the nest which now contained only 4 oriole eggs. A striking feature at nests 75-81, 84, and 109 was the speed with which the females left the nest after most pecking sessions. I suspect they carried eggs or parts of eggs on these departures and left quickly so as to avoid dropping eggs back into the nest.

(4) Nest 75-112 was parasitized at 11:00 with an artificial egg. An adult male scolded while I was at the nest. I watched the nest until 11:14. During this time the male stayed in the tree with the nest but never came within 2 m of it. As the male was not scolding and showed no "nervous" behavior, my presence about 25 m away was probably not responsible for his failure to go to the nest. A female was not detected.

(5) At 15:24 I added an artificial egg to nest 75-123 while scolded by a female. I did not see the female arrive at the nest but 3.5 min later I noticed her, up-ended and pecking into the nest. After about 30 sec she flew to a tree roughly 60 m away and was joined by an adult male. About 30 sec later she returned to the nest, up-ended for about 90 sec and then went all the way into the nest and apparently sat on the eggs. I flushed the female from the nest at 15:34.5. The cowbird egg had 15–30 peck marks. The one oriole egg I had left in the nest was undamaged.

(6) I parasitized nest 75-101 at 18:08, flushing a female from the nest. The nest was watched until 18:20 but no orioles were seen.

(7) Nest 75-88 was parasitized with a House Sparrow egg at 18:15. A male and female scolded while the egg was inserted. The sparrow egg was missing when I returned at 18:49 and a female was incubating.

(8) I parasitized nest 75-103 at 10:25 with a House Sparrow egg. No orioles were detected. When I returned at 10:35 a bird was on the nest and the undamaged sparrow egg was present. At 11:00 the egg was gone and a bird was again on the nest.

These observations suggest ejection usually occurs shortly after a female returns to her nest as was the case at nests 75-81, 84, 109, and 123. The speed with which birds carried ejected eggs made it impossible to determine how the eggs were carried. Pecking motions that preceded ejections indicate eggshells were pierced before removal but whether the eggs, still virtually intact, were speared on the bill or whether the eggs were broken in the nest and pieces carried away separately is uncertain. The former is more likely but the latter may have occurred at 75-109 as the oriole made 2 rapid departures from the nest. My observations indicate most ejected eggs are dropped at least several m from the nest. Orioles are known to drop naturally deposited cowbird eggs directly from the nest (Friedmann 1963, Smith 1972) but these cases of natural parasitism were detected only because eggs were dropped from the nest. Each of the 4 rejections I observed was by a female, suggesting males do not usually reject. Furthermore a male, but not a female, was present and scolded when I parasitized nest 75-112, yet the male did not inspect the nest as had females at other nests. Whether males totally lack rejection behavior remains an important question and is critical to the population genetics of the rejection trait (Rothstein 1975b).

Breakage and disappearance of oriole eggs.—Some but not all oriole eggs disappeared from or were broken in 11 of 18 nests parasitized with artificial eggs. I suggest orioles broke their own eggs while attempting to eject artificial eggs and that they later removed some of these broken eggs. Birds remove their own eggs if these have holes (Poulsen 1953, McClure 1945). This interpretation is supported by several lines of evidence. The incidence of missing or broken oriole eggs at nests parasitized with real eggs (1 in 5) is significantly ($P < 0.05$) less than for nests that received artificial eggs. That orioles removed their own broken eggs is suggested by the fact that at some nests, eggs seen to be damaged on one nest check were missing on a subsequent check. Finally the female at nest 75-81 ejected a House Sparrow egg without breaking any of her own eggs. I then added an artificial egg. The next day the nest contained a damaged artificial egg and pieces of oriole eggshell. Pieces of oriole eggshell were also on the ground beneath the nest, which was deserted. Breakage of oriole eggs probably occurred when an oriole's bill or the plaster egg rebounded against the oriole eggs during pecking or when a plaster egg was dropped on the oriole eggs. Possibly orioles actively pecked their own eggs during redirected behavior occurring when their frustrated attempts to eject the plaster egg conflicted with another tendency such as incubation.

Effects of nest stage.—As orioles parasitized during all 3 nest stages rejected (Table 1) there is no correlation between nest stage and acceptance or rejection of cowbird eggs. However, there is a possible correlation between nest stage and amount of effort exerted in rejection. The fact that artificial eggs can't be ejected easily provides a measure of rejection effort because different amounts of effort may produce different results. By contrast, with real cowbird eggs, rejection effort, even if it does change with the breeding cycle, may always be sufficiently strong to result in the same response—rapid ejection. In response to artificial cowbird eggs, intense rejection effort is likely to lead to ejection. rather than only egg damage. The incidence of missing oriole eggs may be correlated with rejection effort because the more intense the attempts to eject the plaster egg the more likely oriole eggs will be damaged. Results from the 13 nests that received artificial eggs and were checked on day 1 (24 h after parasitization) are relevant. On day 1, 5 of 7 L and L-I nests showed ejection of the plaster egg or disappearance of at least 1 oriole egg whereas these events occurred at none of 6 I nests ($P < 0.025$). This suggests rejection effort decreases after the first 3 days of incubation.

THE NORTHERN ORIOLE AS A REJECTER SPECIES

Because rejection occurred at each experimental nest the Northern Oriole conforms to the responses of previously designated rejecter species. These species reject cowbird eggs at rates of 88 to 100% (Rothstein 1975b). Experiments on orioles were conducted in 4 widely spaced regions (California, Ontario, Manitoba, Connecticut) suggesting rejection is characteristic of the entire species. However, because only 1 nest was tested in 2 regions and because the species is polytypic in morphology (Rising 1970, Misra and Short 1974) experiments in other regions should be done.

There is little doubt that orioles that damaged artificial eggs would have ejected real ones. This must mean that the natural parasitism that is observed is just a fraction of the actual parasitism that occurs. The rapidity with which cowbird eggs can be ejected is shown by nests observed immediately after they were parasitized experimentally. The point is also demonstrated by the fact that rejection occurred within 24 h at 17 of 18 experimental nests visited on day 1 (Table 1). Methods to estimate the rate of natural parasitism are described elsewhere (Friedmann et al. 1977).

The Northern Oriole's status as a rejecter contrasts with other Icteridae. Two well studied icterids. Red-winged Blackbird (*Agelaius phoeniceus*) and Common Grackle (*Quiscalus quiscula*) are accepter species (Rothstein 1975a). The contrast between the oriole and Red-wing is especially interesting because their eggs are similar (Fig. 1). The presence of a definite rejecter species within the Icteridae strengthens the generalization (Rothstein 1975a) that species within a family often differ as regards rejecter-accepter status.

COMPARISONS BETWEEN THE NORTHERN ORIOLE AND OTHER REJECTER SPECIES

Fourteen of 18 (77.8%) oriole rejections of artificial cowbird eggs were by damage. Only 6 of 201 (3.0%) rejections of artificial cowbird eggs by 7 other rejecters were by damage and all of these were by the Cedar Waxwing (*Bombycilla cedrorum*) (data in Rothstein 1975a). Orioles rejected by damaging significantly ($P < 0.005$) more frequently than every other rejecter species, except the Western Kingbird (*Tyrannus verticalis*), for which I tested only 2 nests. The waxwing and oriole differ in the type of damage they inflicted. In contrast to the numerous shallow peck marks on cowbird eggs damaged by orioles, eggs from waxwing nests had nearly all the damage restricted to several large depressions dug into the plaster. Damaged eggs were probably more prevalent among orioles because this species ejects cowbird eggs by spiking them. Other rejecters usually lift cowbird eggs in their mandibles (Rothstein 1975a). While the occurrence of damaged cowbird eggs left in nests is probably an artifact of using plaster eggs (i.e., real cowbird eggs would have been removed) it leads to the discovery that the oriole differs from other rejecters in its ejection technique—a finding that would not have resulted as easily from experiments using real cowbird eggs.

Ejection by spiking would not seem to be as adaptive as ejection by carrying eggs in the mandibles. Even if a broken egg is quickly removed it may leak its contents and this endangers the other eggs (Rothstein 1975a). A bird spiking an egg might cause the egg or its bill to rebound against other eggs, thereby breaking them. Why then does the Northern Oriole eject by spiking instead of by carrying eggs in its bill? I suggest a bird would have difficulty removing an egg from the deep pendant nest characteristic of orioles unless the egg were securely impaled on the bird's bill. Otherwise, the egg might fall back into the nest and damage the bird's own eggs. By contrast other rejecter species I studied have the cup-shaped, shallow nests typical of most passerines. Corroborative evidence is provided by N. G. Smith's findings (pers. comm.: see also Smith 1968) that oropendolas and caciques, whose nests are even deeper than those of the oriole, also eject by spiking. The shape of the oriole's bill may also introduce some difficulties in ejection. Other rejecters have either slightly decurved or hooked bills but the oriole's bill is straight and this may make it difficult for orioles to lift eggs. Also, among known rejecters the oriole has the smallest bill after the Cedar Waxwing.

The oriole and waxwing differ from other rejecters in the incidence with which some but not all of their own eggs were found broken or missing from the nest. Missing or damaged "host" eggs occurred at 12 of 23 (52.2%) oriole nests and at 25 of 58 (43.2%) waxwing nests subjected to experimental cowbird parasitism. Breakage or disappearance of host eggs occurred at only 5 of 190 (2.6%) experimental nests of the other rejecters (Rothstein 1976).

The loss of oriole eggs in experimentally parasitized nests is not totally lacking in biological significance. One nest parasitized with a real egg (75-84, Table 1) lost an oriole egg during the ejection process. The remaining oriole eggs had wet egg contents on them and this may have caused further losses. Another nest I parasitized with a real egg (75-109) showed a potential for the loss of oriole eggs. About 15 min after the female ejected a real cowbird egg, 2 of the 4 oriole eggs had wet egg white on them. A third had a small feather and some cottony nest lining glued to it. These eggs were incubated successfully but my handling may have decreased the likelihood that they would be glued to one another or the nest. I suggest that orioles reject cowbird eggs at some risk to their own eggs. This risk explains the possible reduction in the oriole's rejection effort during the I stage (see above). Selection may favor a reduction in rejection effort during the I stage because cowbird eggs laid then pose little threat to the oriole's reproductive output but sustained efforts to eject such eggs could result in loss of oriole eggs. A similar explanation accounts for the fact that Cedar Waxwings shift from 87.5% rejection during the L and L-I stages to 40.0% rejection during the I stage (Rothstein 1976).

TRUE EGG RECOGNITION VERSUS RECOGNITION ON THE BASIS OF DISCORDANCY

Oriole and "parasitic" eggs in experiments reported above differed in appearance and numerical representation in the clutch (the parasitic eggs were outnumbered by oriole eggs). Thus do orioles reject eggs on the basis of appearance or on the basis of which egg is in the minority? I shall refer to these 2 mechanisms as true egg recognition and recognition on the basis of discordancy. If the latter occurs orioles should reject their own egg if it is outnumbered by foreign eggs. Experiments on other species demonstrated true egg recognition (Victoria 1972. Rothstein 1975c).

Data for 2 nests (75-107 and 123) in Table 1 indicate true egg recognition. Artificial cowbird eggs were rejected even though only 1 oriole egg was present. Thus the orioles at these nests rejected the foreign egg even though it and their own egg type were represented equally.

After artificial cowbird eggs had been rejected, experiments were conducted at 2 nests to distinguish between the 2 modes of egg recognition. On 13 May nest 74-79 (Table 1) contained 5 oriole eggs. At 16:55 I replaced 4 of these with 3 Loggerhead Shrike (*Lanius ludovicianus*) eggs. When next checked, on 14 May at 14:11, the nest contained only an undamaged oriole egg. The nest was still active as 2 orioles scolded intensely. I found no trace of the missing shrike eggs in an area 3 to 5 m around the point under the nest. When next visited on 20 May the nest was abandoned and curiously the still intact oriole egg was buried under 10 to 25 mm of new nesting material. On 13 May, nest 74-86 contained 4 oriole eggs and one heavily damaged cowbird egg (Table 1). I removed the latter at 12:16 and at 12:50 I replaced 3 oriole eggs with 4 shrike eggs. At 13:27 I removed 1 shrike egg because the combined mass of 4 shrike and 1 oriole egg was too large for the eggs to lie on the nest floor in 1 layer. The eggs were being incubated when checked at

13:27. When next visited on 14 May at 18:35 the nest contained only the oriole egg. The egg was cold and had a hole that measured about 3 by 2 mm. No orioles were in attendance. The shrike eggs were not found beneath the oriole nest.

The orioles at nests 74-79 and 74-86 demonstrated true egg recognition. Both nests were probably eventually abandoned because the single oriole egg that remained was not a sufficient stimulus to release incubation behavior. The shrike eggs were larger than the orioles' eggs. At nest 74-79 the oriole egg left with the shrike eggs measured 22.67 × 15.95 mm. Measurements are unavailable for the 3 shrike eggs placed in the nest but 2 eggs from the same shrike clutch measured 23.70 × 18.40 and 24.92 × 18.97 mm. Measurements are unavailable for the shrike eggs used at nest 74-86 but these eggs were also larger than the oriole egg (unpubl. photograph). Thus these experiments present no evidence that orioles prefer large eggs or that large eggs are a supernormal stimulus, as has been found in some nonpasserines (see Tinbergen 1951).

SUMMARY

Experiments on 28 Northern Oriole nests showed this species does not tolerate cowbird parasitism. Artificial or real cowbird eggs or real House Sparrow eggs, which simulate cowbird eggs, were rejected at every nest. Real eggs were ejected whereas most artificial (plaster) ones were damaged and left in the nest. Observations at nests immediately after they were parasitized showed: (1) 4 of 4 rejections were by females, (2) cowbird eggs are often ejected within min, (3) cowbird eggs are usually dropped at least several m from the nest. The oriole's rapid removal of cowbird eggs indicates that the natural parasitism that is observed is a fraction of the total parasitism that occurs.

The Northern Oriole corresponds closely to species previously designated as rejecters —these species reject cowbird eggs at rates close to 100%. But other rejecters usually remove artificial cowbird eggs whereas most orioles damaged them and left them in the nest. This difference demonstrates orioles eject cowbird eggs by spiking although other species do so by lifting the egg in their mandibles. The oriole's special ejection technique is probably an adaption to its pendant nest. Although orioles reject cowbird eggs throughout the egg stage, the effort exerted in rejection seems to weaken during incubation. This decrease in rejection effort may have been selected for because cowbird eggs laid during the oriole's incubation pose little threat to the oriole's offspring but ejecting them endangers the oriole's own eggs. Orioles correctly distinguished between their own and foreign eggs even when the latter outnumbered their eggs, as orioles at 2 experimental nests ejected 3 and 4 real Loggerhead Shrike eggs even though only 1 oriole egg was present.

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OBSERVATIONS ON THE RED-NECKED GREBE NESTING IN MICHIGAN

Michael L. Chamberlin

The Red-necked Grebe (*Podiceps grisegena*) in Michigan is a regular transient although generally uncommon. Zimmerman and Van Tyne (1959) give only 5 summer sight records through August 1958. From 1959–1974 Michigan Summer Bird Surveys recorded only one observation, a group of 12 on 30 August 1962 that were likely migrants (Mahan 1963). The nearest nesting records are for Wisconsin, Minnesota, and Ontario (Jones 1938, Speirs et al. 1944, A.O.U. 1957). The following account is the first record of Red-necked Grebes nesting in Michigan.

STUDY AREA AND METHODS

On 16 June 1975, Steve Goodman and I located a Red-necked Grebe nest containing 7 eggs in a marshy section of Cedarville Bay, Cedarville, Mackinac Co., Michigan. Four days later, on 20 June, we sighted 2 adult Red-necked Grebes in the same marsh. The marsh covered approximately 15 ha of the west shore of the bay (Fig. 1). The near-shore area of the marsh was a dense growth of cattail (*Typha latifolia*) and sedge (*Carex* sp.). The deeper waters contained pondweed (*Potamogeton* sp.), bulrush (*Scirpus* sp.), pickerelweed (*Pontederia* sp.), smartweed (*Polygonum* sp.), spatterdock (*Nuphar* sp.), water milfoil (*Myriophyllum* sp.), and bladderwort (*Utricularia* sp.).

I observed the pair almost daily from 20 June to 29 August 1975, for a total of 259 hours and 37 min. A single sighting was also made on 28 September. I attempted to distribute observations evenly throughout the day from 06:00 to 22:00. Observations before and after the incubation period, when the birds were the most mobile, were made with 7 × 35 binoculars from a canoe. Observations during incubation were made with a 20× scope from a black rowboat anchored among the cattails 67 m from the nest. The birds appeared to become accustomed to the boat and frequently swam within several meters of it. To avoid losing this familiarity the more disturbing visits to check nest contents were made from the aluminum canoe and the nest was approached from the opposite direction of the observation boat's route. Daily nest checks were made until the first egg was laid, after which the nest contents were checked once a week. Although the Red-necked Grebe is a monomorphic species I believe the sexes were distinguishable by the male's brighter plumage, thicker neck, and stockier head.

COURTSHIP

On 5 occasions (23 June–5 July) nesting material was presented by one bird to the other, although unassociated with a nest site or actual nest construction (Fig. 2). One bird picked up a piece of vegetation floating on the water, turned and swam to within several centimeters of the other and dropped it. A lily pad was presented once; a bulrush and then some unidentified vegetation was presented; strands of water milfoil were presented 3 times; and

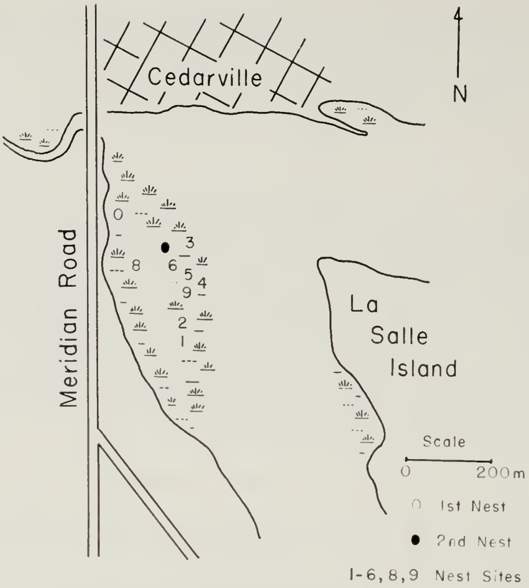

Fig. 1. Location of Red-necked Grebe nests. Cedarville Bay, Clark Township, Mackinac County, Michigan.

unidentified vegetation was presented once. During a fifth presentation both birds simultaneously presented vegetation to the other and then turned away. Immediately after one presentation both birds called in unison and after another the birds turned tail-to-tail (bodies almost touching) and simultaneously dipped their bills and shook their heads.

Courtship observations were few, brief, and involved only 3 (Weed Tricks, Head Shaking, and Turning Away) of the many postures and displays given by Wobus (1964) as part of the Red-necked Grebe's courting repertoire. I believe most of the courtship activities occurred prior to my first sighting the pair on 20 June and possibly some occurred even before their arrival in the marsh. Storer (1969) observed courtship behavior in the Horned Grebe (*Podiceps auritus*) along its migration route and suspected it also occurred on its wintering grounds. Bent (1919) and McAllister (1958) wrote that Eared Grebes (*Podiceps nigricollis*) appeared mated on their arrival in the spring, however, McAllister (1958) further noted that they may change mates on the breeding grounds. Although I never saw the birds on the first nest (found on 16 June) its presence also suggested that all observations were of a renesting attempt and probably courtship and pair bond formation initially occurred in May.

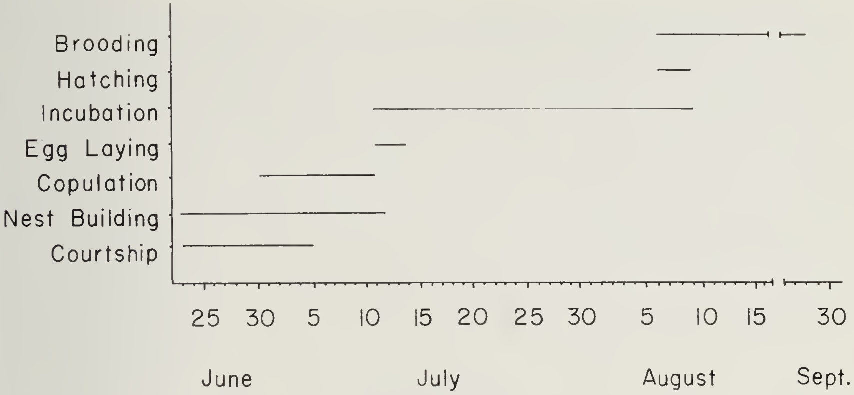

FIG. 2. Duration of breeding activities of the Red-necked Grebe, 23 June to 29 August 1975.

NEST BUILDING

On 25 occasions (23 June–12 July) I observed nest construction. Observations ranged from 1–90 min duration (Fig. 2). The very brief periods of nest building (1–4 min) appeared to have more significance as post-copulatory behavior than actual nest construction. The mean duration of nest building bouts, excluding those occurring immediately after copulation, was 21 min.

Nest building was observed at 9 locations which were from 2–70 m apart (Fig. 1). On several occasions the 2 closest nests were worked on simultaneously. The number of days each nest site was attended by the pair is depicted in Fig. 3. The construction of numerous nests apparently is not uncommon. Speirs et al. (1964) recorded 7 nests built by one pair of Rednecks on Lake Ontario.

The nest site appeared to be chosen by the male either by poking at the future site with his bill, by starting to carry nest materials to a particular spot, or by Invitation. On one occasion the male left the female on a nest site they had been working on for 4 days and had copulated on, swam 6 m to another clump of cattails and assumed the Inviting posture (i.e. lying flat with neck outstretched and low and the bill pointed forward and almost touching the water). The female called several times but the male did not move. After 1 min the female joined the male and both began building at the new site.

All nest sites were among the bulrushes and on floating clumps (less than 1 m in diameter) of cattail roots and stems. Bulrushes, water milfoil, and lily pads were incorporated into the nest. These materials were collected within approximately a 5-m radius of the nest. Bulrush stems were picked up

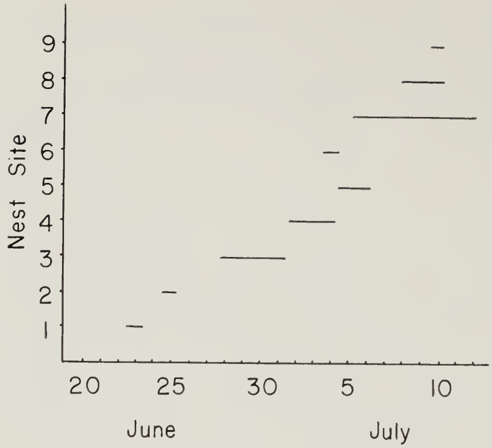

FIG. 3. Duration of nest building activities at 9 nest sites, 23 June to 12 July 1975.

singly and carried crosswise in the bill. Water milfoil was obtained during a brief dive. Lily pads were half-carried, half-dragged through the water and lifted onto the nest.

Nest construction appeared to involve 2 steps. First, bulrushes, lily pads, and some water milfoil were placed on a clump of cattails. This provided a floating platform capable of supporting eggs and an incubating bird. Second, a simple depression was formed by one bird on the nest receiving materials (almost exclusively submergent vegetation brought up from the bottom) from its mate and pulling these around itself into a low rim. Most of the rim was constructed during the first 2 days of incubation.

Nest building was performed by both birds, although the male was the principal builder during the early stages and was observed vigorously piling vegetation on the nest while the female swam back and forth, rested, or preened a couple meters away. Later, the male frequently carried materials to the nest where the female, on the nest, arranged them around herself. As the day of the laying of the first egg approached both birds were often simultaneously involved in the nest building and on one occasion they worked together continuously for 74 min. On several occasions I saw the female building alone.

During the nest building period the birds rarely approached the nest site alone, although one frequently departed before the other. When one finished foraging before the other, it called, preened, and waited until the other joined it. Only when the birds were together did they cautiously return to the nest site several body lengths apart.

The nest in which the eggs were ultimately laid was the seventh nest begun by the pair (excluding the nest with the 7 eggs) and was among the bulrushes at the edge of the inner open water area in 1.1 m of water (Fig. 1). It had an inside diameter of 15–16 cm and an outside diameter of 38–42 cm. The depth of the depression was 2.5 cm and the top of the rim was only 5 cm above the water level. The first nest (found on 16 June) was floating in 0.5 m of water, 25 m from the shore, and only 30 m from a road. I suspect it became detached at its anchorage, drifted into the shore, and was consequently abandoned. The nest was a sodden mass of bulrushes and water milfoil with a 33-cm outside diameter above water and a 61-cm diameter under water. The top of the nest was 6 cm above water and the depression containing the eggs was 15 cm in diameter.

COPULATION

I observed copulation 6 times from 30 June to 11 July (Fig. 2). The procedure for all copulations was essentially the same: (1) The female climbed onto the nest platform and Invited. On 2 occasions the female uttered a faint, plaintive call. (2) Within 0.5–2.0 min the male mounted the female and copulated, while on the nest. Copulation was 3–7 sec in duration and accompanied each time by the copulating call ("Rattern") described by Wobus (1964). (3) Immediately after copulation the male walked over the female's head and shoulders and into the water at which time both birds raised their heads. This was followed by (4) Head Shaking by one or both birds or both birds, Slow Swaying ("Wegsehen"), and (5) either both birds preened briefly or the female preened while the male briefly collected nest material.

My observations were in accord with those of Wobus (1960, 1964). The faint vocalization of the female in the Inviting posture may correspond with the platform call of the Horned Grebe described by Storer (1969).

EGG LAYING

Three eggs were laid. The first egg was laid on 11 July and had a bluish matrix which became, by the time it hatched, dark brown due to staining from wet vegetation. I don't know the exact dates of the laying of the second and third eggs. Wobus (1964) found that the average clutch size for July-nesting birds was 2.5.

INCUBATION

I observed incubation for 151 h and 39 min from 11 July to 9 August (Fig. 2). Incubation was shared by the sexes, the male incubating 41% of the time and the female 59%. For comparison I divided the day into two 8-hour blocks; one representing mid-day (10:00 to 17:59) and the other morning and evening (06:00 to 09:59 and 18:00 to 22:00). In the morning and evening intervals the female incubated 65% of the time, whereas during the

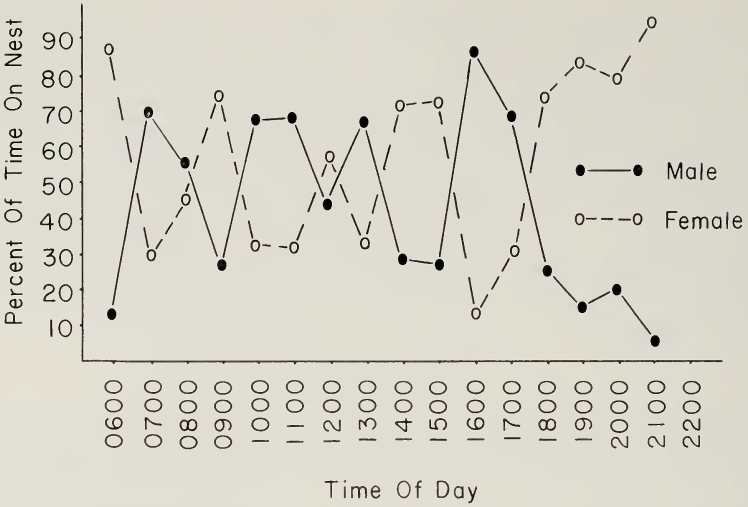

FIG. 4. Average percent of time spent on the nest by sex and time of day. Each time block represents a minimum of 5 hours of observation.

middle of the day she was on the nest only 41%. During all observations before sunrise and after sunset the female was on the nest, suggesting that she performed most of the night-time incubating. From day to day each sex tended to incubate at approximately the same times (Fig. 4).

As the birds adjusted to the incubation routine, the average duration of their individual attentive periods increased. The average attentive period lasted 87 min during the first week but increased to 132 min during the second with a corresponding decrease in the number of periods per day from 10 to 7. The last few days of incubation were similar to the first days of incubation in that the mean duration of the attentive periods decreased to 78 min and the frequency of change-overs increased back up to 10 per day. Wobus (1964) found the average duration of attentiveness to be 1–2 h.

An all-day observation on the third day of incubation revealed that incubation was continuous, or nearly so, during the egg-laying and early incubation periods. During the first 3 days incubation was infrequently interrupted by brief periods of nest building and copulation but from the fourth day on the eggs were very rarely and briefly left unattended.

During the nest reliefs, or change-overs, the returning bird's behavior appeared dependent not only on the strength of its own urge to incubate but also on the incubating bird's readiness or reluctance to leave the nest. Occasionally during extremely hot weather (e.g. 32°C) and after unusually long periods of attentiveness (e.g. 3½–4 h), the mere presence of the returning bird was sufficient to induce the incubating bird to leave the nest. Head Shaking by the returning bird was the dominant component of nest reliefs and in most cases induced its mate to leave the nest. Head Shaking was part of 49 (68%) of the 72 nest reliefs I observed. During the first week's nest reliefs the returning bird Head Shook as many as 6 times and often the incubating bird also participated in Head Shaking. By the second week Head Shaking was primarily by the returning bird and only done once or twice per nest relief. If Head Shaking failed the returning bird often sat next to the nest (usually to the rear of the incubating bird) and performed comfort movements or poked at the nest for several min. When its mate still remained on the nest the returning bird made brief nest building actions. Twice the male simply "gave up" after these attempts and left for a while; once the female jumped onto the nest forcing the male off. Herring Gulls (*Larus argentatus*) demonstrate a similar behavioral progression during nest reliefs (Tinbergen 1960, pers. observ.). The returning gull's inducements ranged from its mere presence on the territory, to Mewing, to Choking, to bringing nest material to the nest, to physically evicting its mate from the nest.

Three times during the first 2 days of incubation the female, on leaving the nest, Reared and Wing Quivered, thus "coaxing" the male onto the nest. These 3 occurrences were the only times I saw Wing Quivering. Storer (1969) discussed this display as the most intense form of soliciting. The Inviting posture, a milder form of soliciting, was assumed by the incubating bird as its returning mate swam towards the nest. Inviting remained as part of the nest relief pattern through the seventh day, after which I no longer saw it. Prior to egg laying the nest platform had been used primarily as a copulation platform. Thus the occurrence of soliciting postures during the first nest reliefs suggested they were a carry-over from copulation, and possibly such actions on the part of the female encouraged the male's transition to incubating behavior.

Also during the first 2 days of incubation, nest reliefs were twice initiated by the female (as the returning bird) carrying nest material to the nest but not depositing it thereon. Instead she swam back and forth in front of the male as if to entice him off the nest by an activity in which he had, until recently, been vigorously involved. Carrying nest material, as well as soliciting, may have reflected the ambivalence present in the birds as they changed from one behavior pattern to another. I saw none of these activities as part of nest reliefs after the first week of incubation. The nest reliefs gradually became less complex (i.e. fewer movements and postures) as various components were "phased out."

Several change-overs occurred in which I saw none of the usual cues, but rather they appeared to be initiated by impatience, rain damage to the nest, or disturbances. On the third evening of incubation the male abandoned the nest after a long period of incubating. Both birds returned 27 min later and the female climbed onto the nest. Once after a 44-min downpour, the male slid off the nest and began nest repairing. The female appeared 2 min later and climbed onto the temporarily abandoned nest. The male continued to repair the nest for an additional 18 min. Change-overs occurred twice when the incubating bird was frightened off the nest by fishing boats and once by one of my nest checks.

The birds approached the nest cautiously from the open water, rather than through the bulrushes. During the first 10 days the birds swam on the surface to the nest, usually with considerable head-bobbing movements. Starting on the eleventh day the female approached the nest underwater, diving from 20–30 m away. Seven times when the female surfaced right next to the nest and face to face with the incubating male they both raised their necks up as tall as possible, crest plumes erect, and called loudly and simultaneously. The same display occurred twice when the incubating bird left the nest at the sight of the returning mate. The birds displayed and called as they swam towards each other, and turned face to face as they passed. This mutual upright posturing and vocalizing apparently was a greeting of mate recognition. According to Storer (pers. comm.) this vocalizing corresponds to the Triumph Ceremony of the Horned Grebe and the greeting trills of the Pied-billed (*Podilymbus podiceps*) and Least grebes (*Podiceps dominicus*).

After each nest relief the departing bird spent 3–20 min (mean = 8) preening before it swam out through the bulrushes to forage in the channel. The male was markedly more vocal than the female and often called during his returns to the nest, although by the 6th day his returns had become silent. I rarely heard vocalizing in the immediate vicinity of the nest after the first week of incubation, except during the aforementioned change-overs and after disturbances.

LATE INCUBATION

During the last 5 days of incubation, nest building was frequent and occurred in conjunction with 7 of the 18 nest reliefs of this period. Except for one instance of nest repair, I had not observed extensive nest building since the second day of incubation when rim construction was completed. Since token nest building was a strong nest relief cue, such behavior may have indicated strong drives to incubate or possibly it was displacement activity reflecting frustrations caused by the sounds of chicks within the eggs and internal changes in the birds' drives from incubating behavior to broodiness.

Two days before hatching a new behavior, which I call Lunging, was incorporated into 6 of the 8 observed nest reliefs. Lunging consisted of a stabbing motion of the bill towards the incubating bird's back and was made by the returning bird as it sat next to the nest. Lunging was apparently an intention movement of feeding the young, during which the adult presents food in the bill to the chicks on the other parent's back.

Several days prior to hatching the incubating bird frequently stood up and either looked down at the eggs or rearranged the nest material around them. Such behavior was most likely stimulated by chick sounds within the eggs. During the earlier days of incubation the birds rarely stood up once comfortably settled on the eggs. During these last days of incubation the non-incubating bird spent considerably more time loafing in the vicinity of the nest than it had before and the birds started approaching the nest through the bulrushes, which they had not done previously.

HATCHING

The 3 eggs hatched on 6, 7, and 9 August (Fig. 2). Since the first egg was laid on 11 July, and incubation began on the same day and was continuous throughout, the incubation period for the first egg was 26 days. Bent (1919) determined the period of incubation to be 22–23 days for eggs he hatched in an incubator. The eggs' constant contact with wet vegetation and the possibility that, although the grebes were continuously on the eggs starting with the laying of the first egg, heat transfer may not have yet been complete might have accounted for the longer incubation period in the wild. Wobus (1964) gave the average incubation period as 23 days but added that it is often longer due to cold weather and/or disturbances.

Hatching occurred in the mid-morning. From 09:49 to 10:24 on the morning the first egg hatched the incubating bird showed considerable uneasiness and stood and looked down at the eggs 6 times. The next day the second egg was intact at 07:30 and the second chick was first observed crawling out from under the incubating adult at 11:45. Two days later at 07:48 the third egg was still intact but during the change-over at 12:38 I saw the chick in the bottom of the nest while the other 2 were in the water. Before settling onto the nest the male picked up the egg shell and dropped it over the rim of the nest.

BROODING

The chicks were brooded on the parents' backs under their wings when the adults were on the nest as well as on the water. This undoubtedly had survival value considering the cold, wet state of the nest and the presence of aquatic predators such as the northern pike (*Esox lucius*). Brooding was performed by both sexes and brooding periods ranged from 57–162 min (mean = 119). During change-overs on the nest the brooding bird stood up, spread its wings, and shook the chicks off its back and into the nest. After the adult dismounted, its mate climbed onto the nest and raised its wings 4–5 cm off its back allowing the chicks to crawl up and under. During change-overs on the water the brooding bird raised itself into a nearly vertical position and shook off the chicks by wing-flapping. At 3 weeks of age the chicks were no longer brooded on the adults' backs.

After the hatching of the third and last chick on 9 August the nest was used during most of the following day, from 09:29 to 20:52, and then abandoned. I never saw the birds using the nest after 10 August.

FEEDING THE CHICKS

Both parents fed the chicks. During the first week the chicks were fed 2- to 5-cm minnows, small unidentified items (probably insects), and an occasional feather. The age of the first chick I observed being fed a feather was 2 days. Wobus (1964) observed chicks being fed feathers, as well as insect larvae, during their first day of life. After the first week the food appeared to be almost exclusively fish in the 4–10 cm range. During the third week the fish were noticeably heavier bodied and once a medium-sized crayfish was fed to one of the chicks.

As the parents swam towards the chicks with a fish they repeatedly dipped the fish in the water and appeared to be manipulating and pinching it in their bills, as described by Sim (1904). This probably killed and softened the fish and made swallowing and digestion easier. The food was held in the tip of the bill and presented to the chicks while they were on the other parent's back. The chicks frequently dropped the minnows during the first several days' feedings but the parents picked up the dropped minnow and presented it repeatedly until the chick finally got it headfirst into its mouth. The brooding parent frequently picked up any dropped items and fed the chicks on its own back. By the second week the chicks were fed on the water where they persistently begged for food and swam out to meet the parents each time they returned with food, and occasionally even pursued their parents underwater.

Feeding periods during the first week ranged from 23–113 min (mean = 75) with a mean of 9 feedings per period (Table 1). Feeding intervals (i.e. the time between individual feedings) ranged from 1–32 min (mean = 8). A 28- to 129-min loafing period (mean = 58), during which the non-brooding bird loafed and/or foraged for itself, immediately preceded or followed each change-over. During the second week feeding periods were one-third as long as during the first week while the number of feedings per period more than doubled due to the 6-fold reduction in the length of time between feedings (Table 1). Thus the chicks' growing demand for food was met by decreasing the time interval between feedings.

TABLE 1

A WEEKLY COMPARISON OF FEEDING AND LOAFING PERIODS

	Week		
	1st	2nd	3rd
Duration of feeding periods (min)	23–113 (75)*	16–34 (25)	4–27 (17)
Number of feedings per period	2–15 (9)	10–31 (19)	7–32 (16)
Feeding intervals (min)	1–32 (8)	0.5–12 (1.4)	0.25–7 (1.1)
Duration of loafing periods (min)	28–129 (58)	32–64 (50)	23–39 (31)
Mean number of feedings per hour	3.5	12.5	18.0

* Means are given in parentheses.

The mean duration of the feeding periods and feeding intervals continued to decrease through the third week (Table 1). The reduced number of feedings per period simply reflected the shorter duration of the periods. The very short time intervals such as 0.25 min between some feedings were probably the result of both parents simultaneously feeding the chicks. Short time intervals probably also occurred when the birds found their prey concentrated in large schools. Once when the chicks were fed 74 times in a 25-min period, every fish appeared to be the same size (4–5 cm) and while the birds fished they moved steadily along as if following a school. During the third week the mean duration of the loafing periods was 47% and 38% shorter than during the first and second weeks, respectively. Thus although the feeding periods were shorter they were also more frequent, as indicated by the reduced amount of time the adults spent loafing in between. As the chicks grew the mean number of feedings per hour increased steadily from 3.5 the first week, to 12.5 during the second week, to 18.0 during the third week (Table 1).

I last observed the family on 28 September 3.5 km from the nest. The 3 chicks, at 51, 53, and 54 days of age, were still being fed by both parents. According to Wobus (1964) the family bonds break up after 8 to 10 weeks.

INTERSPECIFIC RELATIONS

Red-winged Blackbirds (*Agelaius phoeniceus*) were in frequent attendance of the grebes' nest building. After the grebes' departure from a nest platform, the Red-wings immediately dropped down to the nest and appeared to be snatching up insects, probably brought up with or attracted to the wet vegetation. Deusing (1939) watched a Long-billed Marsh Wren (*Telmatodytes palustris*) catching insects on a Pied-billed Grebe's nest.

The incubating grebes tolerated the passing and activities of other marsh nesters such as the Pied-billed Grebe. American Coot (*Fulica americana*), Black Tern (*Chlidonias niger*) and Red-winged Blackbird near the nest. The several species of ducks (*Anas platyrhynchos, A. rubripes, A. discors*, and *Aix sponsa*) common in the marsh were tolerated as they fed near the nest prior to the hatching of the grebe chicks.

The grebes assumed a defensive posture (neck and head upstretched with the bill directed towards the cause of the alarm) whenever Herring Gulls flew low and noisily over the nest. Once 2 immature Ring-billed Gulls (*Larus delawarensis*) dived at one of the 3-week-old chicks and stimulated a half-running, half-flying attack by both adults. These same 2 gulls also tried to rob the male grebe of a crayfish, but only forced him to dive out of their reach. A female Marsh Hawk (*Circus cyaneus*), gliding only 4–5 m directly over the nest, caused the male, with the chicks on his back, to leave the nest.

At hatching the male became strikingly territorial towards other species. On one occasion the male drove off 2 immature Pied-billed Grebes that were foraging at least 40 m from the nest. The male approached one of the Pied-bills in a very pronounced threat attitude, hunched very low on the water. The male dived and in the same instant the Pied-bill half-ran, half-flew 3–4 m across the water. The male surfaced and continued to pursue the Pied-bill in a threat attitude. When the male dived a second time the Pied-bill flew off. The male then turned his attention to the other young grebe and with a similar sequence of actions drove it away. According to Storer (1967) grebes seem to fear underwater attacks and so do not remain on the surface if an aggressive grebe dives.

In aggressive situations diving is "understood" as a threat between different species, and even genera, of grebes but apparently not between higher taxonomic groups. When the male approached a Mallard feeding 10 m from the nest in a threat attitude, the duck continued feeding, and as the male dived the duck remained oblivious to the grebe's actions. However, several seconds after the male dived the Mallard sprang into the air and, quacking loudly, flew off. Apparently the duck did not "interpret" the dive as a threat and so fled only after (presumably) being physically attacked from underwater.

The pair's interspecific territoriality appeared to be in defense of the brood and not the nest site or any fixed area of the marsh. This was suggested by the rarity of agonistic behavior prior to and during incubation and the sudden aggressiveness at hatching. Also, their aggressiveness extended far beyond the nest site and even after the nest had been abandoned. As the brood moved so did the territory. Both adults frequently chased away Pied-billed Grebes, Mallards, a female goldeneye (*Bucephala clangula*), and a Great Blue Heron (*Ardea herodias*) that came close to the brood as they traveled along the marshy shorelines of the channel.

Twice during the hatching period a muskrat (*Ondatra zibethica*) swimming close to the nest was threatened by the male. When the muskrat dived the grebe immediately followed. Shortly, the muskrat surfaced and continued on its way and the male returned to the nest. The only other interaction with muskrats was that the abandonment of nest site #4, after 4 days of use by the grebes, coincided with muskrats starting to use it for one of their feeding platforms.

SUMMARY

A pair of Red-necked Grebes (*Podiceps grisegena*) was studied in a northern Lake Huron marsh from 20 June to 29 August 1975. Observations were of a renesting attempt and courtship behavior was brief and infrequent. Copulation occurred on the nest platform from shortly after nest building began into the egg-laying period.

The nest site was selected by the male although both sexes built the nest. The pair constructed 9 nest platforms, one of which ultimately became the nest in which 3 eggs were laid. Incubation began with the laying of the first egg and both sexes incubated, although the male incubated more during the mid-day and the female more in the morning and evening hours. Nest reliefs were initiated primarily by Head Shaking by the returning bird.

The first egg had a 26-day incubation period. Hatching occurred in mid-morning. The nest was abandoned 2 days after the hatching of the last chick. The chicks were brooded on the adults' backs under their wings. Both sexes brooded and fed the young. Food items consisted of minnows, crayfish, and probably insects. The mean number of feedings per hour increased from 3.5 to 12.5 to 18.0 during the first, second, and third weeks, respectively. Three chicks were successfully raised to over 7 weeks of age.

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NEW LIFE MEMBER

Mr. Hubert P. Zernickow is a new life member of the Wilson Ornithological Society. Mr. Zernickow is an Advisory Systems Engineer with the IBM Corporation at Lansing, Michigan. His ornithological interests are primarily as an observer and photographer, and he has a special interest in owls. Mr. Zernickow is a member of the AOU and is presently president of the Michigan Audubon Society. He is married and his wife, Norene, shares his enthusiasm for birding. In addition to his ornithological interests, Mr. Zernickow enjoys botany, hiking, and canoeing.

GROWTH AND DEVELOPMENT OF THE PLAIN CHACHALACA IN SOUTH TEXAS

WAYNE R. MARION

Growth and development of many game birds have received thorough investigation, but this is not true for the Plain Chachalaca (*Ortalis vetula*). I studied growth and development of chachalacas as part of a larger study (Marion 1974) of the ecology of this species in Texas.

METHODS

Research was conducted from January 1971 to August 1972 at Santa Ana National Wildlife Refuge, and 3 other study areas in the Lower Rio Grande Valley, Hidalgo and Starr counties, Texas. Data reported in this paper were obtained from captive birds, live-trapped birds, and collected specimens.

Captive chachalacas were reared in 2 weld-wire pens at Santa Ana National Wildlife Refuge headquarters. An attempt was made to keep the pens as natural as possible; they included several small trees and additional plant materials which provided cover, shade, and sites for perching and nesting. One pen (4.6 × 3.0 × 2.4 m) contained 3 adult birds (1♂, 2♀♀). Another slightly larger pen (6.1 × 7.2 × 2.4 m) contained 7–9 immature birds (2–3♀♀, remainder♂♂). Captive juveniles were hatched in an incubator from eggs collected from 4 nests during 1971. Fresh water and commercial foods were provided ad libitum. Captive birds were fed commercial starter, grower, and maintenance rations, corresponding to stage of maturation. Natural foods were frequently provided to supplement commercial foods.

Chachalacas were live-trapped at the main study area in 25 × 50 mm mesh weld-wire traps (1.2 × 1.2 × 0.6 m) with funnel entrances similar to those described by Taber and Cowan (1963:261). Twelve traps were operated at randomly selected sites during late winter and early spring of both years of this study. Traps were baited with fresh cabbage and grain sorghum placed within the enclosure and near the funnel entrances. To avoid excessive stress on handled birds due to overheating, trapping was restricted to the cool morning and evening hours. Trapped birds were marked with aluminum bands and colored leg streamers for subsequent individual field recognition.

Chachalaca specimens were shot in a nonselective manner on all study areas between September 1971 and August 1972. Many birds were collected in the morning and evening when they were more active; fewer were collected at midday. Data from carcasses of chachalacas found dead during this study also were recorded.

There is no obvious sexual dimorphism in this species, but all birds handled were sexed using at least 1 of 4 known methods. Two of these methods, convenient for sexing live birds, were related to the presence or absence of a looped trachea. The adult male has a trachea lengthened by a loop which is easily felt between ventral musculature of the breast and the skin; this looped structure is lacking in young males and females (Merrill 1878). During this study, inspection of gonads of sacrificed birds verified this sexual difference in tracheal development of adult birds. Determination of the presence or absence of the tracheal loop by feeling the breast was the major technique used in sexing older juveniles and adults.

Generally the longer and wider the trachea, the deeper the bird's voice; the shorter and narrower the trachea, the higher the voice. Adult males have a longer trachea and their voice is a full octave lower than that of females and young males (Sutton 1951:127). The pitch of the voice was a second method used in sex determination when live birds were heard calling.

Chachalaca males have a penis which can be readily observed by cloacal examination, but this technique was rarely used because it required more handling of birds than the previously described tracheal loop method. All collected specimens were sexed by examination of the gonads.

Definitive aging criteria for chachalacas have apparently not been reported. I recorded tracheal loop lengths, measured externally from the distal portion of the loop to the point of entry into the thorax, for use as aging criteria for male birds. Total length and diameter (at each end and near the middle) of the trachea of all collected specimens were measured to determine sex and age differences. Vernier calipers, permitting readings to the nearest 0.1 mm, were used in measuring tracheal diameters.

Postal scales were used to measure total body weight to the nearest 0.5 ounce. These data were later converted to equivalent values in grams. Several standard length measurements for birds, including total body, wing chord, tail, exposed culmen, tarsus (tarsometatarsus), middle toe, and total extent of wings, as described by Baldwin et al. (1931) and Pettingill (1946:323–325), were taken to the nearest 1 mm using a pair of dividers and a ruler. These measurements were recorded for captive (at intervals of 1 month or less), live-trapped, and collected birds. Plumages and molt patterns of all handled birds also were examined.

RESULTS AND DISCUSSION

I live-trapped, color-marked, and released 222 chachalacas (144 in 1971, 78 in 1972). Ten of the marked birds from 1971 were recaptured in 1972. An additional 64 chachalacas (32 in each year) were sacrificed at the 4 study areas, with the majority from Santa Ana National Wildlife Refuge.

Sex and age determination.—Tracheal development in chachalacas was successfully used to determine sexual differences and to distinguish juvenile from adult males. Measurements of total tracheal length could not be taken externally and were all obtained from sacrificed birds. The mean total length of the trachea for 48 sacrificed adult males was 329.8 ± 20.6 mm (range 245–385 mm), more than twice the average tracheal length for 23 sacrificed adult females (141.7 ± 10.3 mm, range 121–168 mm). Measurements of maximum diameter of the trachea, taken near each end and at the middle, also showed sexual differences. Mean tracheal diameters were significantly larger for adult males than for adult females at the anterior (upper) end ($t = 3.5$, $P < 0.01$), near the middle ($t = 4.5$, $P < 0.01$), and at the posterior (lower) end ($t = 3.5$, $P < 0.01$).

The tracheal loop began to develop in juvenile males at about 8 weeks of age and was easily felt on the anterior breast at 10 weeks. Tracheal loop lengths were measured either internally or externally; the former measurement required that birds be sacrificed, whereas, the latter was used without harming living birds. Length of the tracheal loop was measured by both methods from the distal end of the loop to the point of entry into the thorax. For comparison, loops of 19 collected adult males were measured using both techniques. Mean external measurements were slightly larger than mean internal measurements (73.0 ± 3.6 mm and 70.4 ± 4.6 mm, respectively). These differences, however, were not significant ($t = 1.9$, $P > 0.05$).

External tracheal loop measurements were recorded for male chachalacas. Mean loop length of captive juveniles was 17.5 ± 7.1 mm (range 13–23) at 9 weeks of age ($N = 2$) and 30.0 ± 7.2 mm (range 34–38 mm) at 10 weeks of age ($N = 3$). The tracheal loop of captive juveniles elongated slower than other body parts; measurements began overlapping those of adults when young males were approximately 9 months old (Fig. 1).

Tracheal loop development was apparently slower in wild juveniles than in captive juveniles. Mean loop lengths for wild juveniles handled during February ($N = 9$) and March 1972 ($N = 4$) were 51.2 ± 4.4 mm (range 46–60 mm) and 54.1 ± 3.5 mm (range 49–57 mm), respectively. The average loop lengths of 5 captive juveniles in February and March were 62.1 ± 4.3 mm (range 58–67 mm) and 64.8 ± 2.4 mm (range 63–68 mm), respectively. These measurements for captive juveniles were significantly larger than those for wild juveniles in February ($t = 4.4$, $P < 0.01$) and in March ($t = 5.5$, $P < 0.01$). Several variables, all related to the exact age of wild (unknown age) vs. captive (known age) juveniles, may be responsible for this difference but the major cause remains unknown.

These data generally indicate that wild juveniles may be distinguished from adults using tracheal loop lengths until at least 9 months of age. By 1 year, tracheal loop development was nearly complete and differences among males were subtle. Further increases in tracheal loop length as males aged were apparently minor. Four banded males, known to be more than 5 years old, had an average loop length of 78.0 ± 3.1 mm (range 75–82 mm). This mean value, although slightly larger than the average loop length of 44 other adult males (74.2 ± 4.4 mm, range 67–87 mm), was not significantly larger ($t = 1.7$, $P > 0.05$).

Significance of color of the upper mandible was investigated as an indicator of age. Presence or absence of a dark tip on the upper mandible was recorded for 17 juvenile males (tracheal loop partially developed) and 17 adult males (tracheal loop well developed) handled between December 1971 and March 1972. Upper mandibles of all 17 juvenile males had dark tips. Only 2 of 17 (11.8%) adult males had dark-tipped upper mandibles. The remaining 15 (88.2%) had uniformly colored (blue horn) bills. These results indicate that dark markings near the tip of the upper mandible are characteristic of juvenile birds.

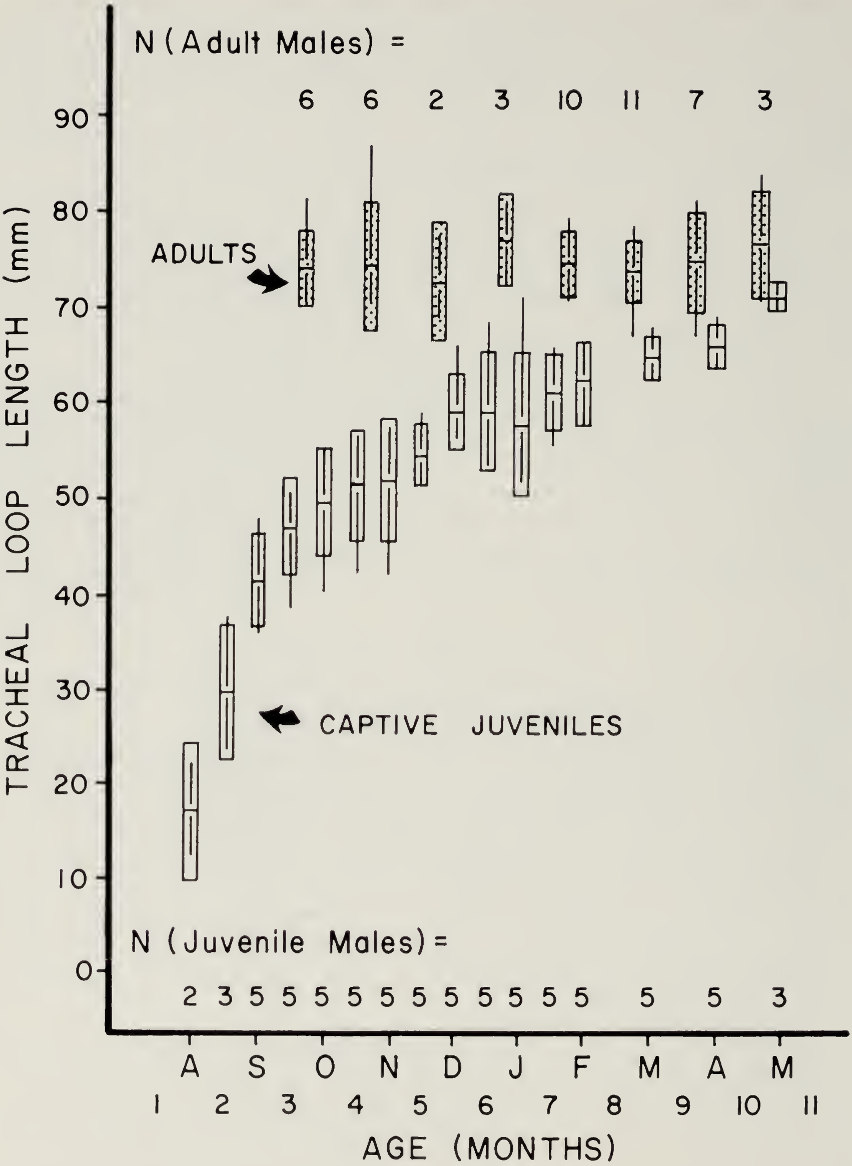

FIG. 1. Tracheal loop lengths of wild adult and captive juvenile chachalacas. External measurements were taken and data presented are means (± SD) and ranges.

Strength of the lower mandible varies with age in many gallinaceous birds. Generally, if a dead bird is supported only by the lower mandible and it breaks, the bird is a juvenile; if the lower mandible does not break, it is an adult (Leopold 1933:166, Taber 1963:134). Lower mandible strength was determined for males of known age (by tracheal loop development) collected between December 1971 and March 1972. When subjected to the "lower mandible test," all 4 juvenile males had mandibles that broke. Each of the 10 adults tested had a lower mandible that supported the bird's weight. Strength of the lower mandible seems to be a valid technique for distinguishing juvenile and adult chachalacas.

Males of known age (determined by tracheal loop development) handled between December 1971 and March 1972 were used to investigate leg color differences between juveniles and adults. Of 18 juveniles, 8 (44.4%) had legs that were slightly orange. The others had darker (blue horn) legs. Of 22 adults, only 2 (9.1%) had slightly orange legs. A significant ($P < 0.05$) chi square value of 6.6 indicates that orange legs are more typical for juveniles than for adults.

Age determination in gallinaceous birds commonly involves plumage characteristics (Taber 1963:128), however, plumage differences between juvenile and adult chachalacas diminish rapidly as young birds mature. At 2 or 3 months of age, slight differences exist in width and shape of flight feathers. Rectrices and remiges of juveniles are relatively narrow and pointed, while those of adults are broad and rounded. Most of these plumage differences are lost with the postjuvenal molt before the juveniles are 6 months old. The outermost juvenal rectrices and primaries, however, may be retained slightly longer.

Growth.—Chachalaca chicks are precocial and leave the nest within a few hours after hatching. Chicks are very active and agile in climbing through trees and shrubs within a few days of hatching and are able to jump and fly at least 1.3 m at 6 days of age.

Weights and measurements of wild adults (males and females) and captive juveniles (1 week and 1 month old) are presented in Table 1. Adult males averaged significantly ($P < 0.01$) larger than adult females in weight, total length, wingspan or extent, wing chord, tail length, exposed culmen length, tarsus length, and middle toe length. Although statistical comparisons of mean values indicate that adult males average larger than adult females, much overlap exists in the ranges of these measurements. These overlapping values reflect subtle sexual differences in size which are not easily recognized in the field.

Mean adult weights were highest during October and November (631 ± 87 g and 646 ± 97 g, respectively), but were relatively constant during other

TABLE 1

WEIGHTS AND MEASUREMENTS OF ADULT, WEEK-OLD, AND MONTH-OLD CHACHALACAS[1]

Age (N)	Weight (g)	Total Length (mm)	Extent (mm)	Wing Chord (mm)	Tail Length (mm)	Exposed Culmen (mm)	Tarsus (mm)	Middle Toe (mm)
Adult Males (106)	584 ± 58 (468–794)	566 ± 24 (502–610)	628 ± 25 (559–669)	210 ± 7 (191–229)	244 ± 10 (210–267)	23.3 ± 2.1 (19.0–27.5)	59.3 ± 4.2 (51.0–69.5)	48.6 ± 2.2 (41.5–51.0)
Adult Females (102)	542 ± 52 (439–709)	536 ± 24 (476–591)	596 ± 27 (534–648)	200 ± 7 (184–216)	235 ± 13 (176–261)	21.7 ± 2.1 (19.0–26.0)	56.6 ± 3.5 (51.0–65.5)	47.0 ± 2.4 (40.5–51.0)
One week (10)	53 ± 8 (40–65)	145 ± 14 (121–165)	216 ± 18 (191–245)	71 ± 6 (63–80)	17 ± 6 (7–26)	12.5 ± 1.8 (9.0–14.5)	23.8 ± 1.5 (22.0–26.0)	25.5 ± 1.3 (23.0–27.0)
One month (9)	149 ± 30 (96–196)	274 ± 32 (232–337)	370 ± 43 (312–438)	123 ± 8 (111–139)	99 ± 12 (79–106)	16.0 ± 1.1 (14.0–17.5)	32.9 ± 3.3 (25.0–36.0)	33.0 ± 2.4 (29.0–36.5)

[1] Data shown are mean ± SD and (range).

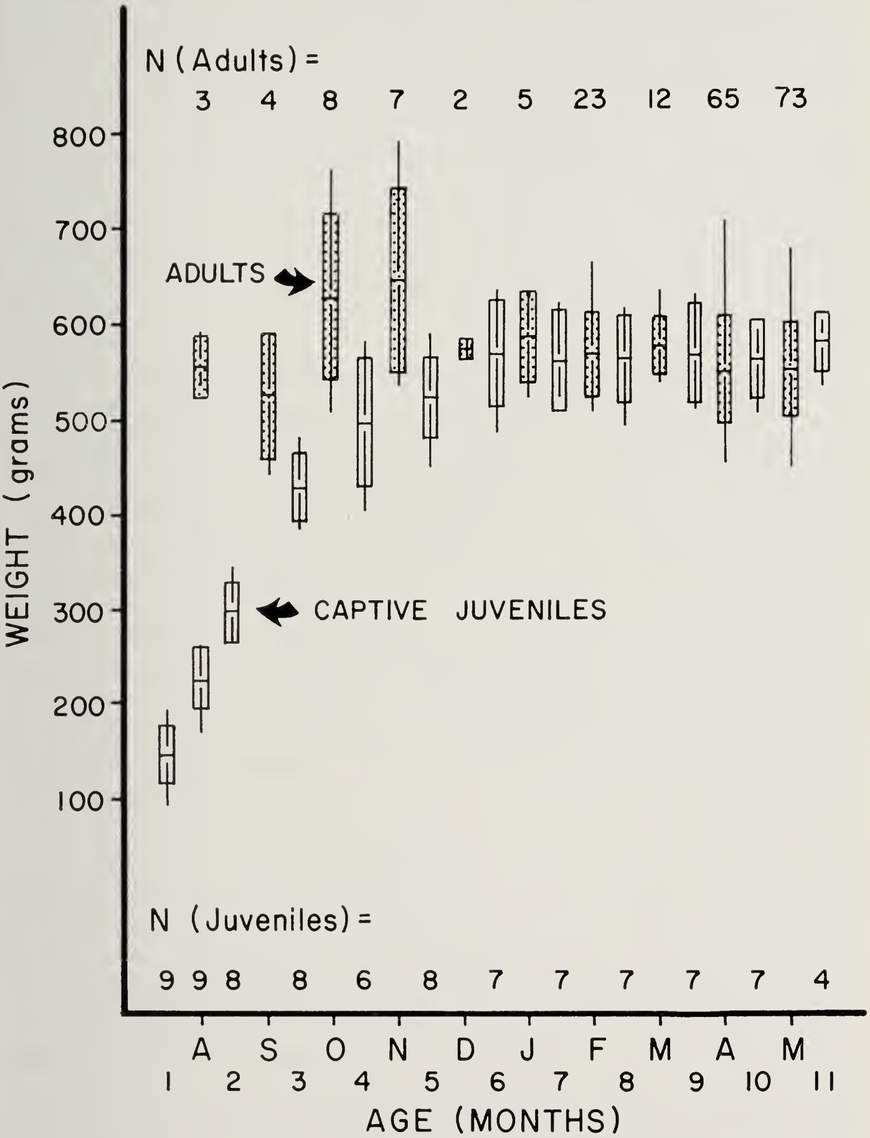

Fig. 2. Weights of wild adults and captive juvenile chachalacas. Data presented are monthly means (± SD) and ranges.

months (Fig. 2). An abundance of natural foods following floods in the fall of 1971 and heavy fat deposition may account for the increased adult weights during October and November. In addition, 11 of the 15 adults measured during these 2 months were males and this may have also contributed to the increase in recorded weights. Average weights of captive juveniles increased rapidly and, at 4 or 5 months of age, approached the 550–600 g level of adults (Fig. 2). Similarly, but at only 3 or 4 months of age, captive juveniles approached adult size in total length, extent or wingspan, wing chord, and lengths of the tail, exposed culmen, tarsus and middle toe. Growth rates for wild juveniles may be slightly slower than this due to the disproportionate sex ratio among the captive juveniles favoring the males (and thus, larger size).

Plumages and molting.—Rectrices begin to develop at less than 1 week of age and grow rapidly. Initial rectrices are uniformly colored and rather narrow with pointed tips which are easily worn and broken. Remiges (except for the outer 3 primaries) are well developed at hatching and continue rapid development for several weeks after hatching.

At approximately 1 month of age, juvenal plumage begins to replace natal plumage and juvenile birds begin to resemble adults. Body feathers of the head and neck region are the last to be replaced by drab olive plumage characteristic of adults. The juvenal plumage stage in this species is relatively short. Juvenile chachalacas replace rectrices and remiges during the postjuvenal molt. Postjuvenal molting of rectrices in captive juveniles occurred between August and December, when the birds were 2–6 months old. Postjuvenal molting began with intermediate pairs (Nos. 3 and 4) in each half of the tail and proceeded both inward and outward until all pairs were replaced. Pair No. 3 was usually replaced slightly before pair No. 4, but both pairs were replaced in late August when juveniles were 2 months old. Replacement of pairs 2 and 5 occurred in late September when the birds were 3 months old. Rectrices 1 and 6 were molted over a longer interval: the central pair (No. 1) was replaced between September and December and the outer pair (No. 6) was replaced between September and January.

Observations of wild juveniles handled during spring banding operations indicated that outer rectrices are occasionally retained until March. These older rectrices are easily recognized since they lack white tips and are obviously old and worn. Following the postjuvenal molt, rectrices of young birds were white-tipped and both remiges and rectrices were relatively broad with rounded tips (as in adults).

After the breeding season each year, feathers are replaced during the postnuptial molt. This molting is gradual and flight is not inhibited. Postnuptial molting of rectrices began as captive juveniles approached 1 year of age and the sequence was extremely irregular compared to the postjuvenal molt which followed a definite sequence (3-4-2-5-1-6). Postnuptial molting of adult rectrices was also irregular, with no obvious pattern or sequence. Most rectrices of adults were molted during August and September, but this occurred as early as May and as late as December.

Molting of primaries was sequential (proximal to distal) for both juvenile and adult birds. Molting observations for remiges of captive juveniles were not recorded prior to the age of 4 months. In the first year, captive juveniles replaced the outer 2 primaries (IX and X) during the postjuvenal molt. In most gallinaceous birds, except Ring-Necked Pheasants (*Phasianus colchicus*), the 2 outer primaries are not replaced during postjuvenal molting (Taber 1963:134).

Captive juveniles began the postnuptial molting of proximal (I and II) primaries in February, 2 months prior to adults and this continued until all distal primaries were replaced in the late summer and fall. Postnuptial molting of adult primaries occurred in an ascending pattern similar to that described for juveniles. Replacement of proximal (I and II) adult primaries began in April and continued until all distal primaries were replaced in the fall. The majority of primary molting in adults occurred during August and September.

Molting of secondary wing feathers was not as distinctly sequential as in primary wing feathers. Secondaries of captive juveniles were molted during all months of year and postjuvenal molt was not clearly distinguishable from the postnuptial molt. Likewise, postnuptial molting of secondaries in adults followed no definite pattern, but most were being replaced during August and September.

SUMMARY

Plain Chachalaca growth and development were investigated in 1971 and 1972 in the Lower Rio Grande Valley of Texas. Chachalaca chicks are precocial and growth and development of juveniles is rapid. At 4 or 5 months of age, juveniles resemble adults and field recognition of differences becomes difficult. Size measurements are valid age criteria only during the summer and fall when juveniles are less than 4 or 5 months old. Differences in tracheal loop development (males), molting of outer primaries and rectrices, color and strength of bills and color of legs are valid criteria for distinguishing juveniles from adults.

Plumage changes also occur rapidly; postjuvenal molting begins in early fall when juveniles are nearly 2 months old. Postjuvenal molting of rectrices follows a definite sequence of pairs (from innermost to outermost) and is usually completed before January of the first year. Juvenal primaries are also molted sequentially from the innermost to the outermost. Postjuvenal molting of secondaries is not distinctly sequential.

Adult rectrices are molted in an irregular pattern during the postnuptial molt (August and September). Adult primaries are molted in a sequential pattern (innermost to outermost), but postnuptial molting of adult secondaries follows no definite pattern.

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SOCIAL DOMINANCE IN WINTER FLOCKS OF CASSIN'S FINCH

Fred B. Samson

Reports of social dominance by females in avian winter flocks are few but have been described in the Bullfinch (*Pyrrhula pyrrhula*; Hinde 1955, 1956; Nicolai 1956) and the House Finch (*Carpodacus mexicanus*; Thompson 1960). I have noted this dominance in the Purple Finch (*Carpodacus p. purpureus*), and it is evident in this study of Cassin's Finch (*Carpodacus cassinii*). The significance of female dominance in winter flocks is not known nor is the importance clearly evident for any pattern of avian social dominance during the winter (Watson and Moss 1970). The purpose of this study of winter flocks in Cassin's Finch was to (1) assess patterns of social dominance, (2) suggest their possible ecological significance, and (3) describe displays involving agonistic or anti-predator behavior.

Cassin's Finch is an irregular winter resident of the Cache Valley in northern Utah (K. L. Dixon, pers. comm.) where I studied flocks during the winters of 1972–73 and 1973–74. I found no flocks in the area in 1971–72 or 1974–75. Aside from fragmentary observations by those engaged in faunistic or winter surveys (Orr 1968 and references cited therein), little is known of the winter behavior or biology of Cassin's Finch.

METHODS

I observed the activity and social dominance of finches almost daily from January to April 1973 and an average of 2 days per week from November 1973 to February 1974.

Five banding stations were established during the winter of 1972–73 at different sites within Cache Valley. All were at least 1 km apart with stations 1 to 4 in residential areas and station 5 at the mouth of Green Canyon. Cassin's Finch visited only stations 2 and 3 during the second winter. I caught few finches in mist nets, but captured most in drop or walk-in traps baited with sunflower seeds and millet. Color of plumage was noted and wing lengths measured for all but 6 of 353 birds captured. Each bird was banded and I marked 131 with distinctive combinations of plastic color leg bands to permit later recognition without recapture.

Cassin's Finch females and yearling males have a similar streaked gray-brown plumage, but all females during the breeding season exhibit an incubation patch and also can be distinguished by wing length (Samson 1976). Wing length measurements in 3 summer populations I studied in northern Utah and those obtained in this study are not significantly different either for older males or gray-brown birds (Samson 1974). A criterion based on wing length similar to that employed for summer populations is used in this study to separate females (wing lengths of 85.0 to 89.9 mm) and yearling males (wing lengths of 90.0 to 96.9 mm). As discussed under head-forward display, feather arrangement also may be used to identify females during agonistic encounters.

I studied patterns of social dominance at or near banding stations. Finches concen-

TABLE 1

LOCATION AND NUMBER OF CASSIN'S FINCHES BANDED AND RECAPTURED

Banding Station	Number Banded	Mean Per Day	Number Recaptured at Banding Stations[1]				
			1	2	3	4	5
			1972–1973				
1	131	9.4	26	26	33	17	2
2	42	14.0	12	11	11	9	
3	64	5.3	8	20	19	10	
4	51	17.0	14	18	23	11	
			1973–1974				
2	38	4.8		29	26		
3	21	2.6		18	19		

[1] An individual bird may have been recaptured at more than 1 location.

trated their activity near the bait and were not observed foraging elsewhere including adjacent mountain and valley terrain which was regularly censused. Criteria of subordination in agonistic encounters included the turning away or lateral body presentation, avoidance, or fleeing of a finch relative to the approach of another individual. I also studied displays and social hierarchies in 2 captive flocks (n = 6, n = 12) maintained in the summer of 1971. Linear social hierarchies constructed from observed encounters among color-marked birds were noted in the 2 captive flocks but not in winter flocks and therefore are not presented in this report. The analysis of social dominance in early 1973 is subdivided by month to consider the influence of possible changes in sex and age ratios on patterns in aggression. Chi-square analyses of data were used to determine statistical significance.

Displays of individual Cassin's Finches were recorded on 111 m of 8 mm color movie film and 25 m of 35 mm black and white film during the second winter for later analysis.

SOCIAL DOMINANCE

Populations.—Of the 288 finches banded in January to April of 1973 (Table 1) 80 were color-banded. Throughout this winter unbanded finches were regularly observed and captured. Whether these birds represented immigrants or unbanded winter residents is not known nor is the total number of winter residents. Finches banded in mid-January were recaptured or observed in early April, suggesting that birds remained for the winter. I caught 59 finches in early winter of 1973–74 (Table 1), and captured or observed few unbanded finches by mid-December 1973. Fifty-one of the 59 captured were color-banded, and these remained in the valley from late November 1973 into February 1974. Only one finch, a female banded in the first winter, was recaptured in the second.

Older males represented 21.9% (63 of 288) of finches banded in the winter

TABLE 2

SOCIAL DOMINANCE IN WINTER FLOCKS OF CASSIN'S FINCH[1]

	Subordinate Bird		
Dominant Bird	Female	Older Male	Yearling Male
January 1973			
Female	7	8	14
Older male	2	9	13
Yearling male	6	15	19
February 1973			
Female	7	21	47
Older male	9	13	39
Yearling male	9	4	22
March 1973			
Female	2	12	17
Older male		16	8
Yearling male		2	23
November 1973–February 1974			
Female	31	134	264
Older male	27	48	263
Yearling male	21	112	140

[1] Numbers refer to victories by group at left over individuals in the respective columns.

of 1972–73 and 54.2% (32 of 59) in 1973–74. Yearling males accounted for 48.6% (140 of 288) of birds banded in the first winter when finches were numerous in contrast to 18.6% (11 of 59) in the second. Females were outnumbered by all males 203:85 in 1972–73 and 43:16 in 1973–74. These sex ratios are similar to disparities favoring males reported by Samson (1976) in 3 breeding populations of Cassin's Finch in northern Utah and to the proportion of males reported in over 15,000 Cassin's Finches banded in North America from 1956 to 1973 (J. Sheppard, pers. comm.).

Patterns of social dominance.—Dominance-subordination in Cassin's Finch winter flocks includes relationships between females, yearling males, and older males as well as between members of each group. Table 2 reflects the general dominance of females over both older and yearling males. The observed dominance by females over both male age classes is significantly different than expected in both winters (Table 3). Although not as successful in winning encounters as females, older males exceeded yearling males in proportion of encounters won in both winters (Table 2) and are dominant over the yearling male age class (Table 3).

TABLE 3

COMPARISON OF SOCIAL DOMINANCE IN WINTER FLOCKS OF CASSIN'S FINCH

	Dominance	
Rate	Result	p[1]
January 1973	females > older males	< .01
	females > yearling males	< .05
	older males > yearling males	< .01
February 1973	females > older males	< .01
	females > yearling males	< .001
	older males > yearling males	< .001
March 1973	females > older males	< .001
	females > yearling males	< .001
	older males > yearling males	< .05
November 1973–February 1974	females > older males	< .001
	females > yearling males	< .001
	older males > yearling males	< .001

[1] Chi-square with df = 1.

Heterosexual encounters most often occurred when a yearling male approached a feeding female or, rarely, when an older male attempted to supplant a female. In neither case were males regularly successful. Encounters of older males and females appeared to involve mistaken sex identification by the male. Females were tolerant of other females, and I noted few interactions in either winter.

Many finches were captured at more than 1 location (Table 1). In both winters, observers at the different locations noted the temporal and spatial association of color-marked birds. Comparison of these records indicates that feeding flocks of Cassin's Finch lack continuity in membership from day to day and from feeder to feeder on any specific day. Pairs did form in these flocks during late winter but well after the establishment of patterns of social dominance. Pair status could not have influenced social dominance exhibited by unpaired females less than a year old over older and yearling males. Thus, the dominance of females as a group appears independent of site, flock composition, or mate status.

Winter disappearance.—The significance of female dominance in Cassin's Finch may relate to improving their survival from breeding season to breeding season. In the winter of 1972–73, 64 of 85 females, 40 of 63 older males and 53 of 140 yearling males were recaptured at least 1 day following the initial banding. Significantly more females ($P < .001$) were recaptured than expected. Conversely, significantly fewer yearling males ($P < .001$) were recaptured than expected. Attempts to locate or observe marked individuals within Cache Valley or adjacent mountain terrain that were not among recaptures were unsuccessful, and I presumed they were dead or had moved from Cache Valley to seek another food source.

Fewer finches were winter residents in 1973–74 (Table 1) and few ($n = 3$) disappeared. The winter of 1973–74 was mild in comparison to 1972–73. Considering that the energy needs of a homeothermic animal increase as temperature decreases, both the milder winter conditions and fewer finches present to exploit available food resources may have contributed to the disappearance of few finches during the 1973–1974 winter.

DISPLAYS

Head-forward.—This display in Cassin's Finch varied in intensity and, as in other finches (Hinde 1955, 1956; Dilger 1960; Coutlee 1967), is divided into 2 categories, the low intensity head-forward display and the high intensity head-forward display. The closed beak is directed toward the opponent, the neck partially extended, legs slightly flexed, with the body tending toward a horizontal posture in the low intensity head-forward display (Fig. 1A). If the aggressor is a female, the feathers of the forehead, breast. and back are "shuffled" (Fig. 1B) as in the House Finch (Thompson 1960). With females and yearling males nearly identical in plumage, this shuffling of feathers serves as a visual cue for sex identification in agonistic encounters. Rarely did females employ any other display to maintain their dominance or preferential access to food or roost. Vocalizations did not accompany this or any other display.

Figure 1C depicts the high intensity head-forward display. The beak is usually but not always open, the head and body feathers are sleeked, and the long axis of the body is horizontal and in line with the opponent. If the opponent was above or below the attacker, the head was directed toward the opponent and the tail slightly raised. During the most intense head-forward displays, both wings were raised through rotation at the shoulder (Fig. 1D). Although performed by females and older males, the high intensity head-forward display was especially evident in encounters between yearling males.

Combat.—I rarely noted combat (Fig. 1E) between older males, among females, or in inter-sex encounters and did not observe it in the milder winter of 1973–74. Combat when evident usually occurred between yearling males. If a high intensity head-forward display was insufficient to dislodge an opponent, the attacker would proceed directly at the opponent with wings raised. If the opponent failed to yield, combat resulted. Combat did not result in noticeable body damage, and in most cases it was of short duration.

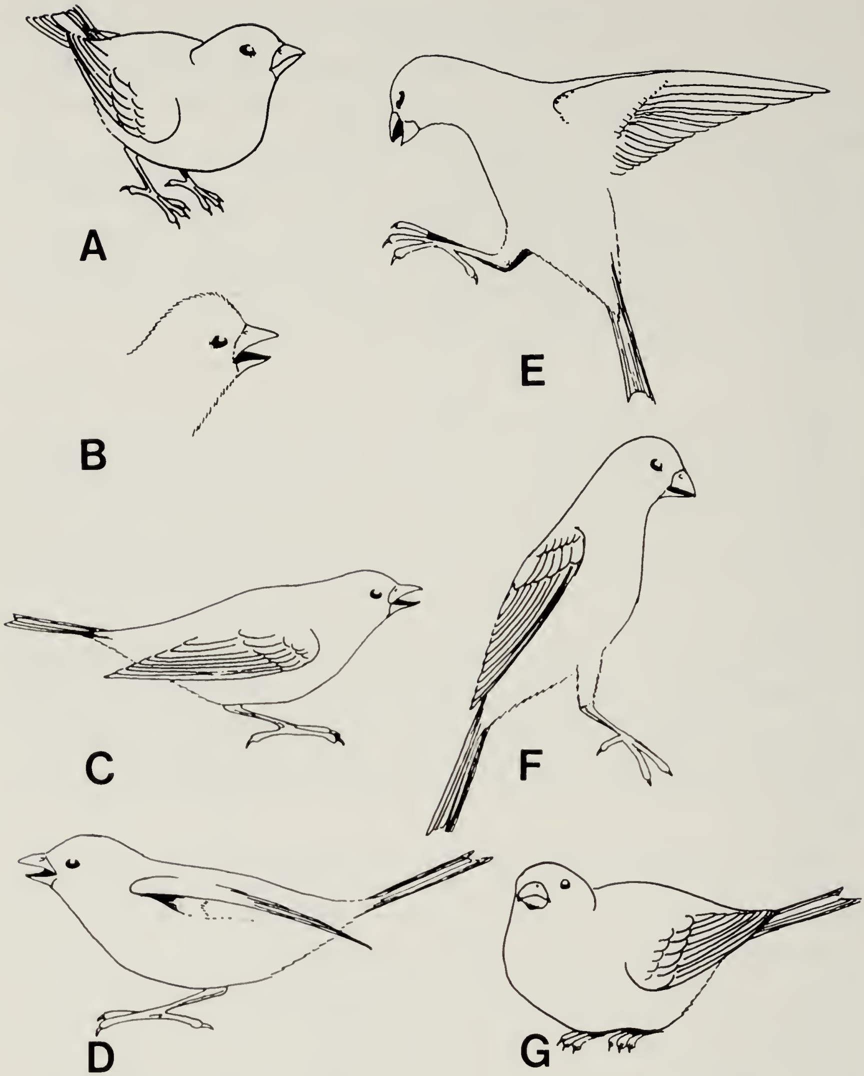

Fig. 1. Postures of Cassin's Finch: (A) low intensity head-forward; (B) female with head, neck and upper breast feathers shuffled; (C) and (D) high intensity head-forward; (E) combat; (F) submissive; and (G) anti-predator.

Often, the birds would fly up almost vertically continuing to engage in combat before one or both birds withdrew to separate perches. Beaks remained open and feet extended during the combat phase of these flights.

Submission.—When approached by an aggressor, submissive birds often assumed an erect, stiff-legged posture leaning away from the attacker (Fig. 1F). If not directly approached but in the presence of a dominant bird, subordinate birds would flex their legs and assume a partially crouched posture similar to that described for other fringillids (Hinde 1956, 1957; Thompson 1960; Coutlee 1967). This posture is similar to that observed when an avian predator was present (Fig. 1G). Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*Accipiter cooperii*), and Northern Shrikes (*Lanius excubitor*) were active and preyed on Cassin's Finches near banding stations. Finches in this posture remained stationary moving only the upper throat until the predator departed. The legs were flexed so that the breast and abdomen nearly rested on the substrate.

Supplanting and avoidance.—As in the House Finch (Thompson 1960), I did not see special behavior by an attacking finch prior to supplanting a second bird. The direct or frontal presentation described for other Fringillidae (Hinde 1955, 1956) is apparent in Cassin's Finch. In nearly all attempted supplants, the attacked bird flew before the attacker landed. When the attacked bird did not flee, a lateral body presentation, a submissive posture, or a slight fluffing of the feathers were considered indicators of avoidance. Aggressive chases among finches associated with supplanting were not observed either winter. Displacement activities (i.e., bill wiping, head scratching, breast preening) were rarely observed in free-flying flocks but were common in the 2 captive flocks.

DISCUSSION

Social dominance is not uncommon in avian winter flocks (Brian 1949, Sabine 1959, Dixon 1963, 1965; Kikkawa 1961, Zahavi 1971). In these studies, males or males and their mates are reported dominant. In the House Finch (Thompson 1960), Purple Finch and Cassin's Finch, the members of this genus which breed in North America, females in winter flocks are either as or more dominant than males in agonistic encounters.

This social dominance in Cassin's Finch is considered independent of location in contrast to the importance of site attachment in other species (Brown 1963, Dixon 1963). It may be related to (1) their lack of annual fidelity to a winter area (Bailey and Niedrach 1965, Buckley 1973), (2) the lack of consistent flock organization as in certain other carduelines (Newton 1972), (3) the mobility of the species, or (4) the variable number of finches at a winter area which may range from none as in Cache Valley in 1971–72, 1974–75 to over 5000 as reported in northern Colorado (Chapin 1958).

Other studies of finch populations during the winter (Fretwell 1969, Pulliam and Enders 1971, Davis 1973) point out that food is important in determining population levels and that intraspecific competition may influence patterns of mortality. Newton (1964) provided evidence in the Bullfinch and Murton et al. (1966) in Wood Pigeon (*Columba palumbus*) that the availability of winter food influences subsequent breeding population numbers. In Cassin's Finch (Samson 1976) as in 2 other montane finches with sex ratios favoring males, the Black Rosy Finch (*Lecousticte atrata*, French 1959) and the Gray-crowned Rosy Finch (*L. tephrocotis*, Johnson 1965), the number of females is considered the limiting resource for reproductive effort. The significance of female dominance in Cassin's Finch appears to involve the protection of this limiting resource during the non-breeding season. Survival of females is enhanced by preferential access to food and roost sites in winter, thus allowing for maximization of reproductive effort during the subsequent breeding season. Considering that Cassin's Finch, lacking a strong fidelity to a wintering area or breeding area, must colonize new wintering and breeding areas annually, a reproductive strategy to maximize reproductive effort may represent an important correlate to their nomadic lifestyle and enhance the efficient use of an unpredictable environment (i.e., food and weather). These habitat and species correlates all pertain to an *r*-strategy (Pianka 1970). Opportunism and reproductive strategy in North American birds have not, however, been intensively studied (Cody 1972).

The displays used by Cassin's Finch in agonistic encounters are generally homologous to those of the House Finch and to other fringillids (Hinde 1955, 1956; Coutlee 1967). Cassin's Finch does differ from many fringillids in that vocalizations did not accompany displays. This was particularly evident in interspecific encounters between the Cassin's Finch and the House Finch, the latter regularly using vocalizations in association with certain intense agonistic displays.

In nearly all phases of its annual cycle, Cassin's Finch tends to flock. The flocks are characterized by an absence of agonistic encounters except in winter and in those of yearling males which remain at high altitudes in late summer after other Cassin's Finches have departed. Except among yearling males, the lack of intense agonistic encounters observed in this study may contribute to the flocking tendency. Aggressive behavior did increase at a food source as in the House Finch (Thompson 1960), but this increase was not as substantial as that observed in early 1973 when weather conditions were severe and finches numerous. Nor, was it as intense as in yearling male flocks in late summer (Samson 1976).

Females and yearling male Cassin's Finches are well camouflaged in their striped gray-brown plumage when roosting on woody branches or foraging under a forest or shrub canopy. This coloration combined with the motionless anti-predator posture may enhance their survival from breeding season to breeding season. However, the explanation for the imbalance in the sex ratios, subadult male plumage, and possible hormonal factors influencing female dominance in Cassin's Finch remains to be resolved.

SUMMARY

Female Cassin's Finches were determined socially dominant over older and yearling males in flocks during 2 winters. Few females disappeared either winter in contrast to males. With number of females limiting for breeding effort, the dominance of females in winter is interpreted as a behavioral modification to maximize reproductive effort. This species' trait and the need to semiannually colonize a new and often unpredictable environment are correlates of an *r*-strategy. Displays in agonistic encounters are considered homologous to other fringillids. Reasons for the observed disparities in sex ratio or hormonal factors influencing female dominance are not known.

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INTER-BROOD MOVEMENTS OF JUVENILE SPRUCE GROUSE

Daniel M. Keppie

Juvenile tetraonids form broods during most of their first summer of life. Undoubtedly this contact between parent and offspring has survival value for the chicks, particularly during development of thermoregulation and perhaps for acquisition of learned behavior. Presumably, a brood consists of a single family, yet a survey of 26 theses and published reports pertaining to brood size and behavior of tetraonids revealed 10 in which the author suspected broods contained chicks from different hens (Lehmann 1941, Wing et al. 1944, Bump et al. 1947:293, Patterson 1952:135, Bendell 1955, Chambers and Sharp 1958, Dalke et al. 1963, Bendell and Elliott 1967, Braun and Rogers 1971, Harju 1974). But the evidence is based only on observations of juveniles of different sizes or estimated ages or, supposedly, an excess number of chicks. Inter-brood movements among tetraonids apparently do not occur on the massive scale reported for aquatic birds (Beard 1964, Gorman and Milne 1972). There is little known about the frequency of occurrence and circumstances surrounding inter-brood movements of grouse.

Herein I document inter-brood movements of juvenile Spruce Grouse (*Canachites canadensis*), calculate their frequency of occurrence, and briefly question the function of broods remaining as individual units over a long period of time.

METHODS

Data were gathered from marked birds incidental to a population study at Gorge Creek (GC) and Blue Rock Creek (BRC), 27–32 km west of Turner Valley, Alberta from 1970 through 1973. Grouse were located by repeatedly searching the study areas with trained pointing dogs. All hens with broods known to be on the study areas were captured and marked. Numbers of juveniles and their survival were determined from counts of brood size and records of marked individuals. Young chicks were marked with numbered wing tags (size no. 1, National Band and Tag, Newport, Ky.); leg bands were used after about 40 days of age. Juvenile age was determined by growth of primaries (McCourt and Keppie 1975).

RESULTS

The efficiency of tagging grouse is shown in Table 1. In 3 of the 4 summers, over 50% of the maximum number of juveniles seen were marked by 14 days of age and about 80% by 42 days of age. All juveniles that survived until the end of the brood period were marked by that time.

Broods were seen on 428 occasions in 4 years: in only 8 instances (2%)

TABLE 1

PERCENTAGES OF JUVENILE SPRUCE GROUSE MARKED BY 7, 14, 28, AND 42 DAYS OF AGE, 1970–73

	Year and Area				
	1970		1971	1972	1973
Age of bird (days)	GC (66)* (53)**	BRC (30) (24)	GC (103) (97)	GC (88) (84)	GC (89) (77)
7	6	0	35	43	39
14	9	3	56	58	54
28	32	13	70	68	71
42	52	23	84	81	79

* Maximum number of different juveniles sighted.
** Number juveniles marked in brood period.

were 2 found within 50 m of each other (Table 2), but brood ranges were not mutually exclusive. Nineteen % of the occupied habitat (all years) was included in overlap, i.e., within home ranges of different hens. Some habitat was within the home range of up to 4 families. In one instance (GC, 1971), 6 broods were present on a 108 ha plot, and although 37% of the area was used by 2 or more broods only 2% (1/44) of the sightings were of 2 broods together. In all years, overlap of brood ranges probably was greater than recorded because sightings of broods were limited.

Among the 8 occasions that 2 broods were together, 33 juveniles were already tagged and 32 of these were seen with the same hen at a later date. The remaining juvenile joined the second hen when the 2 broods came together. In one sighting of 2 broods, both hens simultaneously called to their chicks from adjacent trees yet the 4 marked juveniles were seen later with the "correct" adult.

There were 12 instances of 11 marked juveniles (7 females, 4 males) moving from a total of 7 broods. Four of the 7 hens were known or assumed to have died. Three juveniles moved from 3 other hens that remained alive, but one of these juveniles was previously orphaned. In all cases in which the hen remained alive (3) only one juvenile moved to a new brood; the only instances (2) of siblings moving together to a new family occurred when the original hen died. All 11 juveniles were at least 11 days old when mixing occurred and all joined broods that occupied overlapping or adjacent home ranges. Ten of these juveniles (91%) survived until at least the end of summer. Survival beyond summer was not determined because many juveniles dispersed in autumn.

Seven hens were known or assumed to have died while with juveniles; 6

TABLE 2

SUMMARY OF BROOD SIGHTINGS AND INTER-BROOD MOVEMENTS OF JUVENILE SPRUCE GROUSE, 1970–73

	Year and Area					
	1970		1971	1972	1973	
	GC	BRC	GC	GC	GC	All Yrs
Size of area (km^2)	5.2	1.6	6.8	6.8	6.8	–
No. broods[1]	15	6	20	20	18	79
broods/km^2	2.9	3.8	3.9	3.9	3.5	–
No. contacts with broods	57	28	118	121	104	428
No. sightings of 2 broods/contact	1	2	1	2	2	8
% of total	1.8	7.1	0.8	1.7	1.9	1.9
No. juveniles alive after about 2 weeks of age	56	29	69	50	62	266
No. marked juvs. known to change broods	1	1	4	1	4	11
% of total	1.8	3.5	5.8	2.0	6.5	4.1

[1] Broods are excluded if all chicks were lost early.

deaths were at least 11 days after hatch (11–22, 17–22, 17–30, 40, 40–43, and 54 days). In this sample, the probable number of chicks alive when the hens died was 27, of which 20 (74%) were still alive at the end of summer (2 others died from handling). By contrast, a hen died at 4–9 days post-hatch and her 3 chicks were not seen again. This brood was rather isolated and if the juveniles did not die at the same time as the hen they may have had difficulty locating another family.

Although data are limited and not clear-cut, the "need" for orphaned juveniles to seek out a new brood may have varied with age. In 3 broods the hen died before 30 days post-hatch; juveniles in 2 of these joined new families within 9 days, and juveniles in the third brood were captured with a new hen 28 days after the death of the hen. A brood count suggested juveniles in this latter brood were present in a new brood 10 days after the original hen died. Three broods were orphaned after 40 days of age and the juveniles were seen later as intact units without a hen. Juveniles of one of these latter broods were without a new hen for at least 26 days, and only one of the 7 chicks then joined a new family; juveniles in the other 2 broods remained together for 8 and 11 days until they dispersed.

The frequency of brood interchange was calculated from the number of juveniles remaining after about 2 weeks of age (Table 2) because this probably excludes most of the high losses from natural mortality (Zwickel and Bendell 1967). Four % of the juveniles surviving beyond about 2 weeks of age were known to join other broods. At GC, slightly greater mixing occurred in 1971 and 1973 and resulted from several siblings, rather than one chick per brood, moving to other families.

DISCUSSION

Although brood ranges of Spruce Grouse were not mutually exclusive, there were few documented exchanges of juveniles between broods. Proportions of juveniles recorded changing broods probably were overestimates for the cohort hatched unless considerable mixing occurred before chicks were marked.

The frequency of 2 broods coming together likely was greater than recorded, but when considered on a temporal basis such gatherings probably still constituted a small proportion of the brood period. Call notes seemingly function to maintain contact between hen and chicks (Zwickel 1967, this study), and individuality of call notes might facilitate proper reorganization when broods come together. Although there were few records of 2 broods together, the observation that juveniles reunited with their respective parent, coupled with individuality of sound, generates the question of whether survival of a juvenile is enhanced by staying with its respective mother. At least short term survival was good for juvenile Spruce Grouse that changed broods; survival also was good for juveniles that were orphaned. Survival of orphaned juveniles might be age related, requiring the full development of thermoregulation, and for young chicks (< 2 weeks old) the proximity of another brood might be critical to survival.

Several authors have speculated on causes of inter-brood movements of grouse, such as the death of a hen (Bump et al. 1947:293), a loose feeding formation and lack of an efficient rallying call (Lehmann 1941), and a concentration of broods (Wing et al. 1944, Bendell 1955). Bendell (1955) further suggested weather as the ultimate cause, by its influence on plant growth and distribution of preferred feeding sites. Death of hen Spruce Grouse seemed to be a cause for juveniles switching broods, but perhaps only when juveniles were young. There was no evidence of a weak cohesion among family members, concentration of broods, nor preferred or localized feeding sites. I do now know whether densities of broods in this study were high for Spruce Grouse; they were generally as high or higher than densities recorded by others (Ellison 1974, McCourt 1969). It is open to question whether higher densities might reduce the effectiveness of calling for maintaining brood organization, resulting in greater exchange of juveniles. There was no effect of movements between broods in summer on mean brood size. Many juveniles temporarily join other families while dispersing in autumn

(Keppie, unpubl. data) and biases on counts of brood size would be greatest at that time.

Whether a specific mechanism or simple chance accounts for separation of grouse broods (Bendell and Elliott 1967, Zwickel 1973, Godfrey 1975; this study) is unknown. Dispersion of broods may result from other factors operating earlier during courtship and nesting. Perhaps brood dispersion enhances survival of the chicks, but present data on survival until autumn for juveniles switching broods do not support this idea. If juveniles that move to a different brood survive, and if juveniles of a certain age can live without a hen, we should focus attention on the purpose of the dispersion pattern and why hen and chicks maintain contact longer than seems necessary.

SUMMARY

Inter-brood movements of juvenile Spruce Grouse were recorded in Alberta from 1970 through 1973. Although brood ranges were not mutually exclusive, broods generally maintained their original constituency. Only 4% of the marked juveniles changed broods; they moved from 7 broods and in 4 cases the hen had died. All juveniles that moved were at least 11 days old and all joined a family in the immediate vicinity. Juveniles that changed broods or which were orphaned survived well until autumn. Although data are limited on the fate of juveniles that mix or which are orphaned, the question arises as to why broods exist as individual units for perhaps longer than necessary to ensure survival of the chicks.

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BREEDING BIOLOGY OF YEAR-OLD AND OLDER FEMALE RED-WINGED AND YELLOW-HEADED BLACKBIRDS

Richard D. Crawford

Age of male Red-winged (*Agelaius phoeniceus*) and Yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) is known to influence their breeding behavior (Orians 1961, Willson 1966), but little effort has been devoted to the comparative breeding biology between age classes of females. Both species are polygynous (Verner and Willson 1969) ; how age might affect the females within this system, however, is unknown. The objective of this study was to compare data on selected parameters of breeding between yearling and older adult females of both species.

Field work was conducted from 1972–1974 on Dewey's Pasture and Dan Green Slough, 2 glacial marshes in northwestern Iowa that have been described by Bennett (1938).

METHODS

Red-wings were aged by using the methods presented by Nero (1954, 1961) and Meanley and Bond (1970) ; yearling females have a pink or salmon epaulet and light pink chin and face, while older females show a more crimson epaulet and dark pink chin and face. To verify this aging technique, I initiated a banding program in 1972. Eighteen females were recaptured in years after their banding, 7 of which were yearlings. Both yearlings and older adults showed patterns similar to those described.

No similar aging technique exists for Yellow-heads, but Bent (1958:112) described the first-year female as "much like the adults, but colors are more veiled." By examining 21 returning marked females (11 yearlings and 10 older adults), I was able to establish that yearlings have lighter breasts, throats, and facial regions than older adults.

A major advantage of the aging techniques for both species is that an observer can readily distinguish ages in the field.

Observations on the nesting activities of both species began in late May of each year. Most females were captured, banded, and classed as either year-old or older. The few females not trapped were aged in the field by the methods described. After incubation had begun, nests were checked only every 2 or 3 days to minimize disturbance; the nestlings used for growth rate studies, however, were checked daily.

The date the first egg was laid was used as an indicator of nesting chronology. If not known precisely, this date was estimated, considering 12 days to be an average incubation period for both species (Nero 1961, Willson 1966). Only first nests were used for analysis. Statistical comparisons were made with Student's t-test (Steel and Torrie 1960).

RESULTS

Nesting chronology, clutch size, and egg size.—Yearling Red-wing and Yellow-head females began nesting an average of 15 and 16 days later, respec-

TABLE 1

DATES OF NEST INITIATION (1972–1974)

	N	Mean ± 2 S.E. (days)	Range
RW yearling[1]	67	8 June ± 5.2	25 May–18 June
RW older adult	41	25 May ± 5.7	19 May– 5 June
YH yearling	71	7 June ± 4.9	22 May–15 June
YH older adult	49	23 May ± 5.4	18 May–29 May

[1] RW = Red-winged Blackbird, YH = Yellow-headed Blackbird.

tively, than older adults (Table 1). The yearlings also showed a greater range in nest initiation dates. The differences between nest initiation dates of yearlings and older adults were highly significant for both species ($P < 0.01$).

Means and frequencies of clutch sizes observed are given in Table 2. Yearling females of both species had significantly smaller clutches than older females ($P < 0.01$). The mean values are similar to those of other studies. The average clutch size was 3.1 for 504 Yellow-head nests in Iowa (Ammann 1938); 3.7 for 118 nests in Utah (Fautin 1941); and 3.6 for 371 nests in Washington (Willson 1966). For the Red-wing, average clutch sizes reported were 3.5 for 926 nests in New York (Case and Hewitt 1963); 3.4 for 243 nests in Oklahoma (Goddard and Board 1967); and 4.2 for 13 nests in Missouri (Crawford 1970).

Yearling females of both species laid significantly shorter eggs than older females ($P < 0.01$) (Table 3). Egg width did not differ significantly for either species ($P > 0.05$). The mean values for both length and width are similar to those found in other studies (Bendire 1895. Reed 1965).

TABLE 2

CLUTCH SIZE AND FLEDGING SUCCESS (1972–1974)

	Clutch Size					Mean Fledged Young Per Nest
	2	3	4	5	Mean	
RW yearling	4[1]	37	34		3.40	0.73 (71)[2]
RW older adult		1	40	6	4.11	1.63 (40)
RW all ages	4	38	74	6	3.67	1.05 (111)
YH yearling	8	49	31		3.30	0.87 (83)
YH older adult			51	6	4.11	1.81 (52)
YH all ages	8	49	82	6	3.62	1.30 (135)

[1] Number of clutches.
[2] Sample size in parentheses.

TABLE 3

EGG SIZES (1972–1974)

	N	Mean (mm) Length	Mean (mm) Width
RW yearling	165	22.1	17.0
RW older adult	145	26.8	18.2
YH yearling	181	23.2	17.3
YH older adult	157	27.1	18.9

Nestling growth and fledging success.—At hatching, nestlings of yearling females averaged only slightly smaller than those of older adults; weights at 10 days of age, however, were significantly lower for nestlings reared by yearling females ($P < 0.01$) (Table 4). Male nestlings of both species have been reported to grow faster and attain greater weights at fledging than females of the same age (Ammann 1938, Williams 1940, Holcomb and Twiest 1971). I assumed in this study that the sex ratio was constant throughout the nestling period and that differences in sex-specific weights would have no net effect.

Fledging success is given in Table 2. Yearling females of both species fledged significantly fewer young than did older females ($P < 0.01$). The fledging successes reported in this study are similar to those reported elsewhere (Wood 1938, Willson 1966, Goddard and Board 1967).

Pairing status of age classes.—Data on pairing status and its relationship to age were collected on 30 Red-wing and 20 Yellow-head territories during

TABLE 4

GROWTH IN WEIGHT (G) OF NESTLINGS (1972–1974)

	Red-wing		Yellow-head	
Age (days)	yearling	older adult	yearling	older adult
1	3.6 (65)[1]	4.0 (44)	3.9 (66)	4.1 (49)
2	5.8 (48)	6.1 (37)	6.8 (50)	7.0 (40)
3	8.8 (47)	9.5 (30)	10.4 (49)	10.8 (36)
4	12.7 (39)	13.7 (27)	16.5 (43)	16.8 (35)
5	16.6 (36)	18.9 (23)	22.0 (40)	22.5 (29)
6	21.1 (28)	24.2 (22)	28.7 (33)	29.9 (24)
7	25.9 (19)	27.3 (20)	33.1 (24)	35.8 (19)
8	28.3 (15)	31.6 (16)	37.3 (16)	40.7 (17)
9	30.4 (11)	34.3 (13)	40.5 (13)	45.1 (15)
10	32.1 (10)	37.4 (12)	43.7 (10)	49.3 (11)

[1] Sample size in parentheses.

TABLE 5

MEAN CLUTCH SIZE AND FLEDGING SUCCESS IN RELATION TO PAIRING STATUS (1973–1974)

	Primary Female			Secondary Female		
	N	CS[1]	FS[1]	N	CS	FS
RW yearling	6	4.0	1.2	29	2.9	0.6
RW older adult	24	4.2	1.8	11	4.1	1.3
YH yearling	7	4.0	2.0	17	2.8	0.8
YH older adult	13	4.1	2.0	4	4.0	1.2

[1] CS = clutch size, FS = fledging success.

1973–74. Herein, I use the terminology of Martin (1974); the first female to nest in a male's territory is referred to as the primary female, and all those nesting subsequently are termed secondary females.

Table 5 presents data for females where pairing status was determined. For the Red-wing, most primary females were older adults. Some older adults were secondary females, but in all such instances, the primary female was also an older adult. Only 6 yearlings were primary females, 4 of which mated monogamously, and the other 2 mated polygynously where the secondary females were also yearlings. In no instance was a yearling female the primary mate and an older female secondary within the same territory.

A similar situation existed for the Yellow-head (Table 5). All yearling primary females mated monogamously, and all older adult secondary females were secondary only to other older adults.

Further evidence to suggest that age is an important factor influencing pairing status was gained by examining data from returning females of known age (Table 6). In most instances, females were secondary as yearlings and primary when 2 years old; 2 females, however, were secondary both as yearlings and as 2-year-old birds, and 1 female was primary when a yearling as well as when she was 2 years old.

To determine if differences in breeding biology existed in relation to pairing status, data were compared between yearling and older females of both species (Table 5). Older adult primary females did not show significantly larger clutches than older adult secondary females ($P > 0.05$), but primary yearling females of both species laid significantly larger clutches than did secondary yearling females ($P < 0.01$). Trends similar to these also were found in the clutch sizes of known-age females (Table 6). Yearling females fledged significantly ($P < 0.01$) fewer young than did older adults for all pairing situations, except for primary Yellow-heads (Table 5). Yearling and older adult primary females of both species fledged significantly more young than did secondary

TABLE 6

PAIRING STATUS AND CLUTCH SIZE OF RETURNING KNOWN-AGE FEMALES (1973–1974)[1]

Species	Female No.	Age	
		Yearling	2 years old
Red-wing	DP74	II° (3)	I° (4)
	DP97	II° (3)	I° (4)
	DP189	II° (2)	II° (3)
	DP191	II° (4)	I° (4)
Yellow-head	DP67	II° (3)	I° (5)
	DP96	II° (3)	I° (4)
	DP157	II° (3)	II° (3)
	DP181	I° (4)	I° (5)
	DP192	II° (3)	I° (4)
	DP197	II° (3)	I° (4)

[1] I° = primary female, II° = secondary female, number in parentheses is clutch size.

females ($P < 0.01$). Egg size within age groups was not influenced by pairing status. Sample sizes were inadequate to analyze differences in nesting chronology or fledgling weight between primary and secondary females.

DISCUSSION

Lighter-colored females have been noted several times in breeding populations of both species (Nero 1954, Bent 1958, Strosnider 1960), but little comment has been made regarding breeding success of these females. Data presented in this paper suggest that these females are yearlings and that they contribute less to total population production than older females.

Why yearling females breed later than older adults is unclear, but apparently Red-wing yearling females migrate later in the spring than older females (Allen 1914, Nero 1956a). Also, females of both species actively defend their sub-territories against trespass by other females (Nero 1956b, Willson 1966). Possibly one or both of these factors may act to delay breeding by yearling females.

Goddard and Board (1967) noted that early Red-wing nests had larger clutches, were more successful, and fledged more young than later nests, but no indications were given as to causative factors involved. Holm (1973) stated that late arriving females and some early arriving females may be forced to occupy territories in poorer habitats. No data were collected on territory quality in this study, but it is possible that late arriving females (apparently yearlings) are forced to occupy sub-optimum territories and, thus, produce smaller clutches and fewer young.

In a study of the adaptations for polygynous breeding in Bobolinks (*Dolichonyx oryzivorus*), Martin (1974) found that yearling females laid smaller clutches than older females, and primary females received more assistance in nestling care by the male, laid larger clutches, and fledged more young than did secondary females. He hypothesized that primary females laid larger clutches than secondary females mainly because males feed nestlings of primary females more often than they do of secondary females. Yellow-head males are known to feed young in primary nests more often than in secondary nests (Willson 1966). Data from other studies suggest that Red-wing males do not feed their young (Nero 1956a, Holm 1973), but some exceptions are noted (Bent 1958, Case and Hewitt 1963). Why this difference exists is unknown.

Why older adult females did not show a significant difference in clutch size relative to pairing status is not clear. Possibly older adult females, being more experienced in nestling care, would be able to raise more young without help from a male than would yearling secondary females.

Data presented here show that age has a pronounced effect on the breeding biology of Red-wings and Yellow-heads. Although a few studies of other species (e.g. Leinonen 1973, Koskimies 1957) indicate that age has little or no effect on some parameters of breeding, I believe that most species will show age-related differences worthy of study. Other studies (e.g. Laskey 1943, Snow 1958, Lack 1966, Crawford 1974, 1975a, 1975b) have discussed other ways in which age may influence reproduction in birds. Further studies should be conducted so that a more complete understanding of reproduction in relation to age may be attained.

SUMMARY

The relationships between age and breeding biology of female Red-winged and Yellow-headed blackbirds were studied in northwestern Iowa during 1972–1974. Yearling females of both species began nesting later, laid shorter eggs, and fledged fewer and slightly smaller young than did older females. Primary (first-nesting) females were mostly older adults while yearlings were typically of secondary status. Yearling primary females laid larger clutches than did yearling secondary females, but both yearling and older adult primary females fledged more young than did secondary females of the same age. Possible factors affecting delayed breeding and subsequent reduced production of yearlings are discussed.

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FOOD HABITS OF OLDSQUAWS WINTERING ON LAKE MICHIGAN

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Several trophic levels in Lake Michigan have been shown to be contaminated with organochlorines (Hickey et al. 1966), and contaminants that are not biodegradable are passed through the food chain from one organism to the next. Knowledge of the food habits of bird species wintering on the lake would be useful in measuring the movement of these contaminants from the aquatic environment and should help us interpret the distribution and activity of the birds on the lake. This report summarizes data on the food habits of Oldsquaws (*Clangula hyemalis*) collected during 2 periods: 1951–1954 and 1969–1972. Cottam (1939), Lagler and Wienert (1948), and Zimmerman (1953) have previously reported on the gizzard contents of a few Oldsquaws collected from commercial fishermen on Lake Michigan.

METHODS

We collected Oldsquaws from commercial fishermen who found them caught in gill nets between November and May. These nets are suspended along the bottom in water 18–46 m deep, with the leads holding the lower part of the net on the substrate and the floats keeping the mesh upright off the bottom. Presumably, since the nets are only about 1.5 m high, any birds captured would be actively feeding at or near the bottom. Even though some birds may have remained in the nets for up to 1 week before removal, the cold water prevented extensive decomposition of the esophageal material. After the specimens were removed from the nets, they were frozen until dissection and examination could be completed.

In the 1951–1954 study, 10 birds were taken from each catch of Oldsquaws and only those which had significant quantities of food were saved. Samples were collected from southeastern Lake Michigan (South Haven, Saugatuck, Holland, Muskegon), southwestern Lake Michigan (Kenosha, Racine), and northern Lake Michigan (Port Washington, Two Rivers, Gills Rock, Washington Island). From this part of the study we analyzed 192 specimens: 41 were of gizzards only and 151 were of gizzards and gullets (esophagus plus proventriculus). Food items were separated and volume to the nearest 0.1 ml and frequency of occurrence of items were recorded.

In the 1969–1972 study, we only recorded material from the esophagus because Dillon (1957), Bartonek and Hickey (1969), and Swanson and Bartonek (1970) demonstrated differences in the contents of the esophagus, proventriculus, and gizzard. Ellarson's (1956) analysis of the 1951–1954 material indicated a rapid decomposition of the material once it reached the proventriculus. In the 1969–1972 study period, specimens were obtained only from Gills Rock and Washington Island (northern Lake Michigan). We examined as many specimens as possible (956) and recorded those specimens with nothing present in the gullet as well as those having fed. Only the total volume of food present in the esophagus and the frequency of occurrence of food items were recorded.

The lipid content of specimens was determined from a 25 g sample of the homogenized carcass (head, wings, feet, feathers, and gastrointestinal tract removed). After a sample was dried in a 40°C oven for 72–96 hours, it was ground with 100 g Na_2SO_4 and extracted 8 hours on a soxhlet extractor using 70 ml ethyl ether and 170 ml petroleum ether. An aliquot of the extract was then reduced to dryness, weighed, and the amount of ether-soluble lipid determined.

RESULTS

Ingested Material

Grit content of gizzards.—The volume of grit in the 1951–1954 sample was constant among gullets. The ratio of grit to total gizzard and gullet content, for all samples, was 24.7%, and the ratio of sand (<2 mm) to gravel (>2 mm) was consistently about 9:1. Besides sand and gravel, grit was composed of coal cinders and ash from steamships as well as limonitic oolites. In the northern part of the lake, ¾ of the total grit content was oolite material. The constant ratios of food to grit and sand to gravel suggest some internal mechanism regulating grit retention in the gizzard. Excessive quantities of sand are possibly ingested with the food organisms and voided into the intestinal tract because the fecal material is gritty and fluoroscopic examination ($n = 2106$) indicated the lower intestinal tract was laden with sand. Sand often occurred in the esophagus when no animal or vegetable matter was present. In the 1969–1972 study, sand occurred in 83% of all esophagi examined and 90% of all esophagi with food organisms present. Gravel occurred in 28 and 30% of these samples respectively.

Crustaceans.—In the 1951–1954 sample, animal matter constituted 99% of the food volume in 151 gizzards and was present in all 192 gullets and gizzards examined (Table 1). Amphipods (*Pontoporeia affinis*) made up 82% of that volume. In the 1951–1954 sample, amphipods rated between 85 and 100% frequency of occurrence, depending on the area where taken, while in the 1969–1972 sample, they were found in 88% of all gullets examined and 95% of all gullets with some material present (Table 2). One gizzard contained 2 chelae of a small crayfish in the 1951–1954 sample.

Mollusks.—Gastropods (snails) and pelecypods (clams) constituted a relatively small proportion of the volume of gizzard contents (3.9% in 1951–1954), but their frequency of occurrence was high (51 to 79% in 1951–1954), second only to amphipods. Clams (Sphaeriidae) were present in 51 to 76% of the 1951–1954 esophagus and gizzard samples and in 61 to 65% of the 1969–1972 esophagus samples, while snails (*Cyraulus* and *Amnicola*) were present in 9 to 20% and 11 to 12% of the respective samples. The clams were generally very small: 25 average-size shells of *Pisidium* had a volume of 0.1 ml.

Insects.—Adult insects and their larvae accounted for 0.4% of the total food

TABLE 1

PERCENT FREQUENCY OF OCCURRENCE AND PERCENT VOLUME OF INGESTED MATERIAL IN OLDSQUAWS COLLECTED ON LAKE MICHIGAN, 1951–1954

Item	Northern Lake Michigan n = 35 (15)*	Southwestern Lake Michigan n =34 (34)	Southeastern Lake Michigan n = 123 (102)
Crustaceans (Amphipoda[a])	97 (52)	100 (96)	85 (82)
Mollusks	51	56	79
Gastropoda	11	9	20
Pelecypoda	51 (1)	56 (3)	76 (5)
Fish	46 (43)	24 (trace[b])	33 (12)
Skeletal remains	11 (trace)	3 (trace)	24 (7)
Eggs	40 (43)	24 (trace)	trace (trace)
Insects	51	15	28
Coleoptera	9	trace	trace
Trichoptera	31 (4)	15 (trace)	trace (trace)
Diptera	6	trace	25
Unidentified	9	trace	trace
Vegetable matter	74	59	85

* Numbers in parentheses refer to % volume.

[a] *Pontoporeia affinis.*

[b] < 0.5 %.

volume in the earlier sample, but in both this and the later sample, the frequency of occurrence was high (15 to 51% in the 1951–1954 sample). Diptera and Trichoptera larvae occurred most often but they were never abundant in any 1 specimen. Diptera larvae occurred in 6 to 25% of the earlier sample and in 15 to 17% of the later sample, while Trichoptera were recorded in 15 to 31% and 3 to 4% of these samples, respectively. Diptera consisted almost exclusively of midge larvae (Tendepedidae), but a few adult forms were found from this family as well as from the order Coleoptera.

Fish.—Fish and fish eggs were the second most important item in the 1951–1954 sample, but relatively infrequent in the 1969–1972 sample. In the earlier sample, fish remains (primarily Cottidae and Percidae) and eggs constituted an average of 13% of the food volume and the frequency ranged from 24 to 46%. In the later sample the frequency of occurrence was 3 to 4%.

The variation in fish and eggs found in Oldsquaws collected during the 2 periods appears to be related to the feeding habits of this species on Lake Michigan. In some groups of Oldsquaws, fish remains or eggs constituted the bulk of the food present, indicating that individual flocks fed on whatever food was readily available in the area. In one small sample of birds from northern Lake Michigan in the 1969–1972 period, practically all the gullets contained large chunks of decayed alewife (*Alosa pseudoharengus*), but it was

TABLE 2

PERCENT FREQUENCY OF OCCURRENCE OF INGESTED MATERIAL IN THE ESOPHAGI OF OLDSQUAWS COLLECTED ON LAKE MICHIGAN, 1969–1973

Item	% of all esophagi examined n = 956	% of all esophagi with material present n = 884
Animal matter		
Crustaceans (Amphipoda[a])	88	95
Mollusks		
Gastropoda	11	12
Pelecypoda	61	65
Fish		
Skeletal remains	4	4
Eggs	3	4
Insects		
Trichoptera	3	4
Diptera	15	17
Mysidacea	5	5
Oligochaetes	4	4
Isopods	7	8
Unidentified	3	4
Vegetable matter (detritus)	31	34
Mineral matter		
Sand (< 2 mm)	83	90
Oolites	75	81
Gravel (> 2 mm)	28	30

[a] *Pontoporeia affinis.*

found in few other samples from the area. In the 1951–1954 sample, Ellarson (1956) recorded a catch of birds from Saugatuck that had been feeding on perch (*Perca flavescens*) about 5 cm long, while other catches of birds from the area at that time were feeding on amphipods.

In northern Lake Michigan, Ellarson found 43% of the volume in 15 gizzards was composed of fish eggs (Table 2), and eggs were present in 40% of 35 birds examined from that area. One of the birds collected in this sample had ingested 35 ml of fish ova, or approximately 2600 eggs. In the 1969–1972 sample from the same area, we found 4% of 884 birds to have eaten fish eggs. No birds in the later sample contained large volumes of ingested ova. We suspect, in view of the selectivity on fish, that our earlier sample contained a few birds feeding exclusively on eggs. Since we did not find many Oldsquaws with ingested ova in the large sample from the same area in 1969–1972, the data suggest Oldsquaws will feed on fish ova when they find them, but that this occurs in isolated localities.

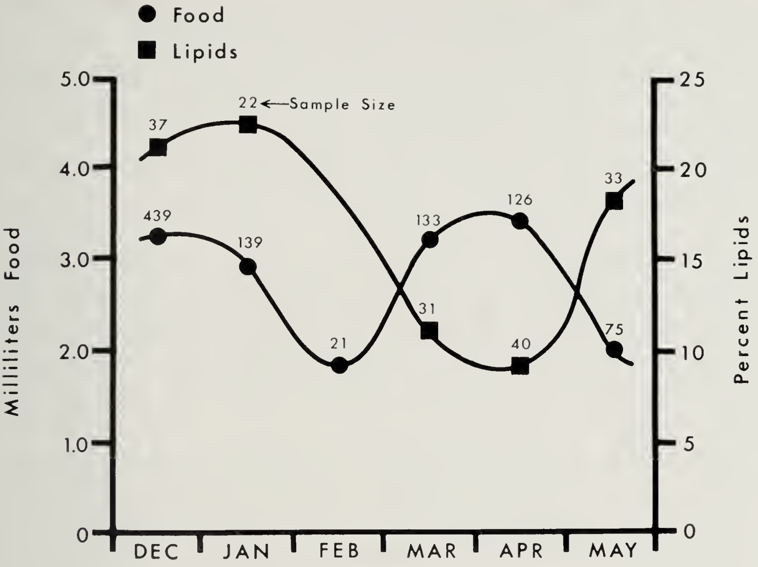

FIG. 1. Seasonal relationship between food ingested and carcass fat in Oldsquaws collected on Lake Michigan, 1969–1972. Curves are hand-fitted.

Vegetable matter.—Pieces of vegetation occurred frequently in our samples (59 to 85% in 1951–1954, and 31 to 34% in 1969–1972), but the volume was generally less than 1%. We doubt that this material is taken as food because most of the vegetation consisted of decomposed fragments characteristic of bottom debris in deep water.

Seasonal Changes in Ingested Volume

Data we have on changes in body weights of Oldsquaws suggest a seasonal rhythm in the lipid levels of this species. Changes in these lipid levels could be due to the availability of food on Lake Michigan: as the ice extends farther out from shore in the winter, Oldsquaws are forced to dive in deeper water for their food, and when either the food is deeper than their diving capability or the amount ingested per dive is less than the energy expended, the birds have to draw upon stored energy reserves. In this section we examine this relationship between food and stored energy in more detail.

Fig. 1 illustrates monthly changes in the volume of food present in Oldsquaws and the relationship to the percent lipids in carcasses. Oldsquaws are readily obtained throughout the winter except in February, when the ice is usually so thick on the northern end of the lake that fishermen cannot get out to tend their nets. The food volume data are not normally distributed about the mean: 42% of 956 esophagi had less than 1 ml present and the range was from 0 to 25 ml. We used the nonparametric Mann-Whitney U-test to check for significant differences among months. Since the sample sizes used to compute U were greater than 20, U was converted to the z distribution and the probabilities determined (Siegel 1956:116).

Our lipid data indicate a peak in deposition occurring in January, followed by a decline through April ($p < .01$), while the volume of food ingested declined from December through February ($p < .07$). In late February, the ice edge begins to retreat and larger average volumes of food ingested were recorded between February and April ($p < .01$). At the same time, lipid levels continue to decline through April, and when lipid deposits are lowest, food ingestion is at a maximum. Between April and May, there is an increase in lipid deposition ($p < .01$), especially in adults, while there is a drop in food intake ($p < .01$).

During the second week of June 1971, we collected a series of Oldsquaws on an arctic breeding ground in northwest Hudson Bay. These breeding pairs had not been on the tundra more than a few days. Lipid analyses indicated these birds had about 17% lipid content, as opposed to an average of 22% lipid content in a similar sample of birds on Lake Michigan prior to migration. However, the Lake Michigan and arctic samples may not be from the same populations.

There was no food present in the esophageal and gastrointestinal tracts in the arctic sample, and the livers as well as the intestinal tracts were much smaller than the average size on Lake Michigan prior to migration. We concluded that the birds in the arctic sample had fed little during migration, and the data in Fig. 1 suggest Lake Michigan birds had started to reduce food intake prior to spring migration.

DISCUSSION

Two important conclusions can be drawn from data on the composition of food in the diet of the Oldsquaw. First, animal matter constitutes the bulk of the ingested material. Our observations confirm what Dement'ev et al. (1952) recorded in the Soviet Union, and Polunin and Eklund (1953) found in an Oldsquaw stomach collected in Ungava. Cottam's (1939) analysis of 190 stomachs from various parts of North America and Madsen's (1954) data from the Danish coast indicate crustaceans and mollusks are the favored food items. On Lake Michigan, our data as well as that collected by Lagler and Wienert (1948) and Zimmerman (1953) indicate this animal matter is primarily amphipods and to a lesser extent clams and snails.

The second important conclusion concerning the composition of the diet is that the Oldsquaw is an opportunist that will take whatever animal matter is most abundant or most available in its feeding area. Mackay commented on this in 1892: "They [Oldsquaws] do not seem to be particular in regard to their food, eating various molluscs, fish and sandfleas." Cottam (1939:76) noted this tendency from his collections when he stated: "The [Oldsquaw], in general, do not seem to show any species preference for either small molluscs or crustaceans, if equally easily obtained;" and Madsen (1954:204) pointed out: "On the whole . . . this Diving Duck is very adaptable in its food selection. . . ."

Eggleton (1937) and Alley (1968:18) found the benthic population of Lake Michigan dominated by 4 groups: *Pontoporeia*, Tubificidae, Sphaeriidae, and Chironomidae, in order of decreasing abundance. The first 3 groups account for approximately 94% of the bottom population, with *Pontoporeia* comprising about ⅔ of the total. Alley (1968) cites Merna (1960) as stating amphipods constituted about 70% of the macrobenthos. Eggleton (1937) and Alley (1968:66) found a zone of concentration for *Pontoporeia* at 35 m, with 8420/m^2 being recorded at 40 m. Marzolf (1962:32) found a maximum of about 14,221/m^2 in Grand Traverse Bay, Lake Michigan.

Amphipods are not only the most abundant bottom organism and the most prevalent in our food samples, but also the region of concentration of this organism is the most frequent depth at which Oldsquaws are taken (Ellarson 1956). The lower limit of the thermocline in Lake Michigan is generally about 35 m, and this coincides with the junction of the sublittoral and profundal zones (Alley 1968). Environmental extremes in the sublittoral zone cause a lower density of amphipods, while cold temperatures and less food cause decreased numbers of amphipods in the profundal zone (Alley 1968).

Field tests indicated a thin detrital film ($<$ 5 mm) was generally present on the bottom of Lake Michigan, and laboratory experiments suggested amphipod densities were positively correlated with the density of bacteria in this organic matter (Marzolf 1962). The sublittoral or inshore areas are constantly subjected to wave action which causes the organic matter to be resuspended and deposited elsewhere, thereby lowering the productivity of the area for bacteria and amphipods (Alley 1968). The decrease in the food base contributes then to less attractive and constantly changing feeding areas for Oldsquaws.

Eggleton (1937) reported Tubificidae to be abundant in the benthic zone of Lake Michigan, but we found relatively few in our samples. Oldsquaws will take members of the Tubificidae, as Rofritz (1972:57) noted: "Sludge worms were overwhelmingly the most important food source for Oldsquaw in the Milwaukee Harbor." Milwaukee Harbor has been dredged to 9 m and the bottom is a hard clay. The sewage treatment plant in the center of the harbor produces conditions suitable for an abundance of "sludge worms" (335,000/m^2 maximum, Rofritz 1972:56), and this food organism is readily available to Oldsquaws owing to the hard bottom. The substrate in Lake Michigan where Oldsquaws are most often taken is largely a mixture of sand and silt. Tubificidae can burrow into these materials and be essentially unavailable to Oldsquaws even though these worms are one of the most prevalent organisms in the benthic zone.

Other data indicate the Oldsquaw is an opportunistic feeder. Several of our samples revealed that a few small groups of birds had been feeding on fish even though the majority of the flocks taken at the same time in the same area had been feeding on amphipods. Ellarson (1956:215) and Hull (1914) have observed Oldsquaws feeding on locally abundant schools of minnows, and Oldsquaws have been seen diving for fish offal discarded by the commercial fishermen on Washington Island. Madsen (1954) noted that the high incidence of mollusks in Oldsquaws collected along the Danish coast reflected the abundance of these bivalves in the marine waters, whereas Cottam's (1939) material showed a preponderance of crustaceans from birds collected largely from freshwater habitats.

An important relationship of Oldsquaws to the gill-net fishery on Lake Michigan exists through the common amphipod food base. Our data indicate this invertebrate is the predominant food organism in Oldsquaws, and Koelz (1927:528), Rawson (1953), and Ellarson (1956) found the principal food of the whitefish (*Coregonus clupeaformis*) was amphipods. Since this bird and this fish are both largely dependent on the same food, it is understandable why both fish and ducks tend to concentrate in areas where amphipods reach maximum density, and why fishermen set their nets in these waters. Oldsquaws are also related to the gill-net fishery by their occasional predation on fish eggs.

The seasonal relationship between the volume of food ingested and the percent of lipids found in the bird is more difficult to explain. Because we do not know the energy requirements of Oldsquaws during the winter, one must interpret the data in Fig. 1 with caution. Surely the decline in lipids between January and April is caused by some stress factor, but whether or not this is due to a decrease in the volume of food ingested, as implied in Fig. 1, is questionable. Oldsquaws need a minimum winter food intake to maintain an energy balance, and when this energy demand is not met, stored energy must be used. As winter temperatures drop and shore ice forces the birds into deeper water, more energy is needed; a decrease in energy intake could cause the observed decline in lipid reserves.

King (1961) observed in White-crowned Sparrows (*Zonotrichia leucophrys*) that just prior to spring migration an increase in lipid deposition was accompanied by an increase in feeding activity that created a positive energy balance. Fig. 1 suggests this is not so for Oldsquaws wintering on Lake Michigan because lipid mobilization does not begin to level off for a month after food intake rises, and an increase in lipid reserves does not occur until about 2 months after the food intake rises. This suggests that, although the difference in the volume of food ingested between February and April may be statistically significant, there is no simple biological relationship between food intake and fat deposition during late winter and spring. As King and Farner (1966) pointed out, a change in lipid deposition is usually the result of changes in metabolism rather than changes in food availability.

The April–May decline in food intake concurrent with increased lipid deposition suggests a negative feedback relationship between the level of fat reserves and appetite, as asserted by Dolnik and Blyumental (1964) for small migratory birds. These authors state that the characteristics of this system are seasonally variable. We believe additional controlled studies are necessary before we can fully interpret the relationship between energy consumption and lipid metabolism in Oldsquaws.

SUMMARY

The food habits of Oldsquaws wintering on Lake Michigan were examined from material collected in 2 periods: 1951–1954 and 1969–1972. Grit averaged 25% of total contents in the earlier sample, and 90% of all grit was sand. Animal food constituted about 99% by volume of the food organisms present in the 1951–1954 sample. The principal food item was an amphipod, *Pontoporeia affinis*, which occurred in 52–96% of the earlier sample and in 88–95% of the 1969–1972 sample. Clams occurred frequently in both samples but the volume ingested was relatively low. The occurrence of fish and fish eggs in the diet varied with the locality and individual flocks. Oldsquaws are related to the coregonid fishery in Lake Michigan through the common food organism *Pontoporeia affinis*. Oldsquaws will also eat fish eggs when available. The decline in Oldsquaw carcass lipids during the winter may be related to a decrease in the volume of food ingested during that period, but a rise in the volume of ingested food during early spring does not appear to be associated with a premigratory increase in lipid deposition. Oldsquaws apparently decrease their feeding activity just prior to migration and do not resume heavy feeding while on spring migration.

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SEXUAL DIMORPHISM IN THE WHITE IBIS

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Sexual dimorphism in body size has been variously accounted for in different species of birds (Selander 1972), though the phenomenon has been little studied in ciconiiforms. In this paper I analyze dimorphism in the White Ibis (*Eudocimus albus*), suggested by the few measurements in Palmer (1962) and briefly noted by Rudegeair (1975). I also discuss the potential significance of this dimorphism, especially related to food use, feeding behavior, and nesting. The morphological analysis is based on a sample of 36 specimens collected from a single population.

METHODS

All White Ibis specimens were collected in the Everglades and Big Cypress Swamp of southern Florida during the 1972 and 1973 nesting seasons. Standard measurements were made of tarsus, middle toe, wing arc, 8th primary, and central rectrix on the left side. Bill was measured as straight line distance (chord) from tip to anterior edge of nares. Body weight was taken after removal of stomach contents. Stomach contents were identified, separated, dried, and expressed as percentage of total dry weight.

RESULTS AND DISCUSSION

Both juvenile and adult males averaged significantly larger than females in all characteristics for which I have adequate samples (Tables 1, 2). Adults were most dimorphic in weight, females averaging 74% the weight of males, and most similar in measurements of the flight structures, females averaging 91% of males. Juveniles differed significantly from adults in several characteristics because of slow post-fledging growth, but sexual dimorphism was still apparent in these as well as adults.

Bills of females averaged 78% as long as bills of males, and also differed in shape and massiveness (Fig. 1). Bill dimorphism is probably the easiest sexual difference to detect in wild birds and is apparent to experienced observers when the sexes are together and in many cases when they are not. The ratio of male to female bill length is 1.25. Such a pronounced difference suggests that the sexes are using different food resources (Schoener 1965, Selander 1966). Differences in leg length, and weight (Hespenheide 1971) have also been related to differential food consumption. Hutchinson (1959) showed that ratios of trophic appendages of different species exhibiting character displacement were about 1.28, while Schoener (1965) found smaller character difference ratios, about 1.14, among species of congeneric sympatric birds and suggested (Schoener 1970) that for animals of similar morphology

TABLE 1

MEAN SIZE (G OR MM), STANDARD ERROR OF THE MEAN, RANGE, AND COEFFICIENT OF VARIATION OF MERISTIC CHARACTERISTICS OF ADULT (MORE THAN 2 YEARS OLD) AND JUVENILE (SECOND YEAR) WHITE IBIS FROM SOUTHERN FLORIDA

	Adult Males				Adult Females			
	n	$\bar{x} \pm$ SE	Range	cv	n	$\bar{x} \pm$ SE	Range	cv
Weight*	12	1036.4 ± 30.3	872.9–1261.0	10.14	16	764.5 ± 17.1	592.7–864.3	8.93
Bill	12	142 ± 1	136–148	3.12	16	111 ± 1	102–121	5.25
Tarsus	12	102 ± 3	91–110	11.81	16	87 ± 1	79–97	5.43
Middle Toe	12	70 ± 1	64–73	5.26	16	61 ± 1	56–68	5.76
Wing arc	12	302 ± 2	295–315	2.00	12	277 ± 3	262–288	3.14
Primary 8	8	216 ± 3	206–225	3.38	13	196 ± 1	188–208	2.12
Tail	11	108 ± 1	104–115	3.28	17	98 ± 1	92–105	2.75
	Juvenile Males				Juvenile Females			
	n	$\bar{x} \pm$ SE	Range	cv	n	$\bar{x} \pm$ SE	Range	cv
Weight	4	905 ± 23.7	854.8–969.1	5.24	1	771.9	–	–
Bill	4	140 ± 23	137–145	2.82	3	110 ± 2	107–113	2.86
Tarsus	3	102 ± 8	99–106	3.57	3	88 ± 1	86–91	2.63
Middle Toe	4	68 ± 1	65–71	3.86	3	56 ± 2	53–59	5.15
Wing arc	4	298 ± 3	292–304	1.90	3	260 ± 6	258–277	3.69
Primary 8	4	201 ± 1	207–212	1.12	3	188 ± 2	185–192	1.92
Tail	4	104 ± 1	103–106	1.10	3	92 ± 1	89–95	3.05

* Weights are minus stomach contents.

TABLE 2

DIFFERENCES OF CHARACTERISTICS OF WHITE IBISES IN SOUTHERN FLORIDA SHOWN IN TABLE 1

	Adult vs Juvenile		Juvenile vs Juvenile	Adult vs Adult	
	♂ vs ♂	♀ vs ♀	♂ vs ♀	♂ vs ♀	DS
Weight	*	*	–	**	73.8
Bill	–	–	**	**	78.3
Tarsus	–	–	**	**	85.8
Middle Toe	–	*	**	**	88.0
Wing arc	–	*	**	*	91.7
Primary 8	–	**	**	**	90.7
Tail	–	–	**	**	91.7

DS = Sexual difference = 100 (mean of females/mean of males), see Selander (1966).
* = Significantly different by t test at $P < 0.05$.
** = Significantly different by t test at $P < 0.01$.
– = Not significantly different.

and feeding behavior, smaller ratios than found by Hutchinson should result in the taking of different foods. The large bill-size ratio of the White Ibis indicates that selection for character dimorphism within this single species has resulted in a difference of similar magnitude to that for competing species.

However, I found little evidence of resource partitioning. In nearly all instances, I observed no discernible difference in the feeding behavior of male and female White Ibis. An alternative method of resource division would be for ibis to forage allopatrically. Because they possess larger bills and legs, males could forage in deeper habitats than females. My limited data show that they do this in only 2 habitats, canal-edge marshes (19 observations of ♂♂, 2 of ♀♀) and offshore on coastal shoals (18 observations of ♂♂, none of ♀♀). However neither habitat is heavily used by ibises. I found no differences between sexes in the mixed species flocks feeding in the Everglades, the primary feeding habitat in southern Florida (70 observations). As feeding site data are somewhat equivocal, I collected males and females feeding in the same locations on 3 occasions in the heavily used fresh water marshes. In no case are large differences in the food taken by the sexes apparent (Table 3). The 2 sets of Everglades samples show overlap between sexes of 98 and 99% and the Cypress Swamp samples have a 75% overlap (Morisita's index of overlap, Horn 1966). Although Earhart and Johnson (1970) suggested that consumption of numerous and relatively small prey items, such as is the case in ibises, results in the lack or reduction of dimorphism, White Ibis appear not to follow this generalization.

It remains possible, of course, that the sexes could be taking different

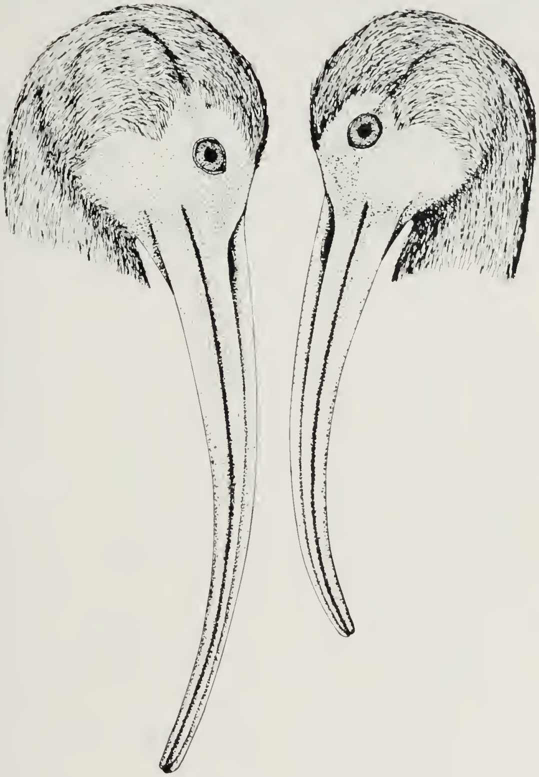

FIG. 1. Sexual dimorphism in the bill length and bill shape of the White Ibis. Male left, female right.

foods, particularly during the non-breeding season when water levels in the interior marshes of southern Florida are deeper and most birds feed along the coast in tidal situations. Male ibises may also take their prey from deeper in the sediment than females and thus take the same prey type without competition.

Sexual dimorphism in the White Ibis, as in many species (Selander 1972), is likely adaptive in reproduction. The larger size and aggressiveness of males is important because males spend much of their time defending the nest. In the first 2 weeks after hatching, the male broods during most of the daylight hours (Kushlan 1976) when predators and other colony members are active and thus protects the nestlings until they are large enough to be left alone.

Dimorphism may also be of advantage to females in nesting. A smaller

TABLE 3

FOOD OF MALE AND FEMALE WHITE IBIS COLLECTED AT THE SAME TIME AND LOCATION*

	Everglades 1		Everglades 2						Cypress Swamp			
	♂	♀	♂	♂	♂	♂	♀	♀	♂	♂	♀	♀
Prawn, *Palaemonetes*						0.2						
Crayfish, *Procambarus*	85.0	79.5					5.1		67.2	99.5	72.0	41.7
Dragonfly, Odonata	2.4	13.6	0.2						0.3		1.0	5.1
Water bugs, Hemiptera	0.5						3.0	9.6				
Diving beetles, *Hydrophilus*	0.1	1.6								1.4		
Snails, Mollusca									32.5		27.1	41.0
Fish, Pisces			95.6	100.0	100.0	95.4	91.8	90.4				
Frog, *Rana*		2.5	4.2			4.4						13.9
Newt, *Diemyctylus*	12.0	2.7										
Plant	0.1	0.02	0.06									

* Data expressed as % of dry weight of stomach contents.

female may be better able to enter the male's territory during pair formation. Dimorphic enlargement of the gular sac of the female also functions during pair formation (pers. obs., Rudegeair 1975). A primary pairing behavior consists of intertwining downward head thrusts described by Meyerriecks (*in* Palmer 1962). In early pair formation, the female when bringing her head upward turns it sideways to the male and holds that posture rigidly, thus displaying in profile the small bill, bright red facial skin and enlarged gular pouch. Rudegeair (1975) suggested a similar function during another display. Thus dimorphic development of the pouch and the female's smaller size probably function together in pair formation. During the first 2 weeks after hatching, the burden of food gathering falls primarily on the female. This is similar to the situation in some raptors in which the male (which is smaller) is the major food provider through the early stages of nesting. It has been argued (e.g., Reynolds 1972) that smaller size is adaptive in increasing foraging efficiency on numerous and agile smaller prey. Such reasoning is not transferable from actively pursuing predators to searching predators, such as White Ibis, that eat passive food items as they are encountered. However, the smaller size of the female ibis does suggest that the amount of food needed for her own metabolism may be less than that of the male (Mosher and Matray 1974) and so a greater percentage of the foraging effort can be allotted to obtaining food for the young. This may be a selective force maintaining the smaller size of the female.

Body size differences may also permit the promiscuous mating behavior that characterizes this species (Kushlan 1973). Irrespective of the adaptiveness or maladaptiveness of promiscuity, the smaller size of the female may make it advantageous for her to permit promiscuous copulation rather than ineffectually attempt defense. The larger size of the male confers advantage in both dominance and mating interactions, much as the case in polygynous systems.

Thus sexual dimorphism in size is a recognizable characteristic of the White Ibis that probably serves several functions within the adaptive complex of the species. My field observations, examination of small numbers of museum specimens of known sex, and comments in the literature suggest that other ciconiiforms including the Roseate Spoonbill (*Ajaia ajaja*), Glossy Ibis (*Plegadis falcinellus*), White-faced Ibis (*Plegadis chihi*), Scarlet Ibis (*Eudocimus ruber*), Sacred Ibis (*Threskiornis aethiopica*), American Wood Stork (*Mycteria americana*), and the Marabou (*Leptoptilos crumeniferus*) are also sexually dimorphic in body size. Herons appear to be less obviously dimorphic, if at all, although statistical differences exist in some species (Browder 1973). For species in which dimorphism is recognizable in the field, body size difference becomes a promising tool in behavioral and ecological study. Because of this, comparative study of character dimorphism in other ciconiiforms is desirable.

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EGGSHELL THICKNESS VARIABILITY IN THE WHITE-FACED IBIS

David E. Capen

Many recent papers have reported the occurrence of persistent chemicals, such as DDT, and the associated thinning of eggshells of birds (Cooke 1973). Eggshell thinning is commonly documented by comparing recently-collected eggs with eggs found in museum collections. There are a number of factors, other than persistent chemicals, which may contribute to the variation in the thickness of eggshells. Some of these factors are geographic location (Anderson and Hickey 1970, 1972); the genetics, physiology, and diet among females (Romanoff and Romanoff 1949); the stage of incubation (Vanderstoep and Richards 1970, Kreitzer 1972); the order in which the eggs are deposited (Romanoff and Romanoff 1949, Berg 1945); and the size of the clutch (Rothstein 1972). Hence, when collecting eggs to study shell thickness, one must be aware of these factors to determine the proper composition of the sample.

I considered it important to conduct a study of eggshell variability of a species nesting in the wild, since most related investigations have been conducted in the laboratory, usually with the domestic chicken (*Gallus gallus*). The purpose of this study was to evaluate variability in the shell thickness of eggs of a population of the White-faced Ibis (*Plegadis chihi*). The parameters studied were (1) the length of incubation, (2) the order in which the eggs were deposited, and (3) the clutch size.

METHODS

During May 1974, White-faced Ibis eggs were collected from active nests in the Bear River delta, Box Elder Co., in northern Utah. More than 1000 pairs of Ibises comprised the study colony. Eggs were taken from 112 of 220 nests where egg deposition was synchronous. The nests were visited each afternoon during the egg-laying period, and all eggs were marked to indicate the order of deposition. Complete clutches most commonly contained either 3 or 4 eggs.

I selected a random sample of 56 nests when egg-laying ceased. From each nest I took 1 egg, also randomly, so that the completed sample contained 8 replicates of the first egg deposited in a nest, 8 replicates of the second egg deposited, etc. Corresponding samples (8 replicates of the first egg, second egg, . . .) were collected from both 3-egg and 4-egg clutches. Thus, the 56-egg sample included 24 eggs from 3-egg clutches and 32 eggs from 4-egg clutches.

A second sample of 56 eggs was collected after incubation had progressed to an average of 17 days, or about 4 days prior to hatching. All eggs contained embryos. This sample was selected in the same manner as before.

After the eggs were removed from the nests, they were refrigerated for 4–6 days, then

TABLE 1
THE COLLECTION DESIGN AND MEAN EGGSHELL THICKNESS (MM) FOR SAMPLES OF WHITE-FACED IBIS EGGS

	Order of Egg Deposition				Sample Means	
	O_1	O_2	O_3	O_4		
6-days Incubation (I_1)[1]						.324
3-egg Clutches (C_1)	.309[2]	.331	.325	—	.322	
4-egg Clutches (C_2)	.321	.314	.341	.325	.325	
17-days Incubation (I_2)						.310
3-egg Clutches (C_1)	.308	.324	.321	—	.318	
4-egg Clutches (C_2)	.302	.307	.306	.300	.304	
Sample Means	.310	.319	.323	.312		.317

[1] Mean incubation for early eggs = 5.8 days; for late eggs = 16.6 days.
[2] Each figure represents a mean for 8 eggs.

cut around the equator, the contents removed, and the eggshells rinsed with warm tapwater. Eggshells were dried on absorbent paper for 24 h in a low-humidity laboratory.

Eggshell thickness measurements were made with a Starrett No. 1010M dial micrometer, read to the nearest .01 mm. Six measurements were taken, equally spaced around the equator of each eggshell.

To obtain a desired precision of 95% for the eggshell thickness measurements, I calculated the variance for the 6 measurements of each eggshell, then computed the number of measurements necessary to be 95% confident of remaining within a 5% limit of error (Steel and Torrie 1960:86). These calculations showed that, on the average, 5.3 measurements from each eggshell were necessary for the desired precision. Since I had taken a sufficient number of measurements, only the mean thicknesses for the eggshells, expressed to the nearest .001 mm, were used in the analyses.

A 2 × 2 × 4 (Incubation [I] × Clutch size [C] × Order of deposition [O]) factorial design (Steel and Torrie 1960:194) was the basis for the collection of eggs (Table 1). A frequency distribution of the data exhibited no kurtosis. For the statistical analyses, the collection design was partitioned into 3 separate factorial designs: a 2 × 2 × 3, a 2 × 4, and a 2 × 3. This was necessary because 2 cells ($I_1C_1O_4$ and $I_2C_1O_4$) do not exist, i.e. there are no fourth eggs deposited in nests with 3-egg clutches. The data were tested by standard analysis of variance techniques.

RESULTS

Sources of variation.—The analysis of variance results are presented in Table 2. The effects of 3 variables on eggshell thickness were investigated in the 2 × 2 × 3 analysis: the length of incubation, the order of egg deposition, and clutch size. The effect of incubation was significant ($P < .01$). Eggs which were incubated for an average of only 5.8 days had shells that were 4.3% thicker than shells from eggs which had undergone 16.6 days of incuba-

Table 2

Analysis of Variance for Shell Thickness of White-faced Ibis Eggs

Designs and Sources of Variation	Degrees of freedom (df)	Mean squares (MS)	F
2 × 2 × 3			
Incubation (I)	1	.00373	8.88***
Order (O)	2	.00149	3.55**
Clutch Size (C)	1	.00048	1.14
I × O	2	.00034	< 1
I × C	1	.00159	3.79*
O × C	2	.00094	2.24
I × O × C	2	.00048	1.14
Error	84	.00042	
Total	95		
2 × 4			
Incubation	1	.00753	18.82***
Order	3	.00056	1.40
I × O	3	.00055	1.38
Error	56	.00040	
Total	63		
2 × 3			
Incubation	1	.00023	< 1
Order	2	.00163	3.70**
I × O	2	.00002	< 1
Error	42	.00044	
Total	47		
Nested factorial			
Incubation	1	.004643	13.66***
Order	5	.000987	2.37**
Clutch Size	1	.000738	< 1
I × O	5	.000340	< 1
I × C	1	.002065	6.08**
Error	98	.000416	
Total	111		

* $P < .10$; ** $P < .05$; *** $P < .01$.

tion. The order of deposition also significantly ($P < .05$) affected the eggshell thickness. In general, the first and last eggs had thinner shells than those in between. The 2 different clutch sizes showed a non-significant ($P > .10$) effect.

Three 2-way interactions and one 3-way interaction were tested. All were non-significant ($P > .10$) except one. A significant ($P < .10$) effect was obtained with the incubation × clutch size interaction. The nature of the implied relationship is illustrated in Fig. 1. Apparently, there was a greater decrease in shell thickness during incubation for eggs in 4-egg clutches than for eggs in 3-egg clutches.

Only the effects of incubation and order of deposition were tested in the 2-factor designs. Data from 4-egg clutches were used in the 2 × 4 analysis. The only significant ($P < .01$) factor was the length of incubation. In the 2 × 3 analysis, however, where only data from 3-egg clutches were used, the significant factor was the order of deposition ($P < .05$). The length of incubation did not significantly affect the shell thickness of eggs from 3-egg clutches. This, to some degree, confirms the interpretation of the significant interaction discussed above.

The data were also analyzed using a nested, factorial design (Sokal and Rohlf 1969:256). Sums of squares for the analysis of variance were obtained using regression techniques for an unbalanced design. Though not as straightforward, this is actually a more powerful analysis since the design used all available data. The results were essentially the same as those of the previous analyses, though more convincing (Table 2). Again, the effect of incubation length was significant ($P < .01$), as was the order of deposition ($P < .05$). The incubation × clutch size interaction was significant ($P < .05$) and more noticeable than before.

DISCUSSION

There was no apparent interference from pecticides in the eggs collected in this study. Eggshells did not differ in thickness from shells of eggs collected prior to 1940 and preserved in museums. The mean thickness for the pre-1940 museum eggs collected in Utah was 0.324 mm ($N = 29$) (unpublished data, Denver Wildlife Research Center, U.S. Fish and Wildlife Service). For a comparable sample of eggs in this study, shell thickness also averaged 0.324 mm ($N = 56$).

Incubation.—I was not surprised to observe the significant decrease in shell thickness between the eggs collected soon after incubation had begun and those taken just prior to hatching. A developing embryo obtains calcium from the eggshell. Simkiss (1967) estimated that 5% of the shell calcium may be used by the chicken embryo. Kreitzer (1972) reported a 7.3% decrease in shell thickness between incubated and unincubated eggs of the Coturnix Quail (*Coturnix japonica*). Rothstein (1972), who studied a species nesting in the wild, the Cedar Waxwing (*Bombycilla cedrorum*), demonstrated a similar association between incubation and eggshell thickness.

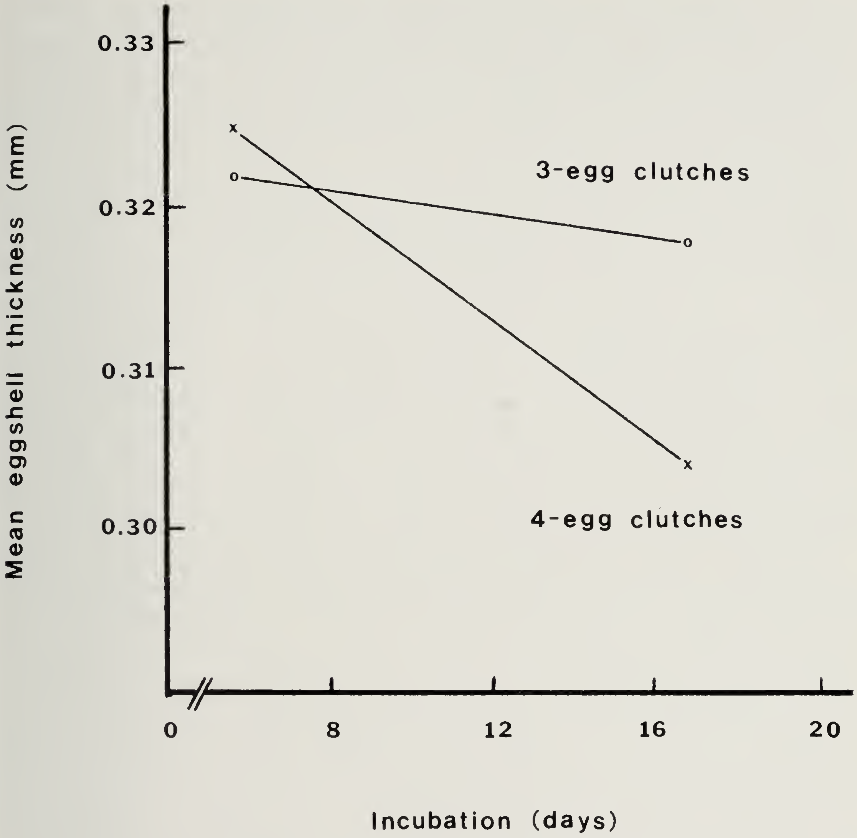

FIG. 1. The effect of incubation on shell thickness in White-faced Ibis eggs from 3- and 4-egg clutches.

The data in this study, showing a 4.3% decrease in shell thickness over approximately 11 days incubation, correspond with other published information. However, most of the decrease is a function of eggs from 4-egg clutches, which showed a 6.5% decrease in shell thickness, while eggs from the 3-egg clutches dropped only 1.2% (Fig. 1). On the average, eggs from 4-egg clutches were incubated only 0.7 days longer than those from 3-egg clutches. There is only a slight probability ($P < .02$) that the relationship is due to sampling error, hence there may be cause for additional study.

Order of deposition.—The relationship between eggshell thickness and the order in which the eggs are laid has apparently not been investigated in wild birds. In the chicken, shell thickness usually changes throughout the laying cycle. Generally, the first and last eggs have the thickest shells (Wilhelm 1940, Berg 1945). My data with the eggs of the White-faced Ibis suggest the opposite relationship, i.e. the first and last eggs are usually the thinnest. Nevertheless, there is noticeable variation (Table 2), and the order of egg deposition should not be overlooked when collecting eggs for determination of shell thickness.

Clutch size.—Complete clutches of both 3 and 4 eggs are common in the White-faced Ibis, and many other species (Lack 1968:330). Thus, I believed that clutch size should be evaluated as a variable which might affect shell thickness. The analyses indicated that clutch size did not have a significant effect on thickness, despite the different responses to incubation discussed above. Rothstein (1972) reported that shell thicknesses were different in eggs of the Cedar Waxwing collected from 3-egg clutches and those collected from 4- and 5-egg clutches. However, Rothstein could not account for variation in the sequence of egg deposition which, as he pointed out, may have confounded the variation attributed to different clutch sizes. The shell thickness–clutch size relationship is worthy of investigation in other species.

Sampling.—There are some practical implications from these results. When collecting eggs to measure shell thickness, one should attempt to take as few eggs as possible, yet sample enough to detect a desired difference, with confidence. Hence, one should select a sampling scheme which provides as little variation as possible among eggs. Klaas et al. (1974) analyzed variation in eggshell thickness in 5 species and concluded that the most efficient sampling procedure was to collect entire clutches. These authors emphasized that this scheme allows for the most efficient use of time and resources, while minimizing the impact on the reproductive success of the species. Their recommendations are valid for many species.

For the White-faced Ibis, I favor a different sampling design. Intuitively, from the data presented in this paper, the most efficient design would be one where the two significant sources of variation in shell thickness are eliminated. Thus, I recommend: (1) collecting eggs before incubation has progressed, and (2) collecting one egg per nest, sampling only the first eggs or only the second eggs laid. Of course, this plan is practical only when the egg laying sequence can be determined.

The following comparison illustrates the efficiency of my recommendations. Klaas et al. (1974) presented eggshell thickness data for the Black-crowned Night Heron (*Nycticorax nycticorax*) and reported the sample estimate of the coefficient of variation (C.V.) as 6.55. For White-faced Ibis eggs (this paper) taken during early incubation, the C.V. was 6.54, thus our samples are clearly comparable. Klaas et al. (1974:162) used a formula (Sokal and Rohlf 1969:247) for estimating the sample size necessary to detect a minimum difference in mean eggshell thickness. These authors estimated that it would be necessary to collect 38 clutches (112 eggs) to show a 5% diffrence in shell thickness with eggs of the Black-crowned Night Heron. Using a different design, collecting one egg at random from a clutch, the authors calculated that 51 eggs would be required. I used the same formula, significance level, and power as Klaas et al. (1974) and calculated that only 34 eggs from the White-faced Ibis would be needed, providing the eggs collected were the first laid in each clutch. My sample for this calculation consisted of 16 eggs. With a similar sample, but taking the second eggs laid in each nest, it was estimated that 41 eggs would be needed.

I must qualify my recommendations where shell thickness comparisons involve museum eggs. The sequence of egg deposition in clutches preserved in museums is rarely, if ever, known, thus eggs in museums are samples which represent all orders of deposition and clutch sizes. The most comparable field sample then, would be either one egg at random from many clutches or the collection of entire clutches. However, for a comparison of shell thickness differences between years or geographical areas, it may be more efficient to eliminate the variability due to the sequence of egg deposition.

My suggested sampling scheme may be the most practical for colony-nesting species. For birds such as the White-faced Ibis, proper synchronization of nesting activities may influence reproductive success; therefore renesting, if it occurs at all, may have much poorer success (unpublished data). Also, there may be more nestlings than adults can feed, and many do not survive. Thus, taking one egg from a nest may not hinder reproductive output. In species possessing these characteristics, the impact of egg collecting may be minimized by selecting one egg per clutch rather than entire clutches. In other species, it may be desirable to collect entire clutches, rather than single eggs. Hence, when collecting wild bird eggs to detect differences in eggshell thickness, one should consider the biology and behavior of the species as well as the factors which contribute to eggshell variability.

SUMMARY

Eggs of the White-faced Ibis were examined for natural variability in shell thickness. Eggs collected soon after they were laid had thicker shells than those collected just prior to hatching. Eggshell thickness also varied with the order in which eggs were laid. Different clutch sizes (3 or 4 eggs) did not contribute to the variability in shell thickness. A design for collecting eggs to determine shell thickness is suggested. The most efficient sampling scheme for eggs of the White-faced Ibis, and perhaps other species, involved collecting only one egg per nest rather than entire clutches.

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CHARACTERISTICS OF A WINTERING POPULATION OF WHITE-TAILED PTARMIGAN IN COLORADO

Richard W. Hoffman and Clait E. Braun

Information concerning White-tailed Ptarmigan (*Lagopus leucurus*) in winter is lacking primarily because of poor access, harsh environmental conditions, and insufficient effort by investigators to study them during this season. Some data on wintering populations of this species have been published (Braun and Schmidt 1971, May and Braun 1972, Moss 1973, 1974, May 1975), but most studies have pertained to behavior (Choate 1960, Schmidt 1969) and general population biology (Weeden 1959, Choate 1963, Braun 1969, Haskins 1969). In order to further understand the biology of this alpine grouse, we collected data opportunistically from 1966 through 1971 and intensively from 1972 through 1974. Objectives were to: (1) document departure and arrival from and to wintering areas, (2) describe sex and age composition of flocks, (3) examine flocking behavior and flock size, and (4) ascertain the affinity of marked birds for individual wintering sites.

STUDY AREA AND METHODS

Guanella Pass, situated in the Front Range of the Rocky Mountains in north central Colorado, was selected as the primary winter study area principally due to the abundance of wintering ptarmigan, accessibility, and availability of information on this area from prior studies (Schmidt 1969, Braun and Schmidt 1971, May and Braun 1972). The area studied encompasses approximately 9 km^2, an unusually large area compared to most known wintering grounds. In addition to studies at Guanella Pass, limited winter investigations were conducted near Waldorf, Naylor Lake, Steven's Gulch, and Horseshoe Basin where small numbers of ptarmigan winter. These sites are located within 3 to 13 km of Guanella Pass and vary in size from 2 to 4 km^2.

Winter use sites can be categorized as: (1) those at or above treeline generally at the head of a drainage, and (2) those below treeline along stream courses. Guanella Pass is an example of the former type of winter use site. Topography of this area is rolling with slopes ranging from 5 to 30% and elevations from 3475 to 3655 m above sea level. The vegetation is complex and may best be described as a mosaic of several communities, mostly dominated by willow (*Salix* spp.), which subtly intergrade with each other. Dominant communities are *Salix-Carex* wet meadows, *Salix* marshes, *Salix-Picea* Krummholz, and *Carex-Trifolium* meadows. Most of the area is snow covered during winter, with snow depths varying considerably. While snow cover is normally in excess of 95%, portions of the area are exposed to prevailing westerly winds. Consequently, bushes of willow are rarely completely snow covered.

Winter groups of ptarmigan were located by concentrated searching on foot with periodic stops to scan surrounding areas for tracks, snow roosts, and/or birds. Upon locating a flock, we tried to count all birds present. Some bias resulted when all birds present could not be counted. This bias was most serious (1) when 30 or more birds were dispersed over a large area such that all individuals could not be seen, (2) when the birds were in snow roosts, and (3) when the flock flushed before all members could be counted. In such instances, only minimum estimates of flock size were obtained. Following Koskimies (1957), 2 or more grouse constituted a flock.

After obtaining counts of flock size, birds were observed through 7 × 50 binoculars in order to ascertain banded to unbanded ratio and to identify marked individuals. Some unbanded ptarmigan and all birds with unreadable bands were pursued until caught or flushed and not relocated. Observations were recorded at the time on standardized cards and locations were subsequently plotted on 7.5 minute U.S. Geological Survey topographic maps.

Ptarmigan were captured with a 5 or 7 m telescoping noose pole as described by Zwickel and Bendell (1967) for Blue Grouse (*Dendragapus obscurus*) and modified by Braun and Rogers (1971) for White-tailed Ptarmigan. Captured birds were banded and classified to age and sex following methods presented by Braun and Rogers (1971). Age categories used were adult (including subadults [1+]), and juvenile (less than 1 yr old).

RESULTS AND DISCUSSION

Arrival and departure.—Winter on the alpine was arbitrarily designated as the period beginning in late October when ptarmigan became entirely white through mid- to late April when the prenuptial molt of males was initiated. In 1971–72 and 1973–74, most birds started arriving on the wintering area by 20 to 26 October and remained until 19 to 30 April when they departed for breeding areas. Birds did not arrive or depart simultaneously; movements to and from winter use sites were gradual extending over a 2-week period. However, climatic conditions had a pronounced influence upon arrival and departure. Prolonged mild weather during the fall of 1972 delayed arrival until 3 to 5 November while extended winter conditions the following spring (1973) delayed departure until 3 to 10 May.

Sex and age composition.—We identified 799 ptarmigan at Guanella Pass from from 1966 through 1974. There were significantly more ($P < 0.005$) adults than juveniles identified, but the proportion of the total birds handled in each age class was not consistent among winters (Table 1). This variation was attributed to differences in nesting success among years. During the summer of 1972, 37 (82.2%) of 45 females encountered on breeding areas surrounding Guanella Pass were accompanied by chicks, whereas in 1973 only 19 (54.2%) of 35 hens located were with broods (Hoffman 1974). Juveniles comprised 42.3 and 27.2% of the birds identified at Guanella Pass during the 1972–73 and 1973–74 winters, respectively, supporting the hypothesis that more juveniles (percent of total identified) occur on the wintering area following summers of good production than after summers of poor production.

Partial segregation of sexes has been documented at Guanella Pass (Braun and Schmidt 1971); however, both sexes are not equally represented on the wintering area. Significantly more ($P < 0.001$) females than males were identified each winter (Table 1), but the proportion of males and females

TABLE 1

SEX AND AGE COMPOSITION OF WHITE-TAILED PTARMIGAN WINTERING AT GUANELLA PASS

Winter[1]	N[2]	% Adults	% Juveniles	% Females	% Males
1967–68	66	54.5	45.5	72.7	27.3
1968–69	43	70.0	30.2	81.4	18.6
1969–70	111	78.4	21.6	78.4	21.6
1970–71	125	61.6	38.4	80.8	19.2
1971–72	142	56.3	43.7	78.9	21.1
1972–73	153	57.7	42.3	77.4	22.6
1973–74	125	72.8	27.2	84.0	16.0
Total	765				
Mean		64.5	35.5	79.0	21.0

[1] The winter of 1966–67 was excluded due to small sample size (34 birds identified).
[2] Total number of birds identified.

occupying the area between winters was not significantly different ($P > 0.50$). Nearly 80% of the estimated 200 to 300 grouse annually wintering at Guanella Pass were females.

Suitable wintering areas for female ptarmigan, such as Guanella Pass, appear to be limited in number; consequently, females from considerable distances are attracted to the few suitable sites (Hoffman and Braun 1975). Areas used by males during winter are scattered throughout the alpine region and each area need only support a small number of males breeding in the immediate vicinity. Winter studies in Colorado indicate that partial segregation of sexes is not unique to the Guanella Pass area. This phenomenon is not only characteristic of White-tailed Ptarmigan as Weeden (1964) reported evidence of sexual segregation in both Rock (*L. mutus*) and Willow ptarmigan (*L. lagopus*). Additional evidence of sexual segregation in Willow Ptarmigan was reported by Irving et al. (1967).

Segregation of sexes of White-tailed Ptarmigan may only be spatial, but generally a difference in habitat preference occurs. Extensive stands of willow do not grow in some locations while in others, the willow may be completely snow covered in winter. Frequently this situation and/or poor snow conditions (lack of available roosting sites) forces both sexes to move below treeline along stream courses. Under these circumstances females were found to winter farther down the same drainage than males; a purely spatial separation. In segregation by habitat, males winter in Krummholz areas alternately dominated by clumps of willow and Engelmann spruce (*Picea engelmannii*). Food availability in these sites is largely dependent upon wind action. Females winter at lower elevations near or at treeline where dense, tall stands of willow grow. Regardless of whether the separation was spatial or an actual difference in habitat preference, males showed a strong tendency to winter closer to breeding areas than females.

Available information concerning segregation of sexes is primarily oriented towards the descriptive aspects of this behavior pattern with no explanation for its occurrence. Obviously there must be an adaptive advantage for sexes to live separately during the winter. Weeden (1964) suggested that another process, migration, must be investigated in detail before segregation of sexes in Rock and Willow ptarmigan could be understood. He also suggested that due to the more sedentary nature and apparently non-migratory behavior of White-tailed Ptarmigan, possibly the 2 processes could be studied independently of each other with this species. However, studies of White-tailed Ptarmigan in Colorado reveal they are migratory and that the processes are very closely related (Hoffman and Braun 1975). The fact that most females traverse long distances to seek out suitable winter habitat and return to the same area year after year is a strong manifestation of migration and that conditions are better for winter survival in these limited areas to offset increased mortality during migration. Principal advantages of wintering in these limited sites appear to be the presence, abundance, and availability of willow which comprises about 89% of the winter diet (May and Braun 1972) and secondarily proper snow conditions for roosting.

It is unclear what advantages are gained by males wintering in exposed sites adjacent to breeding areas and not undergoing long migrations typical of females. No marked differences occur in winter diets of the sexes to necessitate separation (May and Braun 1972). However, food resources are not sufficient at high elevations to support large numbers of wintering birds. Thus it would appear advantageous for survival that a segment of the population migrate to areas where food is abundant. Under Colorado conditions, ptarmigan not only gained weight throughout the winter, indicating no food shortage (Braun and Schmidt 1971, May 1975), but also more efficiently used the winter resources that were available. Possibly it is advantageous for male ptarmigan to winter adjacent to areas where they breed in order to successfully compete for territories the following spring.

Flocking behavior.—Like most grouse, ptarmigan are gregarious, associating in flocks most of the year. Flocks are temporarily fragmented from late April until mid-July due to breeding activities. Flocking tendencies are most evident from late October to late April when ptarmigan are concentrated on winter use sites. From 1966 through 1974, 172 winter flocks and 13 lone ptarmigan totaling over 3178 birds were observed on the Guanella Pass wintering area.

Winter flock size varied from fewer than 5 to over 80 birds. Number and

TABLE 2

YEARLY TRENDS IN FLOCK SIZE OF WHITE-TAILED PTARMIGAN AT GUANELLA PASS

Year[1]	No. flocks observed	No. birds involved	Mean yearly flock size	Yearly range in flock size
1969–70	29	342	11.8	2–50
1970–71	23	340	14.9	3–42
1971–72	29	432	14.9	2–40
1972–73	33	689	20.9	2–75
1973–74	21	316	15.0	2–80

[1] Data from winters of 1966–67, 1967–68, and 1968–69 were excluded due to small sample sizes (< 15 flocks observed per winter).

frequency of encounters of 172 winter flocks and 13 lone birds were as follows: (1) 13 (7.0%) lone birds, (2) 127 (68.7%) flocks with 2 to 25 individuals, (3) 35 (18.9%) flocks with 26 to 50 individuals, and (4) 10 (5.4%) flocks with more than 50 individuals. Flocks of males were small (< 15 birds) while females typically congregated in flocks of larger size (20 to 30 birds). Only infrequently were ptarmigan observed singly, indicating their highly social nature during the winter period.

Mean flock size was not significantly different ($P > 0.05$) among winters for the 5 winters of 1969–74 (Table 2). The 135 flocks observed over the 5 winters averaged 15.5 birds. Similarly, mean flock size did not differ significantly ($P > 0.05$) among the 7 winter months, as average flock size varied from 16.0 to 23.8 birds (Table 3). Flocks tended to be smaller in October and April being 16.0 and 16.2 birds per flock, respectively. Both months represent transition periods when birds are either arriving on (October) or departing from (April) winter use sites. Since birds do not

TABLE 3

MONTHLY TRENDS IN FLOCK SIZE OF WHITE-TAILED PTARMIGAN AT GUANELLA PASS

Months[1]	No. flocks observed	No. birds involved	Mean monthly flock size	Monthly range in flock size
Oct.	8	128	16.0	12–30
Nov.	27	644	23.8	3–60
Dec.	30	664	22.1	2–80
Jan.	30	510	17.0	2–70
Feb.	18	316	17.6	4–75
Mar.	28	491	17.5	2–75
Apr.	31	501	16.2	2–60

[1] Pooled data for winters of 1966–67 through 1973–74.

arrive or depart simultaneously, fewer birds were present at these times to form flocks.

Koskimies (1957) suggested increased population numbers of Capercaillie (*Tetrao urogallus*) and Black Grouse (*Lyrurus tetrix*) and good nesting success led to larger flocks, and to a lesser degree, more flocks. Considering the failure to detect a significant difference in mean flock size among years, even though nesting success varied from year to year, there was no indication that nesting success influenced winter flock size of White-tailed Ptarmigan. However, 2.37 flocks were observed per day on the wintering area following the good production in 1972, while only 1.29 flocks were located per day following the poor production in 1973. Assuming more birds are present on a wintering area after a summer of good production, they apparently form more flocks instead of gathering into larger flocks.

Winter flocks were not composed of family units nor did the same individuals associate together throughout the winter. Ptarmigan broods disperse in late September or early October (Braun 1969) prior to their arrival on wintering areas. No females nor any of their chicks banded together during the summer were relocated in the same winter flock. Considerable interchange of birds occurred between flocks with no noticeable aggressive behavior exhibited towards new flock members. Although exact numbers cannot be cited, many individual birds banded at Guanella Pass were relocated several times throughout the winter associating with flocks of various sizes comprised of different individuals at different locations.

Affinity for wintering areas.—Data obtained from 90 birds initially banded at Guanella Pass and subsequently relocated on breeding or summering sites were used to ascertain the affinity of individual birds for the wintering area. The sample included 62 females and 28 males of which 45 (50.0%) returned in succeeding winters. A bird needed only to return once to be included in the sample, but some individuals returned up to 4 consecutive winters. Occasionally there was an intervening winter when a marked bird was not observed. Birds in this category were probably present on the wintering area but not located.

Fifteen of the 45 birds failing to return were known to be lost from the population (12 hunting mortalities, 2 collections, and 1 trapping mortality) before having a chance to return. To obtain a more accurate estimate of the percentage of birds returning that were available, the 15 birds having no opportunity to return were excluded. Consequently, the sample consisted of 75 birds (22 adult females, 32 juvenile females, 8 adult males, and 13 juvenile males) with at least 45 (60.0%) returning. This estimate must be considered conservative since it was assumed that all birds not returning were either dead or wintering elsewhere; whereas, possibly some birds returned that were not located. Thus, ptarmigan demonstrate a high fidelity to wintering areas similar to their attachment to breeding sites (Schmidt 1969).

Using a 2 × 2 contingency table, differences between the number of birds returning were tested for adults vs juveniles, males vs females, juvenile females vs adult females, and juvenile males vs juvenile females. Comparisons involving adult males were not possible because of small sample size (expected frequencies less than 5; Simpson et al. 1960). Number and frequency of each age and sex class returning were as follows: 16 (72.7%) adult females, 17 (53.1%) juvenile females, 6 (75.0%) adult males, and 7 (46.2%) juvenile males. No comparisons were statistically significant ($P > 0.05$); however, for the pooled sample of both sexes the comparison between adults vs juveniles closely approached significance (< 0.055). In all cases, proportionally more adults (73.3%) than juveniles (51.1%) returned. Juveniles suffer higher mortality than adults (Braun 1969); consequently, fewer are available to return. In addition, juveniles have no prior attachment to breeding sites and upon leaving the wintering area in spring they frequently travel long distances in search of vacant territories where they can become established as breeding birds (Hoffman 1974). Some of these birds probably winter closer to their territories and do not return. Of 40 birds identified on other nearby winter use sites, 4 (10%) were originally banded at Guanella Pass. All were banded as juveniles. Although the sample is small, it does indicate that ptarmigan banded as juveniles are more likely to disperse from wintering areas where they were initially banded and subsequently winter elsewhere.

No differences were apparent in the proportion of adult males (75.0%) and females (72.7%) returning to Guanella Pass. Based on the return of marked birds to breeding territories, Braun (1969) reported a 25 and 30% annual turnover of adult males and females, respectively. Annual turnover of adult males and females estimated by Braun (1969) is similar to the mortality rates for birds wintering at Guanella Pass indicated by data collected in this study. Since adults show a high fidelity to wintering sites, it can be reasonably assumed that most not returning are dead; consequently, percentage of non-returning adults approximates annual turnover rates. A similar assumption cannot be made for juveniles because non-returning juveniles are not necessarily lost from the population. Also, percent of birds not returning cannot be considered an approximation of annual turnover for the entire population as loss of chicks prior to their arrival on the wintering area is not included.

SUMMARY

Studies of the characteristics of a wintering population of White-tailed Ptarmigan were conducted in alpine areas in north central Colorado, primarily at Guanella Pass. Of 799 Ptarmigan identified on the wintering area, 80% were females and 65% were adults. Numbers of juveniles identified varied with year depending upon production success.

Climatic conditions had a pronounced influence upon the timing of arrival and departure to and from winter use sites. Partial segregation of sexes coincided with the arrival of birds on wintering areas with males usually remaining closer to breeding areas. Large concentrations of females wintered in areas at lower elevations near treeline where dense, tall stands of willow occurred. At times sex separation was only spatial, but usually habitat separation occurred.

Winter flocks ranged in size from 2 to over 80 birds with about 69% of all flocks (172) encountered consisting of 2 to 25 members. Flock sizes did not change significantly among years or months. Following a summer of good production, ptarmigan formed more flocks instead of gathering into larger groups. Due to greater mobility and higher mortality, fewer juveniles than adults returned in subsequent winters, but all age and sex classes exhibited a high fidelity (60% return) to the wintering area.

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BREEDING DENSITIES AND MIGRATION PERIODS OF COMMON SNIPE IN COLORADO

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Common Snipe (*Capella gallinago*) occur seasonally throughout most of North America (Bent 1927). Despite their widespread occurrence, little is known about their breeding status and timing of migration outside of northern and southern localities. Knowledge of snipe in Colorado is limited with published records pertaining to distribution and seasonal occurrences (Anon. 1886, Bailey and Niedrach 1965, Niedrach and Rockwell 1939). Because of the paucity of data on this common wetland species in the central portion of its range, this investigation was initiated in late 1973. Primary objectives were to estimate densities of breeding snipe and timing of migration in representative habitat types in Colorado.

METHODS AND STUDY AREAS

Three study sites were selected in each of 4 locations in Colorado. These locations were the Fort Collins (sites 1–3) and North Park (sites 4–6) areas in north central Colorado; Yampa Valley (sites 7–9) in the northwest, and San Luis Valley (sites 10–12) in south central Colorado. Total area studied was 245.1 ha. Size of sites studied in each location ranged from 25.2 ha near Fort Collins, 63.5 ha in the Yampa Valley, 63.6 ha in the San Luis Valley to 92.8 ha in North Park. Elevation extremes were from 1480 to 2510 m above sea level.

Vegetation of each site was described as to dominant species based on frequency of occurrence and percent coverage. All sites were seasonally wet through either irrigation flow or proximity to permanent water sources such as streams or ponds. Seven sites were dominated by species of *Carex*. Other important species on these sites were *Typha* spp., *Scirpus americanus*, *Hordeum jubatum*, *Trifolium* spp., *S. lacustris*, *Lemna* spp., and *Taraxacum* spp. in decreasing frequency of occurrence. The other 5 sites varied in composition of dominant vegetation from *Carex* spp. and *Salix* spp. to *Eleocharis* spp. and *Juncus arcticus*. Ten of the sites were seasonally grazed by livestock varying from late March to early July into October. One of the remaining sites was mowed for hay in late summer.

Climatic conditions varied with location depending upon elevation and proximity to mountains. All locations are semi-arid (<60 cm of moisture per year; range 18–59 cm) and relatively cool (mean annual temp. = 2–9°C) with short (56 days, North Park; 81 days, Yampa Valley) to average (103 days, San Luis Valley; 139 days, near Fort Collins) frost-free seasons (Colorado State Planning Division 1964).

Soils on study sites in 3 of the 4 locations are similar (unpublished data from U.S.D.A. Soil Conservation Service). They are deep, poorly drained, often alluvial in origin with excellent moisture holding capacity and slow to fair air, water, and root penetration. Surface layers ranged from clay loam to fine sandy loam often covered with a thin organic mat. Soils in the Yampa Valley were more variable ranging from deep, well-drained loam or clay loam to saline-alkali rich media with silty clay loam textures.

Measurements of soil compaction on each site were made with a Soiltest penetrometer following standard procedures. Selected water characteristics were measured on each study site using a Hach Model AL-36-B test kit and ranged from 50 to 510 mg/l (as $CaCO_3$) for total alkalinity, 30 to 2100 mg/l (as $CaCO_3$) for hardness, and 7.2 to 9.5 for pH.

Systematic strip censuses were used to estimate snipe numbers on each study site. Censuses consisted of walking linear transects at 20 to 25 m intervals with census routes and locations of snipe flushed, alighting, or displaying recorded on field maps of each site. Censuses were conducted at 2-week intervals from early May to mid-October in 1974 and from late March to late June in 1975 on all sites except near Fort Collins where censuses were conducted on a weekly basis.

Nests encountered during field investigations were inconspicuously marked for later relocation to record nesting progress. Dates of onset of incubation were estimated using the water flotation technique (Westerskov 1950) based on a 19-day incubation period. Egg measurements were taken with vernier calipers graduated to the nearest 0.1 mm.

RESULTS AND DISCUSSION

Breeding density.—The relation between numbers of snipe recorded during censuses and actual number breeding on a given area proved difficult to evaluate. Censuses prior to early May may have overestimated breeding densities due to the possible presence of migrants. Censuses after early May possibly underestimated breeding densities by excluding nesting snipe which were difficult to flush. In order to minimize these problems, the estimated breeding density for each site was derived by using the mean value for all censuses conducted on the site during May.

Densities of snipe using study sites during May varied from 0.2 to 2.1 per ha (Table 1). Of the 4 locations studied, highest densities were recorded near Fort Collins. This appeared to be the result of smaller sites (average = 8.4 ha) and uniformly suitable habitat on these sites. Sites studied in the other locations were generally larger (average size = 24.4 ha), and contained more diverse habitats, some of which were not suitable for snipe. The slightly lower densities recorded in 1974 may be an artifact resulting from conducting more censuses later in May.

Numbers of snipe varied with water depth and coverage, vegetation height and density, and soil conditions. Areas providing most suitable habitats for snipe contained shallow, stable, discontinuous water levels. Vegetation was low (10–30 cm in late May), often grazed or mowed, and sparse. Soils were moist to saturated and frequently characterized by hummocks. Areas with highest densities of snipe generally had ground compactions from less than 0.1 to 0.75 kg/cm^2 and occasionally to 1.5 kg/cm^2 in areas of dense vegetation. Areas having ground compactions of 2.5 kg/cm^2 and greater were slightly moist or dry and seldom provided feeding sites for snipe.

Seven study sites were partially flooded pastures and had densities from 0.4

TABLE 1

ESTIMATED SNIPE BREEDING DENSITIES ON SELECTED STUDY SITES, COLORADO, 1974–1975

Location	Size (Ha)	Snipe/ha (range)[1] 1974	1975
Fort Collins	25.2	1.3 (0.8–1.7)	1.7 (1.2–2.1)
North Park	92.8	0.6 (0.4–0.9)	0.6 (0.3–1.2)
Yampa Valley	63.5	0.5 (0.4–1.1)	0.7 (0.5–1.2)
San Luis Valley	63.6	0.5 (0.2–0.7)	0.5 (0.3–0.8)
Total	245.1		
Averages		0.6	0.7

[1] Estimated densities are averages of the 3 sites studied per location.

to 1.9 snipe/ha (average = 0.8). Of the 5 remaining sites, 2 in the Yampa Valley had relatively high densities (1.2 and 1.0 snipe/ha). These sites had stable water levels through May and were ungrazed. Vegetation heights on these 2 sites ranged from 5 to 30 cm in late May. Three study sites (1 in North Park, 2 in the San Luis Valley) provided few suitable habitats for snipe and had low breeding densities (0.3 to 0.5 snipe/ha). None of the 3 sites were grazed prior to late June. Heights of vegetation in early June at these sites ranged from 20 to 70 cm. Water levels on 2 of these sites were relatively stable but decreased on the third throughout May into June.

Nesting.—During the course of field investigations, 28 snipe nests (18 in 1974, 10 in 1975) were located. Nest sites were typically in grasses or sedges 20 to 40 cm in height on moist but unflooded ground near water. One atypical site was at the base of 3-m high willow (*Salix* spp.) in the center of a stand of willows approximately 30 m wide.

Estimated onset of incubation ranged from 2 May through 4 July, with the bulk of nesting activity occurring in May. Incubation of 12 of the 18 nests located in 1974 (67%) had begun in May. Additional nesting records for Colorado are limited, ranging from 1 May to 1 July with most nests located in May and early June (Niedrach and Rockwell 1939, Bailey and Niedrach 1965). In Utah, nesting dates range from 29 April to 24 July (Johnson 1899, Bent 1927). In California, a late nest was located on 1 September (Bryant 1915).

Complete clutches of 4 eggs were found in 26 nests (93%) and 3 eggs in 2 nests (7%). Forty-nine eggs were measured and had a mean length of 38.5 mm (SD = ± 1.3 mm, range = 36.6–41.6 mm) and width of 28.4 mm (SD = ± 0.7 mm, range = 27.2–29.7 mm). Nesting success and chick survival rates were not determined.

TABLE 2

MAXIMUM DENSITIES OF SNIPE AND DATES OF OCCURRENCE DURING SPRING (1975) AND FALL (1974) MIGRATION IN COLORADO

Location	Spring 1975 (Snipe/ha)	Dates	Fall 1974 (Snipe/ha)	Dates
Fort Collins	5.6	10–13 April	2.9	17 September
North Park	1.2	21–23 April	3.4	21 September
Yampa Valley	1.1	22–23 April	NC[1]	NC[1]
San Luis Valley	1.0	14–16 April	0.3	15–16 September

[1] Censuses were not conducted.

Spring migration.—From data collected on the 12 study sites, the extent and peak of the 1975 spring migration appeared indistinct. During censuses in late March and early April, a few snipe, probably migrants, were observed on most study sites which were snow and ice-free. Previously published arrival dates for snipe in Colorado include 10 March for Denver, 19 March for Boulder, 26 March for Sweetwater Lake (Bent 1927) and 17 April for Rocky Mountain National Park (Packard 1945). By mid-April, highest numbers of snipe were recorded in all locations with Fort Collins having a peak of 5.6 snipe/ha on 10–13 April, North Park with 1.2 snipe/ha on 21–23 April, Yampa Valley with 1.1 snipe/ha on 22–23 April (omitting one site which was snow covered until late May), and the San Luis Valley with 1.0 snipe/ha on 14–16 April (Table 2).

Numbers of snipe declined slightly through early May probably because of continued northward migration. A second decline occurred from early to late May which may have been caused in part, by a continuing northward migration. Although migrating snipe begin arriving in Canada during April and early May (Tuck 1972), breeding populations may not peak until late May (Arnold 1976). Local movements to areas such as irrigated haylands and pasture which had been dry previously and the onset of nesting and incubation making snipe more difficult to flush probably added to the apparent decrease. After late May, numbers of snipe stabilized on most study sites.

Fall migration.—Numbers of snipe were monitored during September and October 1974 to document timing of the fall migration. Data collected indicated that the fall migration was in progress by early September. During fall censuses, highest numbers of snipe were observed in the San Luis Valley with 0.3 snipe/ha on 15–16 September, near Fort Collins with 2.9 snipe/ha on 17 September, and in North Park with 3.4 snipe/ha on 21 September (Table 2). Study sites in the Yampa Valley were omitted because of unfavorable habitat conditions. These data indicate that the peak fall migration period for 1974 occurred about the third week of September. Numbers of snipe declined markedly after late September and by mid-October the fall migration was near completion.

In Colorado, the majority of fall migrants evidently passed through during September; however, substantial increases in numbers of snipe were observed in August. Censuses near Fort Collins and in the San Luis Valley during early August indicated increases on 4 study sites. Censuses in late July in North Park and the Yampa Valley did not reveal increases. Densities of snipe in the San Luis Valley reached 0.9 snipe/ha on 9–10 August, exceeding the September maximum of 0.3 snipe/ha. This increase may indicate that the fall migration was underway by early August or that juvenile snipe had concentrated on favorable feeding grounds. Tuck (1972) reported that in Newfoundland juveniles aggregated in groups of a few birds in late July to flocks of 100 or more in mid-August and were likely to migrate together prior to adults.

SUMMARY

Breeding densities and migration periods of Common Snipe in Colorado were investigated in 1974–75. Sites studied were near Fort Collins and in North Park, both in north central Colorado; in the Yampa Valley in northwestern Colorado; and in the San Luis Valley in south central Colorado.

Estimated densities of breeding snipe based on censuses conducted during May 1974 and 1975 were, by region: 1.3–1.7 snipe/ha near Fort Collins; 0.6 snipe/ha in North Park; 0.5–0.7 snipe/ha in the Yampa Valley; and 0.5 snipe/ha in the San Luis Valley. Overall mean densities were 0.6 and 0.7 snipe/ha in 1974 and 1975 respectively. On individual study sites, densities of snipe ranged from 0.2 to 2.1 snipe/ha. Areas with shallow, stable, discontinuous water levels, sparse, short vegetation, and soft organic soils had the highest densities.

Twenty-eight nests were located having a mean clutch size of 3.9 eggs. Estimated onset of incubation ranged from 2 May through 4 July. Most nests were initiated in May.

Spring migration extended from late March through early May. Highest densities of snipe were recorded in all regions during 10–23 April. Fall migration was underway by early September and was completed by mid-October with highest densities occurring about the third week in September. High numbers of snipe noted in early August may have been early migrants or locally produced juveniles concentrating on favorable feeding areas.

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PRINCIPAL COMPONENT ANALYSIS OF WOODPECKER NESTING HABITAT

Richard N. Conner and Curtis S. Adkisson

Biologists have long been able to associate species of birds in a general way, with their characteristic habitats. Yet, for most species few such studies of a quantitative nature have been published. James (1971) used principal component and discriminant function analyses to ordinate breeding habitats of 46 species of breeding birds in Arkansas on vegetational continua. These kinds of analyses enable habitat relationships among a set of different species of birds to be detected and expressed more readily than do univariate techniques. They emphasize the detection of relationships among species rather than attempting to achieve the fine resolution possible in evaluating single species.

We have applied principal component analysis to the nesting habitats of 5 species of woodpeckers: The Downy (*Picoides pubescens*), Hairy (*P. villosus*), Pileated (*Dryocopus pileatus*), and Red-headed (*Melanerpes erythrocephalus*) woodpeckers and the Common Flicker (*Colaptes auratus*). Red-bellied Woodpeckers (*Melanerpes carolinus*) were not abundant in our study area and were not included in the analysis because of an insufficient number of nests. We selected a set of habitat variables that we felt were pertinent to these cavity nesting species. Woodpeckers are unique among the cavity nesters in that they can exercise a choice as to where they excavate. Most other cavity nesters use cavities where they find them.

METHODS

The study area (20 km^2) was located mainly on the upper Craig and Poverty creek drainages, Blacksburg Ranger District, Jefferson National Forest in southwestern Virginia. A small part of the area was on the Virginia Polytechnic Institute and State University farm and consisted of large mature woodlots.

We searched intensively for active woodpecker nests during the springs of 1972, 1973, 1974 to locate as many nests as possible. Stand condition maps of the Ranger District were used to assure that all habitat types were searched. Vocalizations and drumming of woodpeckers were used initially to locate territories. Subsequent movement of the birds was observed to locate nest trees. We felt that the actual location of the nest would yield a more accurate representation of nesting habitat requirements than measurements of only the nesting territory.

At each active nest tree 8 variables were measured: (macrohabitat) basal area and density of stems greater than 7 cm DBH (diameter at breast height) within a 20-m radius of the nest tree, canopy height to crown top, distance from the nest tree to the nearest clearing, (microhabitat) DBH of the nest tree, diameter of the nest tree at the

TABLE 1

CORRELATION MATRIX (r) FOR 8 HABITAT VARIABLES MEASURED AT WOODPECKER NEST TREES

	BA*	DOS	CH	DTC	DNT	PTA	DAN
DOS*	0.27						
CH	0.72**	0.03					
DTC	0.17	0.48**	0.08				
DNT	0.41**	–0.40**	0.57**	–0.18			
PTA	0.27	–0.31	0.52**	–0.28	0.52**		
DAN	0.47**	–0.11	0.37	–0.05	0.61**	0.17	
NH	0.59**	–0.24	0.70**	0.03	0.68**	0.51**	0.39**

* Variable abbreviations are: BA = basal area, DOS = density of stems, CH = canopy height, DTC = distance of nest tree to nearest clearing, DNT = DBH of nest tree, PTA = percent of nest tree alive, DAN = diameter of tree at nest cavity, NH = nest height.

** Significant at = 0.01.

cavity, height of the nest, and a subjective estimate of percentage of live wood in each nest tree.

A correlation matrix was calculated for the 8 habitat variables (Table 1). As would be expected, basal area was highly correlated with canopy height, and DBH of the nest tree was highly correlated with the diameter of the nest tree at the cavity and with height of the nest. Diameter of the nest tree was significantly correlated with almost everything and distance from the nest tree to the nearest clearing was correlated with almost nothing.

Variation within and among these variables was analyzed using the principal component analysis available in Biomedical Computer Programs BMDO1M (Dixon 1974).

RESULTS

We found 19 Pileated, 20 Downy, 13 Hairy, 11 Red-headed, and 29 flicker nests. Over ⅓ of the flicker nests were found in trees left within clearcuts; most of the remaining nests were found on the edges of the old mature woodlots. The 11 Red-headed Woodpecker nests were found in old mature woodlots on the University campus. Nests of the remaining species were more widely distributed.

More than 86% of the cumulative total variance was accounted for by the first 4 principal components (Table 2). The first component accounted for 44.9% of the total variance. Most habitat variables were positively correlated with the first component; density of stems and distance to a clearing were the exceptions. The highest correlations were with basal area, canopy height, DBH of the nest tree, and height of the nest. High values on the first component correspond to habitat with high basal area, tall canopy, large DBH nest trees, and nest cavities that are high above the ground. Thus the first component represents, with increasing values, a trend from clearcuts to old mature forests.

TABLE 2

RESULTS OF THE PRINCIPLE COMPONENTS ANALYSIS OF 8 NESTING HABITAT VARIABLES FOR 5 SPECIES OF WOODPECKERS

		Component			
		I	II	III	IV
Percentage of total variance accounted for		44.9	22.8	11.0	8.1
Cumulative percentage of total variance accounted for		44.9	67.7	78.7	86.8
Correlations of components to original variables					
	BA*	0.71	0.53	0.01	0.25
	DOS	-0.25	0.83	-0.08	0.35
	CH	0.84	0.28	-0.24	0.07
	DTC	-0.11	0.77	-0.02	-0.58
	DNT	0.85	-0.23	0.21	-0.15
	PTA	0.66	-0.32	-0.50	0.11
	DAN	0.64	0.06	0.70	0.11
	NH	0.86	0.05	-0.14	-0.26

* Variable abbreviations as in Table 1.

The second component accounted for an additional 22.8% of the total variance (Table 2). This component was negatively correlated with DBH of the nest tree and percent of the tree that was alive, and positively correlated with the remaining 6 variables. Density of stems and distance to a clearing were the variables most correlated with the second component. High values on the second component correspond to a high density of stems and great distances from clearings. The second component emphasizes the relationships between dense forest (weighted on stems, but not on maturity factors such as canopy height and basal area) and cleared areas.

The third component accounted for 11.0% of the total variance. The diameter of the nest tree at the nest cavity (positive correlation) was highly correlated with the third component. The fourth component accounted for an additional 8.1% of the total variance but no single factor made a prominent contribution.

Habitat relationships among the 5 species of woodpeckers can be observed when mean values for each species are plotted on the first 3 components (Fig. 1). As can be seen on the first component axis, Red-headed Woodpeckers preferred to nest in areas of high basal area and tall canopy and to nest relatively high above the ground in trees with great DBH and large diameter at the nest. The Downy Woodpecker preferred to nest in areas with

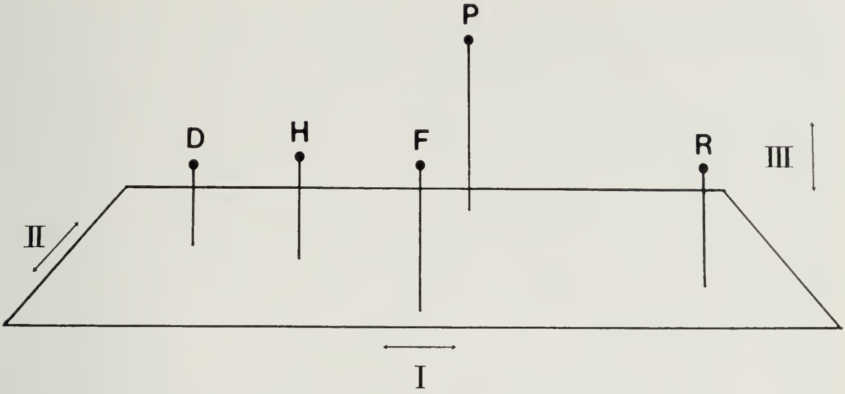

FIG. 1. Three-dimensional ordination of nesting habitat relationships among 5 species of woodpeckers on the first 3 principal components. Contributions of variables to each component are summarized in text. The first component, left to right, represents a change from less mature forest to mature forest. The second component, front to back, represents a change from open areas to dense forests. The third component, low to high, represents a change from small diameter nest cavities to large. Total variance explained by this ordination is 78.7%. (Dots indicate means, D—Downy, H—Hairy, F—Flicker, P—Pileated, and R—Red-headed.)

lower basal area and lower canopy height than the other 4 species of woodpeckers. The Pileated and Hairy woodpeckers and Common Flicker nested in habitat intermediate to the Downy and Red-headed woodpeckers.

On the second component the Pileated, Downy, and Hairy woodpeckers have high values, indicating a preference for nesting areas of high density of stems, while the Red-headed Woodpeckers and the Common Flicker preferred to nest near clearings in areas with a low density of stems (Fig. 1).

On the third component, as the size of the woodpecker increased, so did the diameter of the tree at the place where the nest cavity was excavated (Fig. 1).

TABLE 3

MATRIX OF SIMILARITY VALUES (S) FOR NESTING HABITAT BETWEEN EACH PAIR OF WOODPECKER SPECIES*

	Flicker	Downy	Hairy	Pileated
Downy	.196			
Hairy	.269	.379		
Pileated	.192	.207	.257	
Red-headed	.189	.000	.026	.090

* Higher values represent greater ecological similarity between species (S = complements of average Euclidian distance in hyperspace).

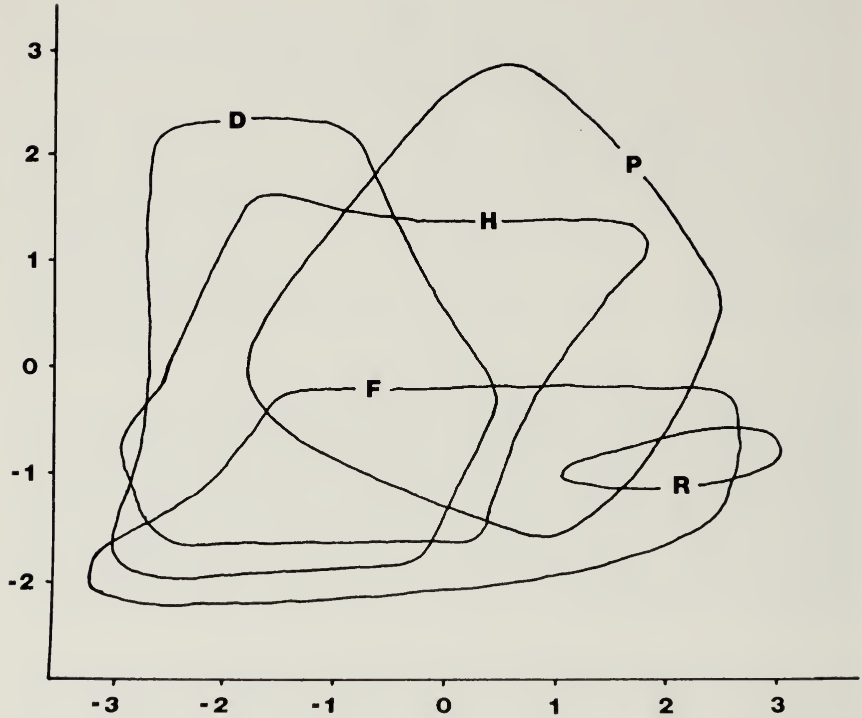

FIG. 2. Two-dimensional ordination of nesting habitat overlap among 5 species of woodpeckers on the first 2 principal components. Contribution of variables to each component is summarized in the text. The first component, left to right, represents a change from less mature to mature forest. The second component, low to high, represents a change from open areas to dense forest. (See Fig. 1 for symbol code.)

A matrix of ecological similarity of nesting habitats for each woodpecker species was calculated using the method described by Power (1971) (Table 3). Higher values in the matrix represent greater similarity among nesting habitats. Red-headed and Downy woodpeckers have the least similar nesting habitats of all the species. The Downy and the Hairy woodpecker had the most similar nesting habitat.

The nesting habitat of each species was plotted on the first 2 principal components and circled to obtain a visual estimation of overlap (Fig. 2). Extensive overlap between the Downy and Hairy woodpeckers is obvious. There is no overlap between the Downy or Hairy and Red-headed woodpeckers. The Pileated Woodpecker and the Common Flicker overlapped with all other species. The habitat area used by the Red-headed Woodpecker was much smaller than the areas used by the other species. This may reflect the limited availability of Red-headed Woodpecker nesting habitat in southwestern Virginia rather than specific nesting habitat requirements.

A rough index of the nesting versatility of each woodpecker species was calculated by summing the variances of each species on each component (the vectors for each component were solved for each species and the variances of these families of values calculated for the respective species) over the first 3 components: Flicker = 5.24, Hairy = 4.14, Pileated = 3.21, Downy = 2.71, and Red-headed = 2.51. The Common Flicker was the most versatile species. by this index, reflecting its ability to nest in conditions varying from mature woodlots to clearcuts, provided that nearby access to open ground was available for foraging. The Red-headed Woodpecker had the lowest versatility and was only found in mature woodlots that lacked a shrub layer and were near clearings.

A short-coming of this technique is that one species might show a great range for one component but be very narrow for one or both of the other components. For example, the Hairy Woodpecker had relatively high variance values on all 3 of the components, while the flicker had high values only on the first and third components, indicating its low tolerance of uncleared areas. The Red-headed Woodpecker had a high variance on only the third component. The Downy and Pileated had high values on the first 2 components and average values on the third component.

DISCUSSION

We believe that the principal component analysis is a valuable tool in evaluating multivariate habitat relations for the 5 woodpecker species. Many of the results were in accord with what is known of the natural histories of these species. General descriptions of Red-headed Woodpecker nesting habitat are abundant. Our results, which indicate that this species prefers areas with high basal area, tall trees, a low density of stems, and an open understory, tend to agree with these previous habitat descriptions (Bent 1939, Stewart and Robbins 1958, Bock et al. 1971, Reller 1972). The open understory and nearness to a clearing (Fig. 1) is compatible with the foraging requirements of this species. Open areas above and on the ground are needed since Red-headed Woodpeckers flycatch and forage on the ground extensively in the summer (Bent 1939, Reller 1972).

Past descriptions depict nesting habitat of the Common Flicker as being diverse (Burns 1900, Bent 1939, Stewart and Robbins 1958). Dennis (1969) thought flickers well adapted to any relatively treeless situation. Our study agrees with all of these observations.

Downy Woodpecker habitat in Maryland was reported as wood margins, open woodland, and forest edge habitat (Stewart and Robbins 1958). Although many of our nests were found in edge type habitats, many were also found in dense stands far from clearings (Fig. 2).

Lawrence (1966) thought that Hairy Woodpeckers could nest in any place where sufficient foraging habitat and a suitable nest tree were present. We found this species to nest over a wide range of basal areas, canopy heights, densities of stems, and distances from cleared areas. Several instances have been reported of Hairy Woodpeckers nesting and foraging in clearcuts (Kilham 1968, Conner et al. 1975, Conner and Crawford 1974).

Hoyt (1957) described Pileated Woodpecker nesting habitat as heavy timber sometimes on mountain slopes, but mainly in moist lowlands such as valleys or bottomland. Kilham (1959) reported Pileated Woodpeckers nesting in swamps in Florida and Maryland. Pileated Woodpeckers in our study typically nested within 75 m of a small stream in stands of high basal area, tall canopy, and usually far from cleared areas. Several reports exist of Pileated Woodpeckers nesting in clearcuts and in forest edge habitat (Bent 1939, Conner et al. 1975).

The large amount of overlap of nesting habitat among some of the woodpeckers in this study (Fig. 2) could be misinterpreted as an indication of competition. Past observations, however, suggest a lack of competition. Lawrence (1966) reported that Hairy Woodpeckers ignored both Common Flickers and Downy Woodpeckers that came near their nest territories. Kilham (1969) reported no agonistic encounters between nesting Hairy and Downy woodpeckers, yet the similarity value between these woodpeckers was the highest (Table 3).

Competition between species might occur only if a resource required by both species is limited. In the past selection favoring a divergence in the size of sympatric populations of Downy and Hairy woodpeckers may have been a factor in reducing competition for nest sites, if any competition existed. Other factors, however, such as foraging technique probably also influenced the evolution of size differences in woodpeckers. A species that fed superficially might not need the larger size and mass of species that fed by excavating through several inches of sound wood to reach arthropod chambers.

It would be difficult to determine if woodpecker nest sites are at present a limited resource. Woodpeckers cannot nest in any tree in a forest, even if the surrounding habitat and diameter and height of the tree are optimum. They require nest trees with fungal heart rots to soften the core of the tree (Conner et al. 1975). A low density of suitably infected trees, especially in forests that are clearcut on a short term rotation, might limit the nest site resource. No data are available at present on the prevalence of heart rots in southwestern Virginia.

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PHENETIC ANALYSIS OF THE SUBFAMILY CARDINALINAE USING EXTERNAL AND SKELETAL CHARACTERS

Jenna J. Hellack and Gary D. Schnell

The subfamily Cardinalinae includes 37 species of cardinals, buntings, and grosbeaks, which have been divided into from 9 (Paynter 1970) to 15 genera (Hellmayr 1938). Previously using skeletal variables, Hellack (1976) investigated phenetic relationships of the subfamily with cluster analysis. In that study 3 species in the genus *Saltator* clustered differently from that suggested in previous classifications (Hellmayr 1938, Paynter 1970). The 3 *Cardinalis* species grouped together only in analyses using 14 skull characters, and all 31 species included in the study were very similar in relative measurements of the pelvic region. In this paper, we examine further the phenetic affinities of the subfamily by analyzing an additional set of external characters.

MATERIALS AND METHODS

We used 75 external morphologic characters in 10 analyses; in 2 of these Hellack's (1976) 49 skeletal characters were included. Table 1 lists the species, the number assigned to each, and common names (nomenclature follows Paynter 1970).

Table 1 of Hellack (1976) indicates the number of skeletons measured. The 49 measurements are from all skeletal regions. Due to lack of skeletal materials, only 31 of the 37 species were compared.

In the analyses of external morphologic characters, similar problems of obtaining materials occurred. The Appendix lists the 75 external morphologic characters, which can be separated into 3 categories: (1) 33 study skin measurements of the tail, wing, toes, and bill; (2) color measurements (dominant wave length) from 8 body regions; (3) contrast characters in which 33 comparisons were made between various regions of the bird (e.g. contrast between the nape and the crown; 0 = no contrast, 1 = contrast). All measurements were taken from adult specimens; the means for each species are in Appendix IV of Hellack (1975).

Hellack measured study skin characters on 10 males and 10 females of each species if specimens were available. When more than one race was involved, measurements were taken from specimens of the nominate race. Study skins were available for females of all 37 species, but only 36 are included in the analysis of males (the only known specimen of *Saltator cinctus* is a female).

Color was measured using the *Munsell Book of Color* (Munsell 1973) which specifies a given color in terms of 3 characters—hue, value, and chroma. We converted these to dominant wave lengths, excitation purity, and % reflectance using tables supplied by the Munsell company (Anonymous 1970); these conversions are discussed by Newhall et al. (1943). Only the dominant wave length of each region was included in the analysis. Color measurements were obtained for males of 34 species and females of 33. *Caryothraustes humeralis*, *Saltator cinctus*, and *S. albicollis* were not included in color analyses of the males. These species plus *S. maxillosus* were not included in color analyses of females.

TABLE 1

SPECIES INCLUDED IN THE STUDY

Species No.	Scientific Name[1]	Common Name[2]	Species No.	Scientific Name[1]	Common Name[2]
1	*Spiza americana*	Dickcissel	22	*S. cinctus*	Masked Saltator
2	*Pheucticus chrysopeplus*	Yellow Grosbeak	23	*S. atricollis*	Black-throated Saltator
3	*P. aureoventris*	Black-backed Grosbeak	24	*S. rufiventris*	Rufous-bellied Saltator[3]
4	*P. ludovicianus*	Rose-breasted Grosbeak	25	*S. albicollis*	Streaked Saltator
5	*P. melanocephalus*	Black-headed Grosbeak	26	*Passerina glaucocaerulea*	Indigo Grosbeak
6	*Cardinalis cardinalis*	Cardinal		(*Cyanoloxia glaucocaerulea*)	
7	*C. phoeniceus*	Vermilion Cardinal	27	*P. cyanoides*	Blue-back Grosbeak
8	*C. sinuatus*	Pyrrhuloxia		(*Cyanocompsa cyanea*)	
9	*Caryothraustes canadensis*	Yellow-green Grosbeak	28	*P. brissonii*	Ultramarine Grosbeak
10	*C. humeralis*	Yellow-shouldered Grosbeak		(*Cyanocompsa cyanea*)	
11	*Rhodothraupis celaeno*	Crimson-collared Grosbeak	29	*P. parellina*	Blue Bunting
12	*Periporphyrus erythromelas*	Red-and-black Grosbeak		(*Cyanocompsa parellina*)	
13	*Pitylus grossus*	Slate-colored Grosbeak	30	*P. caerulea*	Blue Grosbeak
14	*Saltator atriceps*	Black-headed Saltator		(*Guiraca caerulea*)	
15	*S. maximus*	Buff-throated Saltator	31	*P. cyanea*	Indigo Bunting
16	*S. atripennis*	Black-winged Saltator	32	*P. amoena*	Lazuli Bunting
17	*S. similis*	Green-winged Saltator	33	*P. versicolor*	Varied Bunting
18	*S. coerulescens*	Grayish Saltator	34	*P. ciris*	Painted Bunting
19	*S. orenocensis*	Orinocan Saltator	35	*P. rositae*	Rose-bellied Bunting
20	*S. maxillosus*	Thick-billed Saltator	36	*P. leclancherii*	Orange-breasted Bunting
21	*S. aurantiirostris*	Golden-billed Saltator	37	*P. caerulescens*	Blue Finch
				(*Porphyrospiza caerulescens*)	

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[1] Scientific names are those of Paynter (1970). In parentheses are names used by other authors (Hellmayr 1938, Peterson and Chalif 1973, A.O.U. Check-list 1957) when at variance with those used by Paynter (1970).

[2] Common names are those used by de Schauensee (1970) or Peterson and Chalif (1973) unless otherwise specified.

[3] Common name from Hellmayr (1938).

When all available characters were used (skeletal, study skin, and color) we had complete data for only 30 of the 37 species. Therefore the analyses of combined data include neither the 4 above mentioned species nor *Periporphyrus erythromelas*, *S. rufiventris*, and *Passerina caerulescens.*

To assess phenetic similarity, we used multivariate statistical programs from the Numerical Taxonomy System (NT-SYS, developed by F. James Rohlf, John Kishpaugh, and David Kirk). Both Q- and R-type studies were conducted.

In the Q-type analysis, characters were standardized so that each had a mean of 0 and a standard deviation of 1. Then a product-moment correlation coefficient or an average distance coefficient was calculated for all pairs of species (Sneath and Sokal 1973). Species were clustered by the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal 1973) and the results summarized in phenograms.

We extracted 3 principal components from a matrix of character correlations in the R-type analysis (Sneath and Sokal 1973), and phenetic relationships are presented as 3-dimensional models of species projected onto these components (Rohlf 1968). A shortest minimally connected network (Rohlf 1970) computed from the original distance matrix is superimposed on the 3-D models to point out possible distortions.

To eliminate or reduce the size factor, study skin characters were used as ratios (see Appendix), and skeletal measurements were divided by the first principal component extracted from a matrix of unstandardized skeletal characters. Skeletal data were handled this way because the method produced the "best" phenetic classification from the skeletal data (see Hellack 1976).

Ten phenetic classifications were produced using the various combinations of the 4 data sets (study skin, contrast, color, and skeletal characters) and 2 similarity coefficients (correlation and distance). Males and females were analyzed separately to: (1) see if there were major differences among the resulting classifications, and (2) include all species in some analyses without having to compare species with complete data with those for which some information was lacking. Various data combinations were made so as to include all the characters available for any one species in an analysis.

When all available data were used they were handled as follows: study skin characters of both males and females were averaged; for contrast and color characters male and female averages were included separately; and skeletal characters were averaged for a species without regard to sex (as done in Hellack 1976). This resulted in 168 "characters" per species.

Matrices were produced from the classification systems of Paynter (1970) and Hellmayr (1938; see Hellack 1976). These 2 matrices, the 10 from the various combinations mentioned above, and 2 from the analyses of skeletal characters (SKEL/COMP I ALL CORR and SKEL/COMP I ALL DIST, Hellack 1976) were compared by computing the coefficient of correlation between each pair of basic similarity matrices. Similarities were summarized as a dendrogram that indicates which basic similarity matrices are most alike; phenograms were compared in a similar manner.

The following abbreviations are used. CORR or DIST refer to the use of correlation or distance to analyze similarity among species. SKIN denotes the use of study skin measurements and contrast characters. COLOR refers to the use of 8 color characters of dominant wave length. SKEL indicates the use of skeletal characters divided by unstandardized principal component I (SKEL/COMP I ALL of Hellack 1976). BSM is the abbreviation for basic similarity matrix.

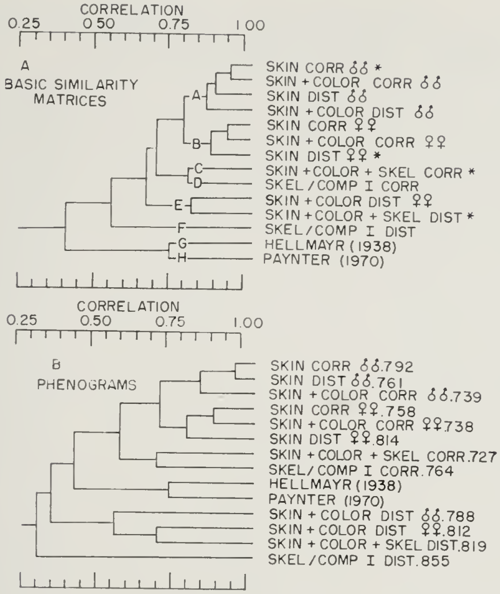

FIG. 1. Dendrograms showing relationships among: (A) basic similarity matrices; (B) phenograms. Letters indicate groups of very similar BSMs. Asterisks indicate the phenogram chosen to represent each of these groups—the one with the highest cophenetic correlation. These representative phenograms are shown in Figs. 2a–b.

RESULTS

Phenograms.—In Fig. 1A, which is a dendrogram of similarities among BSMs, 9 groups are labeled. The 4 BSMs of group A (in which only males are compared) differ in similarity coefficient and/or the number of characters (the BSMs also differ in the number of species included, although the dendrogram, Fig. 1A, is comparing placement of only those species each pair of analyses has in common). Group B has 3 BSMs (where only females were compared) which like those of group A, differ in similarity coefficient and/or the number of characters. The 2 BSMs of group E differ in character set but are alike in the similarity coefficient used. The 5 remaining groups contain 1 BSM each.

The main difference between the dendrogram showing similarities among phenograms (Fig. 1B) and Fig. 1A is that 1 BSM of group A (SKIN + COLOR DIST ♂♂) clusters in group E. Also distance analyses of groups E and F show less similarity to the other clusters than they did in Fig. 1A.

BSMs within groups A, B, and E are very similar (Fig. 1A). We have depicted only 1 from each—the phenogram with the highest cophenetic cor-

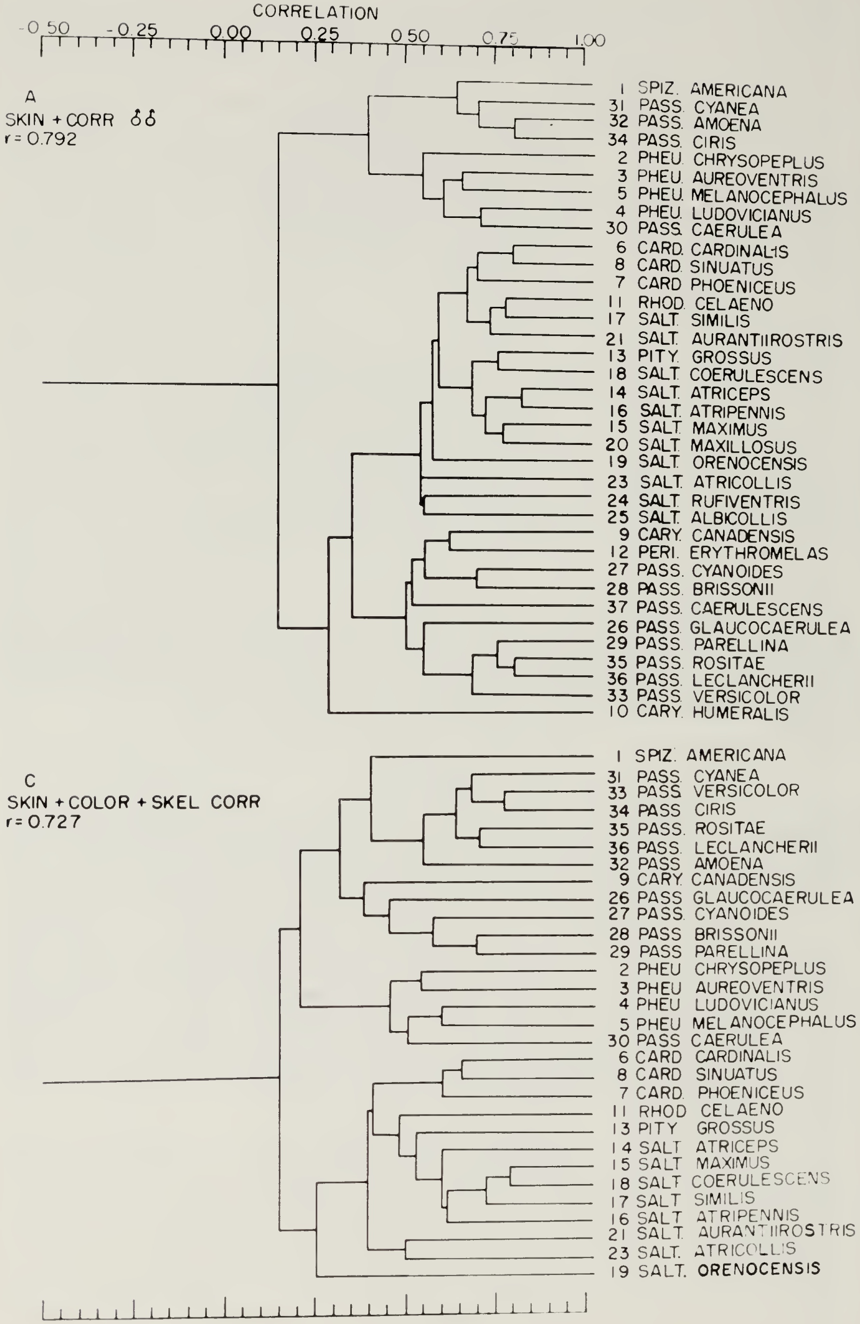

FIG. 2 a. Phenogram representatives of groups A and C of Fig. 1: (A) study skin characters of males with correlations; (C) all characters and correlations.

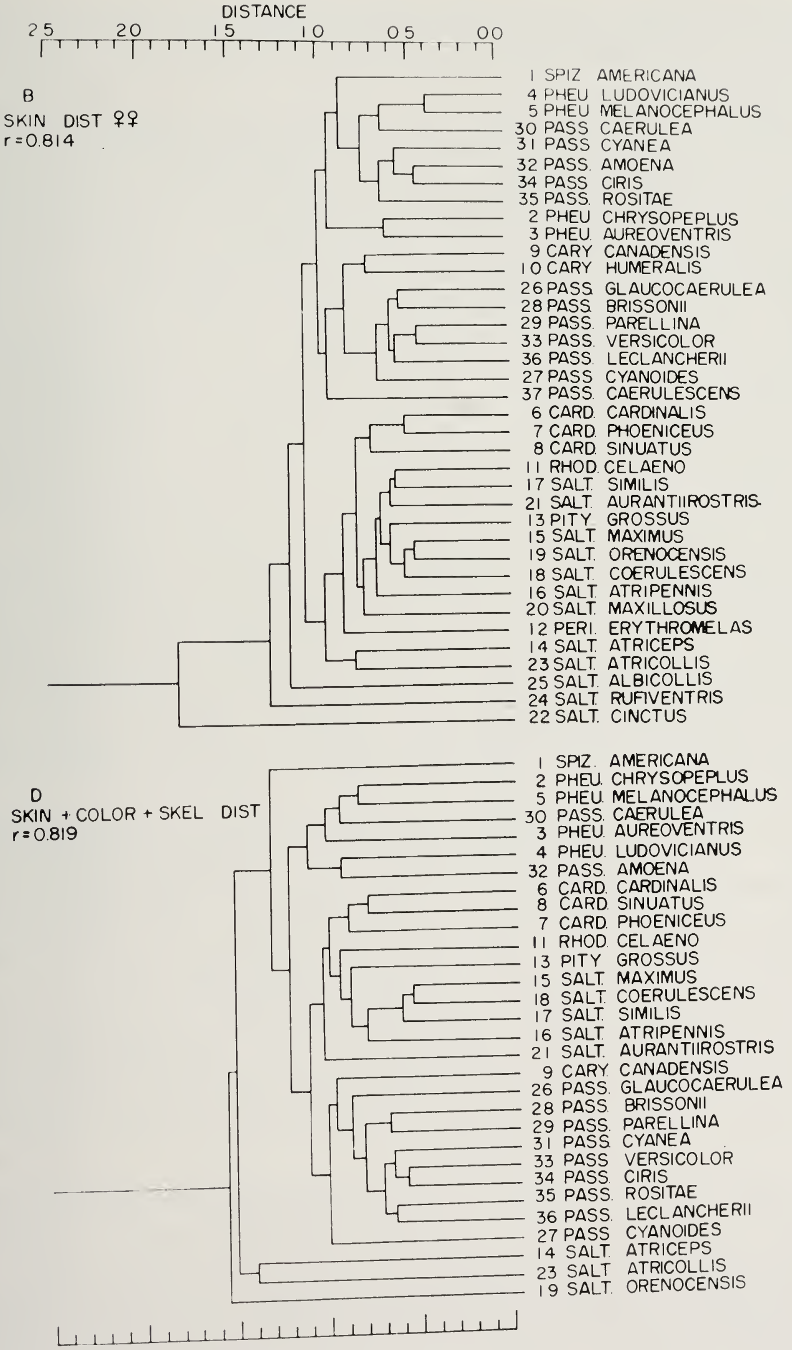

FIG. 2 b. Phenogram representatives of groups B and D of Fig. 1: (B) study skin characters of females with distances; (D) all characters and distances.

relation coefficient (see Fig. 1B for these values). Any substantial difference in placement of species in phenograms within each group will be described below.

Group A consists of 4 very similar BSMs, and is represented by SKIN CORR ♂♂ (Fig. 2A), which differs little from SKIN DIST ♂♂ (not figured). Adding 8 color characters (SKIN + COLOR CORR ♂♂, not figured) caused 2 species to cluster differently from that shown in Fig. 2A. *Passerina versicolor* grouped with *P. ciris*, and *Periporphyrus erythromelas* showed little similarity to any species cluster. SKIN + COLOR DIST ♂♂ (not figured) is the most divergent, but major clusters are much the same. Adding color characters resulted in *Passerina amoena* not being in the cluster of buntings; and *Rhodothraupis caelaeno*, *Periporphyrus erythromelas*, *Saltator orenocensis*, and *S. atriceps* showing little similarity to the other species.

The 3 BSMs of group B, all resulting from analyses of females only, are represented by SKIN DIST ♀♀ (Fig. 2B). In the 2 phenograms not figured, *S. rufiventris* clusters with the other saltators, and *Caryothraustes humeralis* and *C. canadensis* are not as closely affiliated as indicated in Fig. 2B.

Group C includes only the analysis with all characters (SKIN + COLOR + SKEL CORR, Fig. 2C). It connects with the BSM of SKEL/COMP I ALL CORR (described in Hellack 1976, not figured here). The cluster bounded by *Passerina glaucocaerulea* and *P. parellina* (Fig. 2C) is not found in SKEL/COMP I ALL CORR (the members of the genus *Passerina* form 1 cluster with the exception of *P. caerulea* and *P. cyanoides*). *Saltator orenocensis* and *Caryothraustes canadensis* cluster with the genus *Pheucticus* in SKEL/COMP I ALL CORR.

Group E, containing 2 BSMs, is represented by SKIN + COLOR + SKEL DIST (Fig. 2D). SKIN + COLOR DIST ♀♀ (not figured) differs in the placement of several species. The buntings (*Passerina*) cluster much the same as they do in SKIN + COLOR + SKEL CORR (Fig. 2C), and not as in SKIN + COLOR + SKEL DIST (Fig. 2D). *Saltator atripennis* shows little similarity to any other species in SKIN + COLOR DIST ♀♀.

Group F contains the BSM for SKEL/COMP I DIST. Its phenogram (figured in Hellack 1976) was considered the "best" classification when only skeletal characters were analyzed (Hellack 1976) and differs from those presented here mainly in the placement of the species in the genus *Cardinalis* (i.e., they do not cluster together).

Principal component analyses.—Four representative 3-D models from R-type analyses are shown in Fig. 3. Character loadings for the first 3 principal components of each are in appendices I, II, and III of Hellack (1975).

Fig. 3A is the analysis of males using study skin and contrast characters. The principal components explain 21.2, 11.7, and 9.0% of the total character

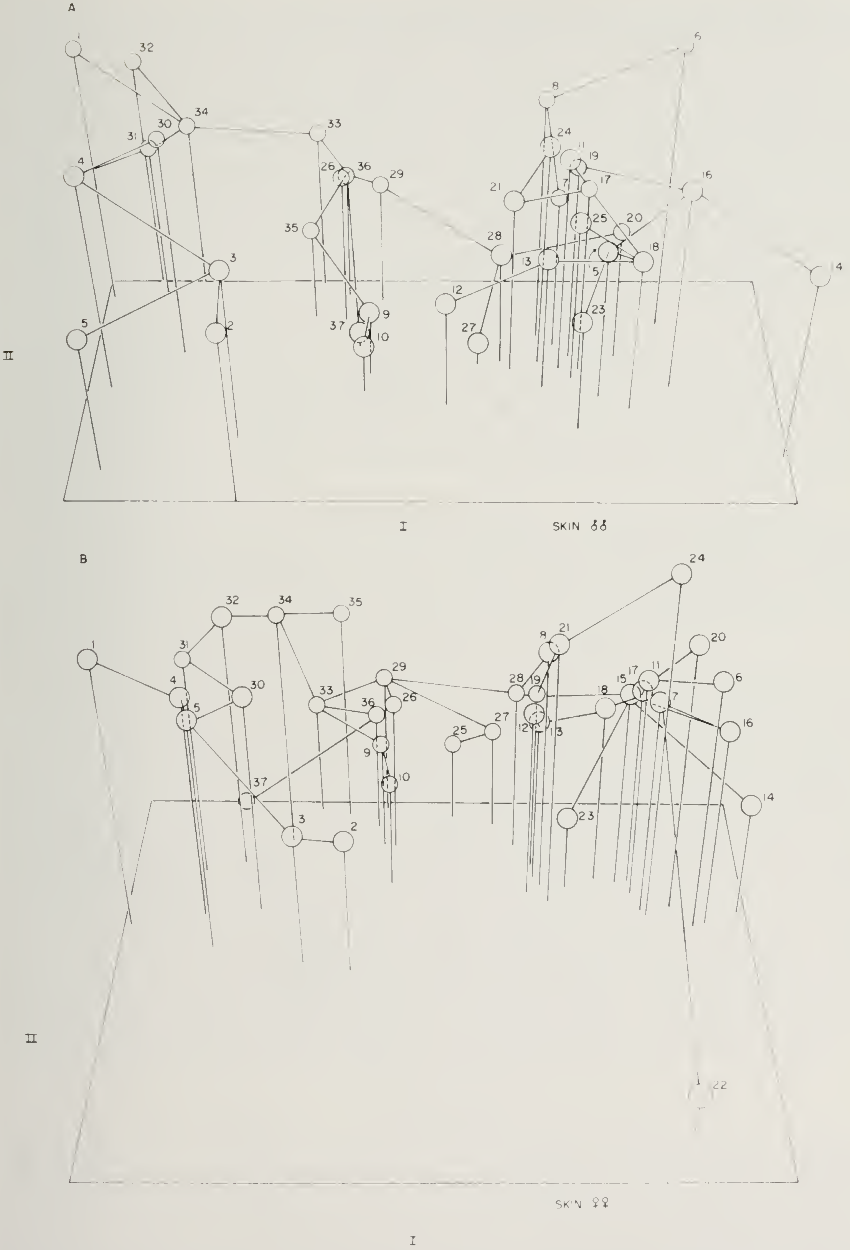

Fig. 3 a. Representative models of species projected onto the first 3 principal components based on (A) male study skin characters and (B) female study skin characters. Species names corresponding to the numbers on the models are in Table 1. Components I and II are labelled, III is the height. The shortest minimally connected network is projected onto each of the models.

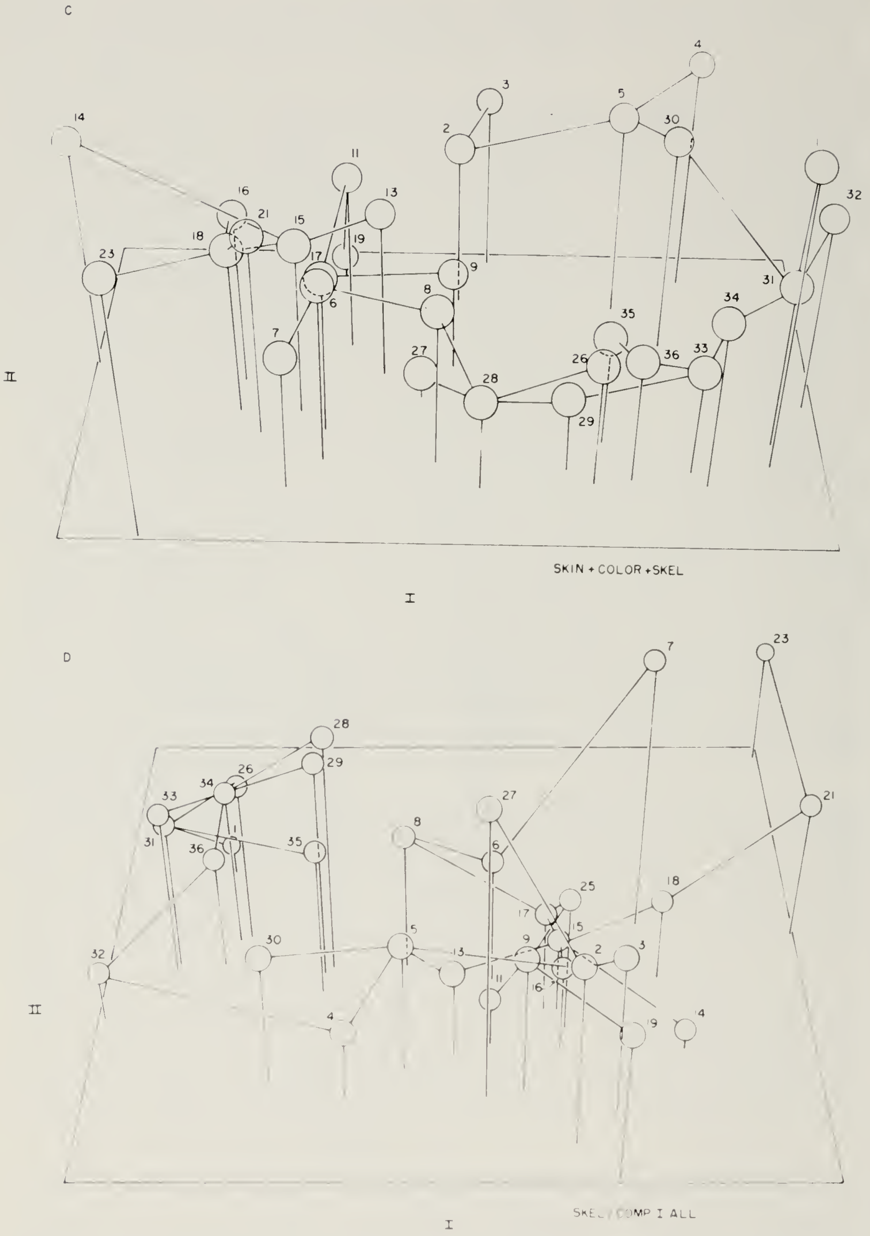

FIG. 3 b. Representative models of species projected onto the first 3 principal components based on (C) all available characters and (D) skeletal characters.

variation, respectively. While only 42% is accounted for, the euclidian distances between species pairs in the 3-D model have a correlation of 0.90 with those in the original distance matrix.

Component I has its highest loadings on the amount of tail covered by the tail coverts and the shape of the wing. Species on the left in the model (Fig. 3A) have less tail exposed and more sharply pointed wings. Component II is a size factor with high loadings on the tail, wing, and hallux lengths, as well as on the contrast characters for white in the wing and tail. The larger birds with considerable white in the wing and tail are in the front of the model. The third component has its highest loadings on the wing vane widths. The species on short stems have relatively wide primaries.

Fig. 3B resulted from an analysis of female study skin and contrast characters. The 3 components explain 20.2, 11.9, and 9.7% of the total variation. The model has a correlation of 0.91 with the original distance matrix. This analysis has high loadings on the same characters as does that of the male analysis (Fig. 3A).

For the model based on all characters (SKIN + COLOR + SKEL) in Fig. 3C, components account for 23.3, 13.0, and 9.2% of the variation. Because there were many more characters than species in this analysis, Gower's (1966) method for computing projections from a matrix of correlation among species was used, and character loadings are not available.

Fig. 3D is a model produced from the analysis of skeletal characters divided by principal component I. The components account for 27.0, 18.2, and 11.2% of the character variation, and the model's correlation with the distance matrix is 0.90. The first component is a contrast with its highest loadings on the keel depth and femur and tibiotarsus widths. Species on the left in the model have relatively deeper keels and narrower femurs and tibiotarsi. Component II has high negative loadings on the long bones of the wing and high positive loadings on the long bones of the leg. Species near the front of Fig. 3D have relatively shorter legs and longer wings than those at the back. The third component has high positive loadings on the skull width and depth, and high negative loadings on the sternum and keel lengths. The species with the shorter stems have relatively narrower skulls and longer sterna and keels.

DISCUSSION

Comparisons of BSMs, phenograms, and previous classifications.—Highly correlated skeletal characters with a large size factor were used by Hellack (1976) in an analysis of Cardinalinae. We found, as in previous studies (Sokal and Michener 1967, Robins and Schnell 1971), that using correlation as a measure of similarity tends to give more uniform results than did the use of the distance coefficient. The analyses in this study in which external characters (SKIN or SKIN + COLOR) were used did not follow this tendency. Except for SKIN + COLOR DIST ♀♀ (not figured), there was considerable correlation among the BSMs of similar character sets irrespective of similarity coefficient (Fig. 1A). That BSMs do not group according to similarity coefficient probably indicates there is no large size factor or other significant trend in the ratios used.

As in analyses of skeletal characters, affinities among phenograms (Fig. 1B) changed some from those expressed for BSMs (Fig. 1A). In the comparison of phenograms (Fig. 1B), SKIN + COLOR DIST ♂♂ (not figured) switched (i.e., clustered with a different group of species or in this case phenograms) affinities, and showed more similarity to SKIN + COLOR DIST ♀♀ (not figured) and SKIN + COLOR + SKEL DIST (Fig. 2D). Switching also occurred in some of the major branches (e.g., 4 distance phenograms show less similarity to other analyses than did their respective BSMs).

In comparing the 12 classifications in this study with those of Hellmayr (1938) and Paynter (1970), 9 BSMs were more similar to previous classifications than were their respective phenograms. All 12 BSMs and 10 phenograms were more similar to Paynter (1970) than to Hellmayr (1938). The 2 phenograms more similar to Hellmayr (1938) are SKIN CORR ♂♂ (Fig. 2A) and SKIN + COLOR CORR ♂♂ (not figured). Correlations between BSMs (as well as phenograms) and previous classifications are very low, indicating that the affinities implied by previous workers are different from those determined in our study.

Comparisons of representative phenograms.—SKIN DIST ♀♀ (Fig. 2B) of group B is the only representative phenogram in which all species included in Cardinalinae by Paynter (1970) were analyzed. The placement of species in the other representative phenograms will be compared below with their placement in SKIN DIST ♀♀ (Fig. 2B).

In the representative phenogram of group A (SKIN CORR ♂♂, Fig. 2A) some changes in close affinities are evident; however, major clusters are composed of many of the same species. *Passerina rositae*, *Saltator albicollis*, *S. rufiventris*, *Periporphyrus erythromelas*, and *Caryothraustes humeralis* in SKIN CORR ♂♂ are not placed in the same groups as they are in SKIN DIST ♀♀.

The phenogram of group C (SKIN + COLOR + SKEL CORR, Fig. 2C) differs primarily in the main stem connections of its smaller clusters. For example, the cluster bounded by *Pheucticus chrysopeplus* and *Passerina caerulea* is found as 2 clusters in SKIN DIST ♀♀ with *Spiza americana* and a few species in the genus *Passerina* added. *Passerina leclancherii* and *P. versicolor* are not included in the same major groups as they are in SKIN DIST ♀♀.

The species showing little affiliation to any of the clusters in SKIN DIST ♀♀ were not included in the phenogram of group C.

SKEL/COMP I CORR (group D, not figured) differs in much the same way as SKIN + COLOR + SKEL CORR (Fig. 2C). In addition to the differences discussed above, the genus *Passerina* does not group in the same way. There is one cluster of 9 species with the other 2 species, *P. caerulea* and *P. cyanea,* not clustering with these.

The phenogram representative of group E (SKIN + COLOR + SKEL DIST) is shown in Fig. 2D. The majority of the clusters are much the same as those of SKIN DIST ♀♀ (Fig. 2B). *Saltator orenocensis* differs in its placement and the species in the genus *Passerina* do not form 2 large groups. Only 2 species, *P. caerulea* and *P. amoena,* do not cluster with the other species of this genus.

Group F contains only SKEL/COMP I ALL DIST, which is in Fig. 5B of Hellack (1976). It was the "best" phenetic classification of Cardinalinae when only skeletal measurements were used. Several differences are noticeable in comparing this phenogram with the others. Only 2 of the species in the genus *Cardinalis* cluster together; the other (*C. phoeniceus*) shows little similarity to them. Most species in the genus *Passerina* cluster together (except *P. cyanea* and *P. caerulea*) rather than forming 2 distinct clusters. Two saltators (*S. aurantiirostris* and *S. orenocensis*) are not found with the other saltators in SKEL/COMP I DIST.

The "best" phenetic classification.—We have presented a number of phenetic classifications of the subfamily Cardinalinae. Each represents a facet of the phenetic relationships of the group. However, it may at times be useful to have one "best" classification of a group.

Schnell (1970) proposed several guides for choosing the "best" phenetic classification, when more than one are available. The phenogram selected should: (1) be based on a large number of characters; (2) have transformations applied to reduce any general size factor and; (3) have a relatively high cophenetic correlation. These guides while useful are not totally sufficient for this study. The phenogram used for general purposes should also have a relatively high correlation with the other phenetic analyses of the study.

For 2 of our analyses, all available characters were used and transformations reduced the size factor—SKIN + COLOR + SKEL CORR (Fig. 2C) and SKIN + COLOR + SKEL DIST (Fig. 2D). The phenogram with the highest cophenetic correlation is SKIN + COLOR + SKEL DIST. However, this phenogram is not as highly correlated to the BSMs and phenograms of the other analyses as is SKIN + COLOR + SKEL CORR. Only SKIN + COLOR DIST ♀♀ (not figured) and SKEL/COMP I DIST (figured in Hellack 1976) of the BSMs are more similar to SKIN + COLOR + SKEL

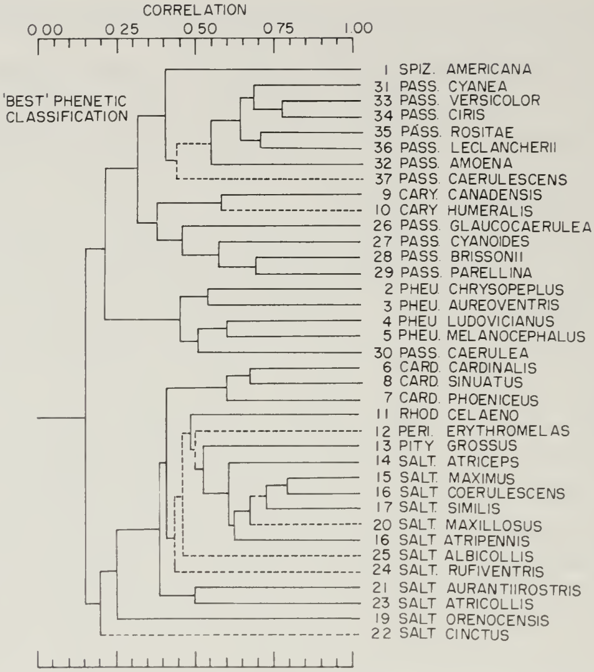

FIG. 4. The "best" phenetic classification of this study. Seven species not included in the SKIN + COLOR + SKEL CORR (Fig. 2A) analysis are represented by dotted lines.

DIST. The 2 phenograms of these analyses plus SKIN + COLOR DIST ♂♂ (not figured) are more similar in the comparison of phenograms. SKIN + COLOR + SKEL CORR (Fig. 2C), while not having the highest cophenetic correlation, is probably the best representative phenogram.

Using all available characters resulted in 7 species not being included in the SKIN + COLOR + SKEL CORR analysis. As these species (*Caryothraustes humeralis*, *Periporphyrus erythromelas*, *Saltator maxillosus*, *S. cinctus*, *S. rufiventris*, *S. albicollis*, and *Passerina caerulescens*) are included in the subfamily by various authors (Hellmayr 1938, Paynter 1970), they should be represented in a "best" phenetic classification of the group. To accomplish this, we evaluated their placement in other phenograms and 3-D models. SKIN + COLOR + SKEL CORR (Fig. 2C) was used for the placement of all species which it included and we positioned the 7 species into the clusters they probably would have joined had they been included in the analysis. This "best" phenetic classification is shown in Fig. 4. The reason or reasons for the placement of each of these species are discussed below.

Caryothraustes humeralis was included only in the analyses of skin and contrast characters. In SKIN DIST ♀♀ (Fig. 2B) and in the 3-D models of both SKIN ♀♀ (Fig. 3B) and SKIN ♂♂ (Fig. 3A), *C. humeralis* is most similar to *C. canadensis.* The average similarity of these 2 in the correlation analyses of both SKIN CORR ♀♀ (not figured) and SKIN CORR ♂♂ (Fig. 2A) is 0.58. This average similarity is used for the placement of *C. humeralis* in the "best" classification (Fig. 4).

Periporphyrus erythromelas was placed between *Rhodothraustes celaeno* and *Pitylus grossus* and near the saltators in the "best" classification. In analyses where *Periporphyrus erythromelas* was included (all of those based on external characters) it was most similar to *P. celaeno* or *Pitylus grossus.* This was true in the phenograms and 3-D models (except for SKIN CORR ♂♂; Fig. 2A).

Saltator maxillosus was included in the analyses of skin and contrast characters (Figs. 2A,B; 3A,B). In the 2 cluster analyses where we evaluated male characters (Fig. 2A), *S. maxillosus* showed close affinity to *S. maximus,* while in the cluster analyses using female characters (Fig. 2B) it was similar to both *S. atripennis* and *S. similis.* In the 3-D models (Fig. 3A,B), *S. maxillosus* separated from the other saltators primarily in component III—the vanes of its primaries are somewhat wider than found in those species of the major saltator cluster. Thus in the "best" classification (Fig. 4) it is placed in the saltator cluster and is depicted as more similar to the central group of species than either *S. atripennis* or *S. atriceps.*

Saltator cinctus was included only in the analyses of female skin and contrast characters. Considerable feather wear was evident in the only specimen of this species. We placed it in the "best" classification (Fig. 4) as we found it in the analyses of female characters (Figs. 2B, 3B), but because of the lack of specimens we are not certain that this appropriately represents the phenetic affinities of this species.

Saltator rufiventris was included in all the external character analyses. It clustered with the saltators; however, it showed no close affinities to any one saltator. Its closest affinities are perhaps to *S. aurantiirostris,* the species to which it is connected by the minimum connecting network of the 3-D models (Fig. 3A,B). *S. rufiventris* separates from the other saltators in component III of the 3-D models. The primaries are relatively narrower. Its placement in Fig. 4 represents more similarity to the major cluster of saltators than to any other species cluster. *S. rufiventris* is also more similar to the saltator cluster than are *S. aurantiirostris* and *S. atricollis.*

Saltator albicollis was represented in all analyses except those in which color was included. It clustered with the saltators in the skeletal analyses (Hellack 1976) and in the analyses of male study skin characters (Figs. 2A, 3A). In the analyses of female study skin characters (Figs. 2B,3B), less similarity to the saltators is shown. Its placement, as that of *S. rufiventris*, is rather arbitrary, but it is apparently most similar to the saltators.

Passerina caerulescens was included in all the external character analyses. It always clustered with species in the genus *Passerina* (Figs. 2A,B; 3A,B), but was relatively less similar to them. In the "best" classification (Fig. 4) it is placed in the cluster which includes *P. leclancherii*, the species to which it appears most similar. Its connection is at some distance from that of the other species to indicate its relatively low affiliation with the group.

Comparison of former classifications with the "best" phenetic classification.— Hellmayr's (1938) and Paynter's (1970) proposed classifications of the 37 species included in this study differ in the placement of species that Paynter (1970) assigned to the genera *Passerina*, *Pheucticus*, and *Cardinalis*. Hellmayr (1938) divides the species of Paynter's (1970) genus *Passerina* into 5 genera (*Passerina*, *Cyanocompsa*, *Cyanoloxia*, *Porphyrospiza*, and *Guiraca*) and the 4 species of *Pheucticus* into 2 genera (*Pheucticus* and *Hedymelas*). Hellmayr (1938) placed the Pyrrhuloxia (*Cardinalis sinuatus*) in a genus by itself (*Pyrrhuloxia sinuatus*).

The "best" phenetic classification (Fig. 4) divides the species into 3 large clusters. While these groups were not found in all the analyses, one or more groups occurred in every analysis (Fig. 2). The 3 groups are: (1) most of the species in the genus *Passerina* plus *Spiza* and *Caryothraustes*; (2) the genus *Pheucticus* plus *Passerina caerulea*; (3) the remaining genera in the subfamily (*Saltator*, *Rhodothraustis*, *Periporphyrus*, *Pitylus*, and *Cardinalis*).

In comparing the "best" phenetic classification to the classifications of Hellmayr (1938) and Paynter (1970), the clusters of the species in the genera *Passerina* and *Pheucticus* are most similar to Hellmayr's groupings. While there is a tendency for *Passerina* to form more than one cluster in all analyses, these groups were often more similar to each other than to any other species cluster. When this was not true, one of the clusters showed more similarity to the genus *Caryothraustes* or species of the genus *Pheucticus*.

Passerina caerulea has been considered very similar to the Indigo Bunting (Phillips et al. 1964; Blake 1969). In this study *P. caerulea* never grouped with the other species included in the genus *Passerina* and in most analyses it clustered with the genus *Pheucticus*. The Pyrrhuloxia clusters with the other species in the genus *Cardinalis*, as suggested by Paynter's (1970) classification.

The groupings of Hellmayr (1938) and Paynter (1970) are the same for the remaining species, but our phenetic analyses differ from the previous classifications in the similarities of the species they both place in the genus *Saltator*. The "best" phenetic classification (Fig. 4) shows one cluster of 6 very similar saltators (*S. atriceps*, *S. maximus*, *S. coerulescens*, *S. similis*, *S.*

maxillosus, and *S. atripennis*). The remaining 6 saltator species show little affiliation to any of the species clusters. It is possible that the material available was inadequate to get a reliable estimate of similarities for the species *S. rufiventris*, *S. albicollis*, and *S. cinctus*. This is not true for *S. atricollis*, *S. aurantiirostris*, and *S. orenocensis*. Ridgway (1901) suggested that several of the South American saltators did not belong in the genus, a conclusion which is supported by this study.

Taxonomic conclusions.—In this study the phenetic similarity found among the species in the subfamily Cardinalinae is somewhat different from the affiliations suggested by previous classifications. This is particularly evident in the genus *Saltator*. Six species of this genus do not show close affinities to any of the other saltators.

The species in the genus *Passerina* show considerable similarity to each other in their skeletal characters (*P. caerulea* being the exception), but separate into groups much like those suggested by Hellmayr (1938) when external measures were considered along with these skeletal measurements. *P. caerulea*, which was never found clustering with the other species Paynter (1970) places in the genus, is particularly noticeable. It has been suggested that this species is closely allied to the Indigo Bunting (Phillips et al. 1964, Blake 1969, Mayr and Short 1970). In our study it was not closely associated with any one group although it clustered most often with the genus *Pheucticus*.

Our results indicate that the genus *Saltator*, as classified at present, is a heterogenous group and consideration should be given to dividing it into several genera. We believe that *S. albicollis* and *S. rufiventris* are saltators and if adequate materials were available they would cluster with the major group of saltators. *S. aurantiirostris*, *S. atricollis*, and *S. orenocensis* are different and should be removed from the genus. We do not feel in a position to comment on *S. cinctus*.

The species in Paynter's (1970) genus *Passerina* could in our opinion be grouped according to either former classification—with the exception of *P. caerulea* which should remain *Guiraca caerulea*. *Pheucticus* appears to be composed of 2 rather different groups as indicated by Hellmayr (1938), and we suggest that his recommendations should be followed. We agree with Paynter on the classification of the genus *Cardinalis* (that it contains *Cardinalis sinuatus*) and the remaining species of this subfamily.

SUMMARY

We analyzed affinities of 37 species in the subfamily Cardinalinae using 75 external morphological characters and 49 skeletal characters. Affinities are presented in phenograms and 3-D models. The phenograms are compared among themselves and with previous classifications. A "best" phenetic classification was constructed using the guide-

lines of Schnell (1970) and taking into account correlation between basic similarity matrices.

The phenogram thus chosen did not include 7 of the species. These 7 species were placed into the clusters they would probably join if they had been included in the analysis. This was accomplished by studying the phenograms and 3-D models in which these species had been included.

This phenogram was then used to look at similarities and compare these similarities with the classifications of Hellmayr (1938) and Paynter (1970). Based on phenetic groupings, several saltators (*S. rufiventris*, *S. albicollis*, *S. cinctus*, *S. atricollis*, *S. aurantiirostris*, and *S. orenocensis*) were found to have little similarity to the remaining saltators. In the case of *S. rufiventris*, *S. albicollis*, and *S. cinctus*, insufficient data may be the reason for their lack of similarity to the saltator cluster. However, *S. atricollis*, *S. orenocensis*, and *S. aurantiirostris* are clearly distinct.

The genus *Pheucticus* clusters much as one would expect from Hellmayr's (1938) classification. The species placed in the genus *Passerina* by Paynter (1970) could be grouped according to either former classification.

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Appendix

DESCRIPTION OF STUDY SKIN, CONTRAST, AND COLOR CHARACTERS

Study skin.—(1) Rectrix length, distance from where skin joins shaft of middle pair of rectrices to tip of longest rectrix. Five characters represent shape of tail and are divided by rectrix length to reduce size factor; measurement is coded as negative until longest feather is measured then positive from longest feather. Characters are as follows: (2) distance from tip of outer rectrix to tip of 2nd, (3) distance from tip of 2nd rectrix to tip of 3rd, (4) distance from tip of the 3rd to tip of 4th rectrix, (5) distance from tip of 4th rectrix to tip of 5th, (6) distance from tip of 5th rectrix to tip of 6th. Two measures of feather widths (from center of feather), each divided by rectrix length to reduce size factor. Characters are: (7) outer rectrix width, and (8) outer vane of outer rectrix. The relative amount of tail covered by coverts was measured by the following 2 characters (divided by rectrix length): (9) distance from tip of under-tail coverts to tip of longest rectrix, (10) distance from tip of the upper-tail coverts to tip of longest rectrix.

Wing length (11), distance from carpal joint (bend of wing to tip of longest primary). Five characters represent shape of wing and are divided by wing length to reduce size factor, coded as negative numbers until longest feather is measured then a positive number. Characters are: (12) distance from tip of 9th primary to tip of 8th, (13) distance from tip of 8th to tip of 7th, (14) distance from tip of 7th primary to tip of 6th, (15) distance from tip of 6th primary to tip of 5th, (16) distance from tip of 5th primary to tip of 4th. Ten characters represent the widths of wing feathers and are divided by wing length in order to reduce size factor (all measurements were taken at the center of the feather). Characters are: (17) width of the 9th primary, (18) width of outer vane of 9th primary, (19) width of 8th primary, (20) width of outer vane of 8th primary, (21) width of 7th primary, (22) width of outer vane of 7th primary, (23) width of 6th primary, (24) width of outer vane of 6th primary, (25) width of 1st secondary, (26) width of outer vane of 1st secondary, (27) distance from the tip of longest secondary to tip of longest primary; measurement divided by wing length.

(28) Hallux length, measured without claw. Three toe lengths divided by hallux length to reduce size factor are: (29) length of middle toe, (30) length of 2nd toe, (31) length of 4th toe. Two angles were recorded from bill: (32) angle of commissural point relative to tomia, and (33) an angle measurement of arc of mandibular ramus.

Contrast characters.—Thirty-three 2-state characters were used. They were recorded as either present or absent characters, or contrast or no contrast characters. They are: (34) white spots in tail, (35) under-tail coverts contrasting to belly, (36) white present at apex of primaries, (37) white at base of primaries, (38) white on primary coverts, (39) white on secondary coverts, (40) marginal coverts contrasting to other coverts, (41) malar region contrasting to auricular, (42) lore region contrasting to forehead, (43) forehead contrasting to crown, (44) occiput contrasting to nape, (45) occiput contrasting to crown, (46) nape contrasting to back, (47) chin contrasting to gular, (48) gular contrasting to jugulum, (49) eye ring, (50) breast streaking, (51) back streaking, (52) side of body streaked, (53) flanks streaked, (54) abdomen contrasting to breast, (55) rump contrasting to back, (56) presence of a crest, (57) color sexual dimorphism, (58) middle wing coverts contrasting to other coverts, (59) superciliary line contrasting to crown, (60) auricular white, (61) white spot at base of lower mandible, (62) stripes on throat, (63) upper-tail coverts contrasting to rump, (64) streaking on crown, (65) flanks contrasting to abdomen, (66) sides contrasting to breast.

Color.—Color characters of the bird were recorded using the dominant wave length as the measurement of color. Color measurements were taken from 8 regions of the bird: (1) crown, (2) back, (3) rump, (4) upper-tail coverts, (5) gular, jugulum region, (6) breast, (7) abdomen, (8) crissum.

GENERAL NOTES

Why Ospreys hover.—Ospreys (*Pandion haliaetus*) fish from a perch or while in flight. Birds hunting from the air interrupt gliding or flapping progression with intermittent 2–10-sec hovering bouts in which they hold themselves stationary in the air column. They dive on fish directly from a gliding "interhover," but more often from a hover (pers. obs. in Florida, Maine, New Jersey, and New Brunswick, Canada). Here I examine the adaptiveness of hovering.

In March of 1974 and 1975, I found the fishing success of Ospreys working Lake George, Lake Co., Florida to be dependent on weather. When the sun was clouded over or the lake surface rippled by wind, the birds' capture rate and dive rate were both significantly depressed. I attribute these effects to reduced visibility into the water (Grubb, Auk 94:146–149, 1977).

To pursue the adaptiveness of hovering, I noted the success of each dive from a hover or interhover (Fig. 1). Although I have no information on energetic costs of gliding and hovering in Ospreys, I presume the latter to be generally more expensive. An exception occurs in strong winds when an Osprey can "glide" with zero ground speed. As it is more costly, for hovering to be adaptive it should result in a large increase in capture rate.

Details on methods are in Grubb (op. cit.). Briefly, I watched Ospreys seeking fish in a 0.2 km^2 rectangular area off Lake George's western shoreline. Numerous parameters of foraging behavior and concomitant weather were recorded.

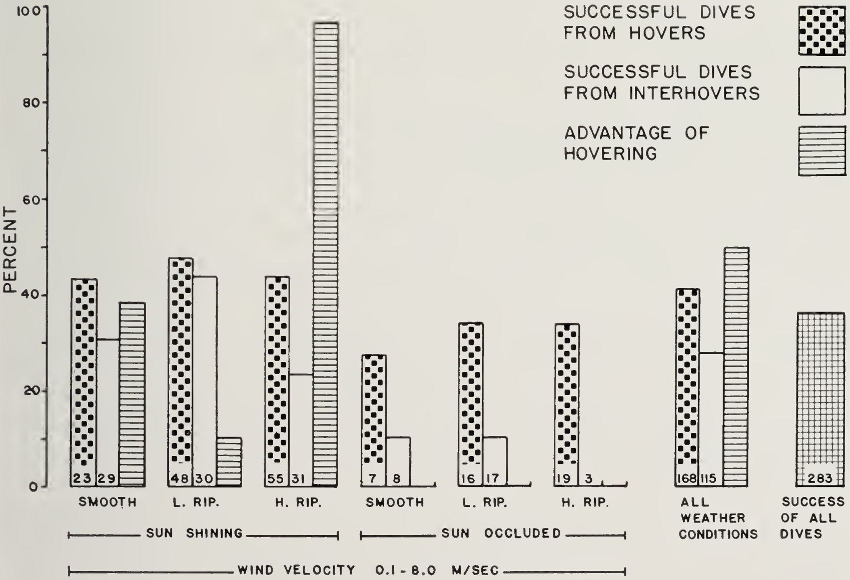

FIG. 1. Success rates of Ospreys diving on fish from a hover or from an interhover under various weather regimes, and advantage of hovering. Hovering advantage is not calculated for sample sizes less than 20. Smooth = calm water surface; L. Rip. = lightly rippled water surface; H. Rip. = heavily rippled water surface.

The success rate of dives from hovers and interhovers under various weather regimes is shown in Fig. 1. Under all weather conditions combined, dives from hovers were 50% more successful than dives from interhovers, a significant difference ($p < .05$; $\chi^2 = 5.90$, $df = 1$).

A complete picture of the adaptiveness of hovering should account for the energetic cost of hovering *vis-à-vis* gliding flight. Unfortunately, I lack the information necessary for such a comparison. The size distributions of fish appeared similar under all weather regimes, whether caught from a hover or a glide. Thus, Ospreys which never dove from a hover would have to save approximately 50% of the energy expended by those diving from hovers to compensate for the hoverers' increased energy intake.

I thank G. H. Grubb and particularly W. M. Shields for field assistance, and K. Bildstein and W. M. Shields for commenting on an earlier draft.—THOMAS C. GRUBB, JR., *Dept. of Zoology, Ohio State Univ., Columbus 43210.* *Accepted 13 Nov. 1975.*

Storage of piñon nuts by the Acorn Woodpecker in New Mexico.—The food habits of the Acorn Woodpecker (*Melanerpes formicivorus*) have attracted considerable attention (MacRoberts, Condor 72:196–204, 1970, and references therein). The most distinctive aspect of this behavior is the species' extensive dependence on stored mast. The nuts, generally acorns, are harvested by groups of birds in the fall, and placed in holes that are especially excavated for this purpose in dead trees, dead limbs of live trees, power poles, fence posts, etc. The stored mast is then communally used and defended from competitors by the groups during the rest of the year. However, most of the information about this and other aspects of the food habits of the Acorn Woodpecker has been obtained from studies of California populations. Relatively little is known about its behavior elsewhere.

As part of a study of the behavior and ecology of this species in the American Southwest, we periodically observed groups of Acorn Woodpeckers from December 1974 to August 1975 in Water Canyon, New Mexico. This canyon, located in the Magdalena Mountains near Socorro, contains riparian vegetation. Gambel's oak (*Quercus gambelii*) and the gray oak (*Q. grisea*) are present, and piñon-juniper (*Pinus edulis* and *Juniperus* spp.) forests are found along the sides of the canyon.

When our observations began, 7 out of the 10 groups of Acorn Woodpeckers which were studied held relatively large stores. Much of this mast consisted of acorns. However, in addition to acorns, we found that many piñon nuts also had been collected. When we examined a section of the storage tree of one of the groups in January, 84 out of 128 holes counted were found to contain piñon nuts, while 17 held acorns and 21 were empty. A recently fallen limb from the storage tree of another group had the remains of piñon nuts in 11 out of 33 holes, while the others were empty. In addition, during the winter and spring, woodpeckers often foraged among the piñon pines along the sides of the canyon, and birds consumed piñon nuts both on the storage trees and at "anvils" located among the pines. While the storage of acorns by southwestern populations of Acorn Woodpeckers has been reported by a number of authors (cf. Bent, U.S. Natl. Mus. Bull. 174, 1939), we know of no published reference to the use of piñon nuts by this species.

These observations suggest that piñon nuts, when available, form an important part of the diet of Acorn Woodpeckers in Water Canyon. California populations of the species have been observed to store other types of nuts besides acorns, including almonds, pecans, and walnuts obtained from orchards. However, according to Ritter (The California Woodpecker and I, Univ. of Calif. Press, Berkeley, 1938), the use of these nuts generally occurs when acorns are in short supply. That this was probably not the case in Water Canyon is suggested by the fact that while piñon nuts were plentiful, the acorn crop also was good. The majority of the groups did not deplete their mast stores over the winter, and many acorns and piñon nuts remained in the storage trees through the summer.

Bock and Bock (Am. Nat. 108:694–698, 1974) recently proposed that the distribution and abundance of the Acorn Woodpecker are affected not only by the abundance of oaks within a habitat, but also by the oak species diversity present. Because there may be an occasional failure of the production of acorns in each oak species, fewer species in an area would increase the probability of a total acorn crop failure. The use of piñon nuts by the woodpeckers in Water Canyon would be significant since there are only 2 oak species present. If the storage and consumption of piñon nuts which we observed is common, it would suggest that the diet of the species in this area has been expanded to regularly include an additional resource. This in turn would increase both resource abundance and diversity, and if the Bocks' hypothesis is correct, would allow the population to both reach and maintain a higher size than would be possible with acorn storage alone.

We thank Carl Bock for his many helpful suggestions, and also Melisse Reichman, who assisted with the field work. L. Kilham and P. L. Stallcup gave valuable comments on the manuscript. Financial assistance was provided by the Chapman Fund of the American Museum of Natural History and the Kathy Lichty Fund of the University of Colorado.—
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Flocking and foraging in the Scarlet-rumped Tanager.—Efficiency in foraging may be an important factor in the evolution of bird flocks (Cody, Theor. Pop. Biol. 2: 142–158, 1971). In order to test this suggestion, it is desirable to have field data showing an association between flocking and foraging behaviors. This note reports data for these behaviors taken on the Scarlet-rumped Tanager (*Ramphocelus passerinii*) in Costa Rica.

Investigations were carried out during August, 1973 at the Tropical Science Center research station near Rincon on the Osa Peninsula in southwestern Costa Rica. Areas of forest edge along roadsides and river banks were searched for Scarlet-rumped Tanagers. The bushes and dense vegetation of these areas are the favored habitat of this tanager, and the close proximity of the forest provided opportunities to occasionally observe Scarlet-rumped Tanagers flocking with species of the forest interior. All observations were made between 05:30 and 11:30. Data were taken only on adult males as their striking plumage made them easier to follow than females.

It is important to differentiate between flocks and aggregations. A flock was defined as a multi-individual group of birds moving in an integrated fashion, i.e. birds moving together as a unit from place to place. An aggregation was a multi-individual group with individuals in close proximity to one another, but which did not move in an integrated manner. For each flock, data on 4 variables were taken: (1) group size—the total number of individuals in the flock. Groups with at least 2 species present were designated mixed-species flocks, groups with only Scarlet-rumped Tanagers were designated single-species flocks; (2) foraging rate—the number of feeding attempts in 15 sec intervals were counted. A feeding attempt was defined as a peck at fruit or insects. Use of an electronic timer and tape recorder allowed continuous observations. It was not possible to obtain an indication of success in these attempts; (3) foraging height—the height of the bird from the ground was estimated in categories of 5 m; (4) group move-

TABLE 1

CORRELATION COEFFICIENTS FOR PAIRS OF ALL VARIABLES FOR ALL FLOCKS (A) AND SINGLE-SPECIES FLOCKS (S)

		Group Size	Foraging Rate	Foraging Height
Foraging	A	0.91*		
Rate	S	0.55*		
Foraging	A	0.78*	0.76*	
Height	S	–0.09	–0.05	
Group	A	0.86*	0.90*	0.77*
Movement	S	–0.03	–0.05	–0.01

* Indicates significance at the $p = 0.05$ level.

ment—the net rate of movement in one direction, i.e. "doubling-back" results in zero net movement. When possible, all data were taken on the first male seen in each flock. An effort was made to see as many flocks as possible.

During the course of the study, 34 flocks were encountered; 29 of these flocks were single-species flocks. Species seen in at least 2 of the 5 mixed-species flocks with Scarlet-rumped Tanagers included the Short-billed Pigeon (*Columba nigrirostris*), Red-capped Manakin (*Pipra mentalis*), Black-crowned Tityra (*Tityra inquisitor*), Masked Tityra (*T. semifasciata*), Green Honeycreeper (*Chlorophanes spiza*), Masked Tanager (*Tangara larvata*), White-shouldered Tanager (*Tachyphonus luctosus*), and Variable Seedeater (*Sporophila aurita*). Relationships between all possible pairs of the 4 variables were examined by correlation analysis. Two sets of correlations were calculated: one set for all data and one set for single-species flocks.

When all flocks are considered, there are significant positive correlations between all possible pairs of the 4 variables (Table 1). This suggests that Scarlet-rumped Tanager males alter their behavior as flocks become larger, showing increased foraging rate, increased group movement, and an increase in the height in the canopy at which the activities are performed. Foraging would seem therefore, to be a functional correlate of flocking. In single-species flocks foraging rate is still positively correlated with group

TABLE 2

A COMPARISON OF SCARLET-RUMPED TANAGERS IN MIXED AND SINGLE-SPECIES FLOCKS ON THE BASIS OF GROUP SIZE AND 3 BEHAVIORAL PARAMETERS*

Flock type	Observation time sec	Group size (S.D.)	Foraging rate pecks/min (S.D.)	Foraging height m (S.D.)	Group movement m/min (S.D.)
Mixed-species	855	21(7.8)	6(2.8)	21(7.4)	8(5.6)
Single-species	4770	4(2.3)	1(0.7)	7(3.9)	1(1.0)
All	5625	7(6.9)	1(2.2)	9(6.7)	2(3.5)

* Values are means with 1 standard deviation in parentheses, except for observation time which is total time.

size (Table 1), but no other pair of variables is significantly correlated. Social factors may be important in single-species flocks, and family members may stay together even when not foraging.

The preceding analysis indicates that it is the combination of the data on mixed-species flocks and those on single-species which produce most of the significant correlations for the data on all flocks. Mixed-species flocks may be functionally distinct from single-species flocks, a point also suggested by examining the mean values for all variables (Table 2). All means are greater for tanagers in mixed-species flocks than for those in single-species flocks (Mann-Whitney U-test, $p < 0.01$), indicating that tanagers move at a faster rate and forage faster and higher in the mixed-species flocks.

Scarlet-rumped Tanagers may gain any number of several advantages from joining large mixed-species flocks. Some possible advantages are: flocks may help the tanagers locate fruiting trees; flocks may "flush" insects; competition may be reduced by monitoring other species with similar food habits; there may be increased protection from predators in a flock which allows the tanagers to increase foraging. These and other ideas pertaining to flocking as an adaptation are discussed along with the pertinent literature elsewhere (Moriarty, Biologist 58: in press, 1976). Some or all of these benefits of flocking may also apply to single-species flocks, but if family relationships are an important aspect of single-species flocks, then it may not be surprising to find the foraging-related aspects of flocking occur more regularly and intensely in mixed-species flocks.

J. R. Karr, D. W. Schemske, C. E. Schnell, and M. F. Willson kindly reviewed the manuscript. Financial support was from the National Science Foundation through the Organization for Tropical Studies.—David J. Moriarty, *Dept. of Ecology, Ethology and Evolution, Vivarium Building, Univ. of Illinois, Champaign 61820.* *Accepted 15 Dec. 1975.*

Yellow Warbler nest used by a Least Flycatcher.—While checking Yellow Warbler (*Dendroica petechia*) nests near the Delta Marsh, Manitoba, I observed a Least Flycatcher (*Empidonax minimus*) making use of a deserted Yellow Warbler nest. The nest, 94 cm above the ground, was placed next to the trunk of a small maple (*Acer negundo*). On 5 June 1975 it contained 5 Yellow Warbler eggs but by 8 June only 1 egg was present and the nest's interior had been disturbed. An active Yellow Warbler nest was located several meters from the deserted nest; the first egg in this nest was laid about 12 June. On 14 June the first nest contained the single Yellow Warbler egg and 2 Least Flycatcher eggs. The nest was shallower now and there was no evidence that the flycatcher had added material to it. The flycatcher clutch was completed by the following day with the addition of a third egg; the Yellow Warbler egg was gone. One Least Flycatcher egg disappeared 6 days later but by 28 June, 2 nestlings were present. An empty nest on 29 June suggested predation had occurred.

Interest in old nests by the Least Flycatcher during the period of nest site selection has been noted by Mumford (unidentified nest, Wilson Bull. 74:98–99, 1962) and de Kiriline (Rose-breasted Grosbeak's nest: Audubon Mag. 50:149–153, 1948). No occupation occurred in either case. Use of nest material from a previous year's Yellow Warbler nest by a Least Flycatcher (pers. observ.) indicates that old nests may be a source of nest material.

It is possible that the Least Flycatcher was physiologically ready to lay, but since its own nest had been destroyed, it took over the available Yellow Warbler nest. I noted Least Flycatcher nest building in the area on 28 May. The present observations were therefore made mid-way through its breeding season. It is possible that this was a renesting attempt. Yellow Warbler nests resemble Least Flycatcher nests (Bent, U.S. Natl. Mus. Bull. 179, 1942); thus the stimulus of a familiar nest structure may have enhanced this opportunistic behavior. As the breeding season progresses, it may be more advantageous to occupy an existing nest and to channel the energy saved into egg production rather than expending it on building another nest.

This behavior may also indicate the initial stages of nest parasitism. Davis (Auk 57: 179–218, 1940) defines a nest parasite as one which builds no nest of its own but rather raises its young in old nests of other birds. The use of deserted or old nests may not illicit competition for the nest site with the original owner thereby allowing egg-laying to occur with minimal disturbance.

This work was funded by grants from the National Research Council of Canada and the University of Manitoba Research Board to S. G. Sealy, whom I thank for assistance in preparing this note. This is paper number 34 of the University of Manitoba Field Station (Delta Marsh).—J. PAUL GOOSSEN, *Dept. of Zoology, Univ. of Manitoba, Winnipeg R3T 2N2.* *Accepted 26 Mar. 1976.*

Pintail reproduction hampered by snowfall and agriculture.—The reproductive strategy of the Pintail (*Anas acuta*) shows several adaptations to the semi-arid variable climate of the prairie pothole region of north central North America where the species is a common breeder. By nesting early and using temporary and seasonal water areas replenished by snow melt waters or early spring rains, the species has successfully occupied broad areas containing limited permanent and semi-permanent water. The Pintail is prone to select new breeding grounds during periods of drought. Smith (J. Wildl. Manage. 34:943–946, 1970) has shown that part of the population moves northward from the prairies and parklands when widespread drought conditions occur there. Though well-suited for the natural prairie pothole environment, this reproductive strategy makes the Pintail vulnerable to spring snowstorms and modern agricultural practices. In recent years, high cereal grain prices have caused most of the prime Pintail breeding areas of eastern North Dakota to be placed under annual cultivation. Because the Pintail is prone to nest on cultivated lands, it is particularly vulnerable to spring farming operations. The magnitude of direct nest loss attributable to agriculture varies with the chronology of planting operations, size of the nesting population, and timing of nesting. These factors are affected by precipitation patterns. A recent study indicated few Pintail and other duck nests survive when nests are initiated on cropland prior to spring planting operations (K. Higgins, J. Wildl. Manage. in press). Field observations of Pintail hens and examination of reproductive tracts of sampled specimens during the spring of 1970 in eastern North Dakota provided an opportunity to identify nesting patterns and to study their relationship to precipitation, including snowfall, and to agricultural operations.

Pintails began arriving in substantial numbers in Stutsman County, North Dakota, on 4 April. Pair dispersal was initially slowed by a lack of water in shallow wetland basins, but in mid-April water conditions improved dramatically following a wet snowfall on 12 and 13 April and additional precipitation on the 15th. Pintail pairs soon occupied the newly flooded habitat and egg laying was in progress by 18 April at the onset of a 10 cm snowfall. Precipitation at Jamestown, North Dakota during April 1970 totaled 5.77 cm (U. S. Dept. Commerce, Climatological Data 79:43–57. 1970).

I collected 5 paired hens (P-45, P-47, P-49, P-50, and P-51) in Stutsman, Barnes, and LaMoure counties from 18 to 23 April while the ground was covered with snow. Examination of the reproductive tracts of the sampled hens indicated all had continued to lay despite apparent disruption of nesting by snow cover. P-45 was collected shortly after the onset of snowfall on 18 April and was nearing completion of its clutch at that time based on number and stage of regression of ruptured follicles. The bird had laid on the date of collection, had an egg in the oviduct, and had 1 enlarged follicle weighing 10.0 g still to be ovulated. P-47 was collected during heavy snowfall on 19 April. Five recently ovulated ovarian follicles, an egg in the oviduct, and normal follicle gradation indicated continued laying activity. Ovary weight was 32.6 g. P-49 had laid 1 egg and its ovary weighed 33.8 g; the largest follicle weighed 15.8 g. Ovulation had not occurred on 20 April but appeared imminent. A series of 6 recently ruptured follicles and an egg in the oviduct indicated P-50 was continuing to lay on 22 April although no enlarged ovarian follicles remained to be ovulated. The ovary of P-51 contained a series of recently ovulated follicles and an enlarged follicle (6.3 g). Three larger follicles had collapsed and were regressing, presumably because of weather-related factors. Continued laying activity by these hens in areas of heavy snow cover suggests eggs were either being dumped or new nest sites chosen. I doubt that many hens relocated their nests the morning of 19 April considering that snowfall began in late afternoon of 18 April and formed a uniform mantle several centimeters deep by the following morning; heavy snowfall continued through the 19th.

Relatively mild temperatures presumably were a major factor contributing to the continuance of laying despite snow cover. Dane and Pearson (Pp. 258–267 *in* Proceedings Snow and Ice in Relation to Wildlife and Recreation Symposium, Iowa Cooperative Wildlife Research Unit, Iowa State Univ., Ames, 1971) indicated that following a snowstorm on 1 May 1967 in North Dakota, all Mallard (*Anas platyrhynchos*) and Pintail pairs in the severe storm area abandoned their territories but some Mallards continued laying in the less intense storm areas. The 1967 storm was accompanied by high winds and temperatures fell to –9°C in the severe storm area causing ice formation of sufficient strength to carry a man (Dane and Pearson, op. cit.). Following the 1970 snowfall, the lowest temperature recorded at Jamestown was –5°C on 22 April. During the 1967 storm, –9°C readings lasted for 3 days whereas in 1970 the temperature dipped to –5°C for only 1 night. Because many wetlands remained at least partially open, invertebrates continued to be available and were fed upon by hens. The 5 hens collected during the snowfall period were feeding and esophagi of 4 contained invertebrates (earthworms or snails, and/or dipteran larvae). Earthworms were obtained from newly flooded shallow wetlands. Invertebrates are the dietary staple of Pintail hens during the period of egg formation (Krapu, Auk 91:278–290, 1974).

The fact that food remained available at certain wetland sites during the period snow covered the ground in 1970 may have contributed to continued laying activity. Nalbandov (Reproductive Physiology, 2nd ed., W. H. Freeman. San Francisco, 1964) indicated that withdrawal of food triggers follicular resorption in laying hens. Some interruption of laying apparently did result from the storm. In addition to ovarian follicular regression noted in P-51 taken towards the end of the snowfall period, ovaries of 2 of 5 hens collected from 24 April through 30 April had enlarged collapsed follicles indicating interruption of a previous nesting attempt. Three of these hens were laying, 1 was about to initiate laying, and 1 showed no evidence of recovery. Heavy nest loss and/or inhibition of nesting as a result of the 18–20 April snowfall presumably contributed substantially to the high transect pair:lone male ratio of 23:19 on 29 April in comparison to a pair:

lone male ratio of 8:24 on that date in 1969 (C. Dane, pers. comm.). Favorable weather conditions prevailed throughout late April 1969.

Following an unusually wet and cold period in late April 1970, a second major nesting effort began on about 1 May and lasted for approximately 10 days. Of 10 hens collected from 3 to 9 May all had ovulated on the date of collection. The Pintail pair:lone male ratios along a transect near Jamestown on 29 April, 5 May, and 12 May were 23:19, 12:17, and 4:20, respectively (C. Dane, pers. comm.). These data also suggest that a major portion of the hens had completed clutches and had initiated incubation by mid-May. Mild weather accompanied this laying effort.

Evidence of substantial nest destruction appeared during late May 1970. Agricultural operations commenced on about 10 May and a massive planting effort was underway by mid-May. Sightings of hens increased on the Drift Prairie as agricultural operations progressed. I obtained a measure of the magnitude of nest losses from data collected during the annual breeding ground survey conducted by the North Dakota Game and Fish Department. Two transects (6 and 7) totaling 643.7 linear km and encompassing an area of 259.1 km^2 occur in the intensively cultivated Drift Prairie of eastern North Dakota. Surveys were conducted on 18–19 May 1969 and 18–21 May 1970. Data from the 2 transects were combined resulting in pair:lone male ratios of 105:364 (1969) and 165:352 (1970) (C. Schroeder, pers. comm.) indicating a marked difference in the proportion of non-incubating hens between years presumably caused by differing nest destruction rates. Favorable weather conditions during the spring of 1969 reduced potential for heavy losses of incubated clutches from planting operations late in the nesting season. In 1970, 11 paired Pintail hens were sampled on the Drift Prairie from 20 to 27 May and all had brood patches suggesting nesting attempts had progressed into incubation. Behavior and activity patterns of these hens suggested nesting attempts had been terminated. Estimates derived by projecting these transect data to the entire Drift Prairie area of North Dakota and interpreting reproductive status on the basis of sampled birds suggest that approximately 43,725 hens had lost one or more nests on the Drift Prairie and were approaching a nesting failure for the season when censused in late May 1970; 15,900 more hens than during a similar period in 1969. The impact of nest loss during years of delayed planting is intensified because of the reduced probability that hens will renest following nest destruction late in the breeding season. Deteriorating water conditions in late May 1970 probably also diminished renesting prospects.

In summary, because most of the prime breeding area of the Pintail in eastern North Dakota is now under annual cultivation, prolonged periods of precipitation in spring that in pristine times either enhanced Pintail reproduction or, as with snowfall, acted only as a temporary setback, now delay agricultural operations and set the stage for destruction of nests over millions of hectares in a few weeks. The problem is magnified from past agricultural periods because few fields are now left idle each spring for a sufficient period to allow clutches to hatch. The Pintail will renest when suitable habitat conditions exist so is capable of partially compensating for these losses.

Agriculture poses an additional threat to the Pintail through destruction of wetland habitat. The degree of success of efforts to preserve a substantial part of the remaining temporary and seasonal wetland habitat of the prairie pothole region will be a major factor determining whether prairie-nesting Pintail populations comparable to those of recent years will continue to exist there. Protection from drainage has been afforded sizable blocks of shallow wetland basins at widely scattered locations in North Dakota through perpetual easements under the Small Wetlands Program administered by the U. S. Fish and Wildlife Service. This continuing effort is an important step toward maintaining the extensive shallow wetland base required by Pintail breeding in the prairie pothole region.

I thank Charles W. Dane and Charles H. Schroeder for use of unpublished data. Dr. Dane also provided editorial assistance and comments on the manuscript.—Gary L. Krapu, *U. S. Fish and Wildlife Service, Northern Prairie Wildlife Research Center, Jamestown, ND 58401.* *Accepted 15 Mar. 1976.*

Ticks as a factor in the 1975 nesting failure of Texas Brown Pelicans.—Fewer than 100 Brown Pelicans (*Pelecanus occidentalis*) remain on the Texas Coast from a population that once numbered 5000 birds. Only a small proportion of these have nested in recent years and most attempts have not been successful (King et al., Southwest. Nat. 21: in press). Pesticides were responsible for mortality of Louisiana pelicans in 1975 (Winn, Audubon Mag. 77:127–129, 1975), but nest failure in Texas was attributed to natural causes. Seven pairs of Brown Pelicans nested on a low-lying island near Aransas National Wildlife Refuge in April, but all deserted their nests before the eggs hatched. The cause of desertion was either storm tides that nearly inundated the island, or more likely, an infestation of nest parasites. A later nesting attempt at Pelican Island in Corpus Christi Bay ultimately produced 9 young.

Adults were first seen building nests near Aransas Refuge on 14 April. On 24 April, 6 nests containing 16 eggs were still active. A 7th had failed, probably due to wave action that partially buried the nest and its single egg. Eight days later, all nests were found deserted. When the eggs were collected on 7 May, an unusually heavy infestation of ticks was noted in and around the nests. On 25 May, 3 nests were collected which yielded a total of 2389 adult and nymphal ticks. Many thousand larvae were also present.

All ticks were identified as *Ornithodoros capensis* by personnel of Naval Medical Research Unit-3 (NAMRU-3) Cairo, Egypt, and United States Public Health Service, Rocky Mountain Laboratory, Hamilton, Montana. *O. capensis* is a common argasid tick infesting many species of aquatic birds in tropical, subtropical, and south temperate climates (Kohls et al., Ann. Entomol. Soc. Am. 58:331–364, 1965; Hoogstraal, *in* Viruses and Invertebrates, A. J. Gibbs (ed.), American Elsevier Publishing Co. Inc., New York, 1973; Hoogstraal et al., J. Med. Entomol. 12:703–704, 1976). Although *O. capensis* is found in many areas of the Old World, its occurrence in continental United States has been reported only once. Twelve specimens were taken from a Roseate Spoonbill (*Ajaia ajaja*) collected on an unnamed island off the coast of Texas in 1940 (Kohls et al., op. cit.). Closely related specimens in the *O. capensis* group, but not true *O. capensis*, have been recorded in Oregon (Clifford et al., J. Med. Entomol. 7:438–445, 1970), California (Radovsky et al., J. Parasitol. 53:890–892, 1967), and Florida (Kohls et al., Ann. Entomol. Soc. Am. 58:331–364, 1965).

Infestations of *O. capensis* have caused nest desertion and perhaps the death of nestlings through the transmission of a lethal arbovirus in some sea-bird colonies. Converse et al., (Am. J. Trop. Med. Hyg. 24:1010–1018, 1975) and Feare (Ibis 118:112–115, 1976) documented the abandonment of 5000 Sooty Tern (*Sterna fuscata*) nests containing eggs and young in a colony of 400,000 pairs on Bird Island in the Seychelles. They found numerous ticks in the deserted portion of the colony but few or none in adjacent areas where reproduction was normal. Not only did the ticks cause desertion, they remained so abundant the following year that the terns did not reoccupy the area. Marshall (Wilson Bull. 54:25–31, 1942) reported nest abandonment of incubating Common Terns (*Sterna* *hirundo*) at night and their return to the sites during the day. The cause of night desertion was not identified but it may have been related to a heavy infestation of ticks such as *O. capensis.*

A Soldado-like virus was isolated from our Texas tick samples sent to Rocky Mountain Laboratory. When *O. capensis* ticks collected from sick Sooty Terns on Bird Island were allowed to feed on young domestic chickens, they transmitted a Soldado virus that caused the death of their host (Converse et al., op. cit.). Feare (op. cit.) found an unusually high number of dead young terns and felt the Soldado virus transmitted by the ticks may have contributed to the die-off.

In our study the occurrence of a spring storm 30 April within the period of desertion (24 April–2 May) complicated defining the cause of nest abandonment. Winds reaching 38 knots and rainfall of 0.41 cm were recorded at the nearest National Weather Service station in Victoria (63 km). However, the 6 nests which had been active on 24 April showed no sign of damage by wind or high water when they were examined on 7 May. We therefore concluded that the infestation of ticks was the probable cause of nest desertion.

In contrast to the complete failure of the Brown Pelican's first nesting attempt, the later nesting on Pelican Island produced young; 9 fledged from 11 nests. We found no *Ornithodoros* ticks associated with the young pelicans, their nests, or in the soil and litter beneath the nests on Pelican Island.

Distribution of *O. capensis* is influenced by bird movements. Our preliminary investigations reveal the occurrence of *O. capensis* in several heronries on the central Texas Coast. Host species noted so far include the Brown Pelican, Roseate Spoonbill, Cattle Egret (*Bubulcus ibis*), Reddish Egret (*Dichromanassa rufescens*), Black-crowned Night Heron (*Nycticorax nycticorax*), Laughing Gull (*Larus atricilla*), and Black Skimmer (*Rynchops nigra*). The long-term effects of ticks on pelicans and other colonial nesting birds remain to be determined.—Kirke A. King, *U. S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Gulf Coast Field Station, P. O. Box 2506, Victoria, TX 77901;* David R. Blankinship and Richard T. Paul, *National Audubon Society, 115 Indian Mound Trail, Tavernier, FL 33070;* Robin C. A. Rice, *Dept. of Entomology, Univ. of Hawaii, 2500 Dole Street, Room 28, Honolulu 96822.* *Accepted 13 July 1976.*

Prairie Warbler feeds from spider web.—A note in the March 1976 Wilson Bulletin described an incident of feeding from a spider web by a Cedar Waxwing (*Bombycilla cedrorum*) (Burtt et al., Wilson Bull. 88:157–158, 1976). It was believed that this represented the first account of such behavior in a passerine.

I observed a somewhat similar incident involving an adult male Prairie Warbler (*Dendroica discolor*) in Everglades National Park, Monroe Co., Florida, on the afternoon of 3 July 1971. The bird was perched low in mangroves about 20 cm from the vertically-oriented web of a golden silk spider (*Nephila clavipes*). Three times during a 30-sec period he flew briefly to the web and each time picked an insect from it with his bill. Upon alighting on his perch, he swallowed each insect and then wiped his bill against a branch as if cleaning silk from it. No spider was seen on the web.

Prairie Warblers are known to eat spiders and to use spider silk in nest-construction (Wetmore, U. S. Dept. Agr. Bull. 326:1–133, 1916; Bent, U. S. Natl. Mus. Bull. 203:1–734, 1953). Webs of *Nephila clavipes* often persist for relatively long periods of time

(Comstock, The spider book, Cornell Univ. Press, Ithaca, 1948), and abandoned ones might serve as effective insect traps for birds detecting them.—JOHN F. DOUGLASS, *Archbold Biological Station of The American Museum of Natural History, Route 2, Box 180, Lake Placid, FL 33852* (Present address: *Dept. of Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor 48109*). *Accepted 27 Sept. 1976.*

Notes on the hummingbirds of Monteverde, Cordillera de Tilarán, Costa Rica.—Monteverde, a lower montane site on the Pacific slope of northwest Costa Rica's Cordillera de Tilarán, supports a strikingly rich avifauna. During the periods October 1971–May 1973 and June–July 1975, I recorded 20 species of hummingbirds—over a third of Costa Rica's total—at Monteverde. Many species were well outside ranges previously described by Slud (Bull. Am. Mus. Nat. Hist. 128, 1964) and others. I present here information on avifaunal affinities of this diverse assemblage as well as data on local distribution, breeding, plumages, and behavior of species seldom studied in the field.

Monteverde lies upon a bench, elevation 1320–1540 m, just below the continental divide, which reaches 1600–1700 m. The approximately 3 km wide belt bounded by the lower edge of the bench and the divide contains a steep gradient of biotic communities, corresponding to the steep moisture gradient produced by trade winds which carry mist over the divide during the November–May "dry season." These communities range from a constantly wet, wind-sculptured elfin forest on the divide proper to a partly deciduous moist forest, subjected to severe dry-season moisture stress, on the lower edge of the bench. One may subjectively divide this gradient into "life zones," though no obvious boundaries exist and elevations are only approximate. Life zones were determined with the aid of Tosi (Mapa ecológico de Costa Rica, Centro Científico Tropical, San José, 1969) and Holdridge (Life zone ecology, Tropical Science Center, San José, 1967; pers. comm. to G. V. N. Powell). They are abbreviated below as follows: MF-WF = Lower Montane Moist Forest-Wet Forest Transition, elevation 1200–1400 m; WF = Lower Montane Wet Forest, elevation 1400–1480 m or higher; WF-RF = Lower Montane Wet Forest-Rain Forest Transition, elevation 1480–1540 m or higher; RF = Lower Montane Rain Forest, elevation over 1540 m; EF = Elfin Forest, crest of divide.

Many of Monteverde's bird species, especially those inhabiting the lower habitats, are characteristic of the dry Pacific northwest or the subtropical belt (*sensu* Slud 1964). Many species of the Caribbean slope stray over the divide, however, and the wetter forests of the higher elevations contain many characteristic highland birds. At these elevations hummingbirds typical of the forests also exploit flowers in the limited second-growth areas. The extensive pasture and scrub habitats of the lower life zones contain a distinct group of species, however, though forest populations contribute scattered individuals (Feinsinger, Organization of a tropical guild of nectivorous birds, Ph.D. thesis, Cornell Univ., 1974).

Though I made observations in all life zones, most studies, mist-netting, and color-marking of hummingbirds—following the method of Stiles and Wolf (Condor 75:244–245, 1973)—took place in MF-WF successional habitats. Within these habitats, hummingbirds fed at flowers of 15 plant species, particularly the herb *Lobelia laxiflora* (Campanulaceae) and the tree *Inga brenesii* (Leguminosae). Aggression was most pronounced during flowering peaks of these species. Territorial species directed most aggression toward flying or feeding birds; only *Philodice bryantae* consistently displaced perched conspecifics. Feeding birds often spread their rectrices as a display, a stabilizing maneuver, or both. Most species vocalized while fighting, feeding, perching, or flying. Additional information on foraging and aggressive behavior is given by Feinsinger (1974) and by Feinsinger and Chaplin (Am. Nat. 109:217–224, 1975).

Phaethornis guy, Green Hermit (resident).—A bird of the humid sub-tropical and lower montane belts of both slopes (Slud 1964), at Monteverde this species resided in mature forest understory from MF-WF through EF. At least one lek site existed in RF. G. V. N. Powell (pers. comm.) discovered a nest with eggs in January 1971.

Phaethornis longuemareus, Little Hermit (vagrant).—The Little Hermit is local in the dry Pacific northwest of Costa Rica and on the lower slopes of the northwestern cordilleras (F. G. Stiles, pers. comm.; see Slud 1964). In April 1970, W. H. Buskirk (pers. comm.) sighted an individual in WF-RF understory. I observed a bird at the lower edge of the Monteverde bench (MF-WF) on 5 May 1972, and netted an adult in the same spot on 21 January 1973.

Doryfera ludovicae, Green-fronted Lancebill (vagrant).—On 16 October 1972, I netted an immature near a flowering *Inga brenesii* tree in a MF-WF pasture. (Immatures were identified by their striated culmens—see Ortiz-Crespo (Auk 89:851–857, 1972).) Previous published records for Costa Rica are restricted to the Caribbean slope of the central highlands (Slud 1964).

Campylopterus hemileucurus, Violet Sabrewing (resident).—A locally common highland species (F. G. Stiles, pers. comm.; Slud 1964), this large hummingbird commonly foraged among banana flowers at Monteverde. Forest-edge and forest understory at all elevations also supported a moderate density of sabrewings. F. G. Stiles (pers. comm.) recorded a lek at Monteverde; however, I noted only single singing males, usually near rich food sources. Males, which weighed more and had shorter bills than females (Feinsinger 1974), exhibited a range of plumages from solid green through mixed green and violet to solid violet. This sequence was correlated with disappearance of culmen striations, indicating a distinct immature male plumage unlike that of the gray-bellied females (*contra* Wetmore, Smithson. Misc. Collect. 150(2), 1968).

Colibri delphinae, Brown Violet-ear (vagrant).—I netted an immature of this species near an *Inga brenesii* tree on 15 October 1972. On 17 October, at least one other Brown Violet-ear fed at a nearby *I. brenesii.* Slud (1964) cites several isolated records from the central and southern mountains and one from the Cordillera de Guanacaste (the next mountain range to the northwest) but none from the Cordillera de Tilarán.

Colibri thalassinus, Green Violet-ear (seasonal).—From October through June, nonforested habitats from MF-WF through RF supported large numbers of this widespread highland species. Singing, presumably by males, took place on exposed perches well away from food sources. Even at particularly rich food sources, Violet-ears made few efforts at defense and were often displaced by smaller birds (Feinsinger 1974). Feeding birds often voiced a repetitious dry chatter.

Chlorostilbon canivetii, Fork-tailed Emerald (seasonal).—From late January through late November, a number of Emeralds resided in the MF-WF study areas. Immature males resembled females but possessed dark-green patches of varying extent on breast and throat. Many individuals of both sexes possessed entirely black mandibles and thus resembled the race—or species (Wetmore 1968)—*assimilis* of southwestern Costa Rica and Panama. Others resembled the race *salvini*, a member of the dry northwest avifauna that is abundant on the lower slopes of the northwestern mountains (Slud 1964). All individuals observed behaved similarly, however, exploiting scattered flowers while giving a soft, wren-like chatter.

Panterpe insignis, Fiery-throated Hummingbird (resident).—This highland species is most typical of the Cordillera Central and Cordillera de Talamanca (Slud 1964). The EF and upper RF at Monteverde also support a conspicuous resident population, discussed by Stiles and Hespenheide (Condor 74:99–101, 1972). Individuals I observed foraged in clearings and at epiphytes in the forest canopy but rarely entered forest understory.

Hylocharis eliciae, Blue-throated Goldentail (seasonal).—Common lower on the Pacific slope (Slud 1964), Goldentails entered Monteverde's MF-WF non-forested habitats only. A few adults and many immatures converged on *Lobelia laxiflora* fields February–April 1972 and 1973. During October and November 1972, some individuals fed at *Inga brenesii* trees. Immatures were dull buff on the underside, with pale pink at the base of the bill and flecks of blue on the throat or upper breast. Adults and immatures alike defended territories, often fighting with each other or with Blue-vented Hummingbirds.

Amazilia saucerottei, Blue-vented Hummingbird (resident).—Typical of the drier Pacific slope and central highlands of Costa Rica (Slud 1964), this species remained abundant year-around in the MF-WF study areas but was seldom seen above 1400 m or in wooded regions. Nearly every rich flower in the study areas supported a Blue-vented Hummingbird territory. Any other hummingbird that attempted to forage among defended flowers and attracted the attention of the territory holder was chased. These high-speed chases often entered other territories and became 3- or 4-bird affairs. Occasionally chase attempts were unsuccessful. Green Violet-ears entering Blue-vented territories in *Lobelia laxiflora* fields often ignored the residents and continued to feed. The numerous heliconiine, ithomiine, and pierid butterflies attracted to large *Hamelia patens* shrubs also ignored resident Blue-vented Hummingbirds despite the birds' continued efforts to eject them. On such occasions, defenders often abandoned their attempts in favor of irregular feeding, presumably a displacement activity.

Two marked Blue-vented Hummingbirds in particular remained in the study areas throughout much of the 1971–73 research period. These moved their territories from one flower concentration to another over the months. Their "shifting territories" (*sensu* Wolf, Condor 72:1–14, 1970) remained within a limited area which might be considered the home range.

Singing and fighting that took place well away from rich flower clumps peaked from early August through October 1972, indicating a possible spurt of mating activity in late wet season. Immatures (as judged by culmen striations) appeared throughout the year, however, and there was a great influx of them in May 1972. I encountered 2 nests, 1 on 2 December 1971 (containing a well-grown juvenile) and 1 on 9 January 1972 (containing eggs). The latter nest was on a dead *Cecropia obtusifolia* branch at secondary forest edge, elevation 1200 m. The nest with the juvenile was on a *Ficus* vine along a pasture edge at 1370 m. On 2 December an adult fed the juvenile at the nest, but on 4 December the latter had fledged and was in the grass beneath the nest. The bird feeding it chased away another adult that landed on the rim of the empty nest and made side-to-side head movements suggestive of feeding. This juvenile possessed duller plumage than most adults or immatures. Primaries and secondaries were medium gray instead of black; coverts and contour feathers on head, neck, and back appeared quite buffy (probably due to buffy edgings); and the rectrices were a light iridescent bluish-green resembling the color of a Green Violet-ear tail. I estimated exposed culmen length at 8 mm, less than half that of an adult. During the May 1972 influx of immatures, several netted had especially deep bill striations as well as duskier plumage and tails lighter in color than adults. These may have recently fledged.

Amazilia tzacatl, Rufous-tailed Hummingbird (resident or seasonal).—Widespread at lower elevations and occurring in clearings to at least 1500 m (F. G. Stiles, pers. comm.; Slud 1964), at Monteverde I observed this species only sporadically. Rufous-tailed Hummingbirds were especially conspicuous in the MF-WF study areas during June 1972, when they wrested control of many large *Hamelia patens* bushes from Blue-vented Hummingbirds. This species breeds at Monteverde: F. G. Stiles (pers. comm.) has discovered nests, and on 13 and 15 November 1971 I observed an adult feeding a juvenile perched on a WF roadside tree. Though its tail was the same striking rufous-brown as the adult's, the juvenile's green plumage appeared much duller (perhaps due to gray or buffy edgings) and its culmen appeared somewhat shorter.

Eupherusa eximia, Stripe-tailed Hummingbird (resident).—A typical mid-elevation species (Slud 1964), the Stripe-tailed Hummingbird was abundant throughout forest-edge and deep forest from MF-WF through EF. Stripe-tails often entered MF-WF clearings as well. They visited a wide variety of flowers, piercing those corollas adapted for longer-billed species. Foraging or fighting individuals often voiced loud buzzes and spread their striking tails for the duration of each buzz.

Elvira cupreiceps. Coppery-headed Emerald (resident).—This normally Caribbean-slope species (Slud 1964) was most abundant in forest-edge and forest habitats in the MF-RF and lower RF. Emeralds also entered MF-WF openings at times, usually to feed at *Inga brenesii* flowers. G. V. N. Powell (pers. comm.) found 2 nests in WF-RF in November 1971 and October 1972.

Lampornis hemileucus, White-bellied Mountain-gem (vagrant).—On 14 February 1973, I netted an immature at 1320 m elevation in the MF-WF study areas. I also observed an immature or female in the same area on 29 May 1972. W. H. Buskirk (pers. comm.) observed this species on the Caribbean slope northeast of Monteverde during dry season. Previously, this species was not recorded further north than the Caribbean slope of the central highlands (Slud 1964).

Lampornis calolaema, Purple-throated Mountain-gem (resident).—I often encountered this common highland hummingbird in all habitats from WF through EF. Some Mountain-gems strayed into the MF-WF study areas to feed at *Inga brenesii*. Although dominant over even Blue-vented Hummingbirds, Mountain-gems gave few displays. Nests with eggs or young were encountered during all seasons in understory trees or shrubs (January, March 1972—WF), on low forest-edge vines (October 1972, WF; December 1972, WF-RF), even in crevices in a clay roadbank (May 1972, August 1972, July 1975—WF-RF and RF).

Heliodoxa jacula, Green-crowned Brilliant (resident).—W. H. Buskirk and G. V. N. Powell (pers. comm.) netted these birds year-around in mature forests of the WF-RF zone. Slud (1964) cites no records from the northwestern cordilleras for this species, more typical of the subtropical-lower montane Caribbean slope.

Heliomaster constantii, Plain-capped Starthroat (seasonal).—A member of the dry-forest avifauna (Slud 1974), this species appeared in the MF-WF study areas. Females or immatures frequently foraged at the vine *Mandevilla veraguasensis* (Apocynaceae) May–August 1972 and July–August 1975.

Philodice bryantae, Magenta-throated Wood-star (seasonal).—Wood-stars were considered "very uncommon" by Slud (1964), who listed several records from the central highlands but only 1 from the Cordillera de Guanacaste and none from the Cordillera de Tilarán. At Monteverde, however, these unique little birds appeared predictably and abundantly from September through April of each year. Though most common at *Inga brenesii* and *Lobelia laxiflora* flower concentrations in the MF-WF study areas, Wood-stars also foraged in openings and forest edges through at least WF-RF.

Intense intraspecific belligerence characterized both sexes of Wood-stars. Rich food sources were vigorously defended. Territory holders perched on dead branches high in trees near the defended flowers. Territorial males sang a complex weak, scratchy melody that often included loud snaps. Songs were often interspersed with preening bouts or with displays that consisted of rotating the head back and forth, presumably exposing the males' brilliant gorgets. Conspecific intruders of either sex, whether feeding or perching, were immediately attacked. If its rapid approach failed to displace the intruder, the attacker hovered back and forth over the trespassing bird, uttering a variety of squeaks and a buzzy *churrrr* and occasionally darting at the other. The slender rectrices were kept spread throughout this action, producing a palmate appearance in contrast to the fanlike spread tails of other species with broader rectrices. These displays seldom failed to elicit either flight or a battle. Both "churrrring" loudly, fighting Wood-stars circled each other 5–30 cm apart and darted back and forth. Still circling and darting, the fighting pair sometimes rose high in the air. More often, however, opponents stayed near ground level; failing to eject one another, both would resort to displacement-feeding, still churrrring. Males performed an aerial display reminiscent of certain North American species. These displays were usually aimed at a male or female trespasser that the defender had been unable to displace, but were occasionally aimed at perched females and thus may have served a mating function as well. A displaying bird swept back and forth pendulum fashion in a shallow, 20–30 m wide arc that centered just above the target individual. At each endpoint, the displayer paused or flew at a tangent for 2–3 sec before sweeping down again. The visual display was accompanied by a loud, snipe-like whistle, undoubtedly produced by the wings, and at the bottom of the arc by 3 to 7 loud manakin-like snaps, perhaps produced by the rectrices. From 1 to 8 such displays were performed in a sequence, the plane of the arc changing all the while. The performer invariably concluded by flying to a nearby perch. I never observed females to sing or to engage in the pendulum display. Nevertheless, females often defended feeding territories, displaced both sexes from flowers or perches, and darted around intruders if necessary.

Perched Wood-stars never uttered the *churrrr.* Foraging birds often did so, however, especially if agitated. A feeding bird never opened its rectrices unless under attack but rather kept the tail closed and pointed up at about a 60° angle from the body plane. Moving methodically from flower to flower, never chirping, wings beating so rapidly and smoothly that a steady loud hum was produced, these stocky, dull-colored birds resembled large hymenopterans. In fact, they may derive some benefit from that resemblance (Feinsinger 1974).

Archilochus colubris, Ruby-throated Hummingbird (seasonal).—A number of females and an occasional male of this species, which is most often observed at lower elevations on the Pacific slope (see Slud 1964, Wolf 1970), appeared in the MF-WF study areas from October–March. Culmen striations showed that all 6 birds netted were birds of the year. Nevertheless, all 4 males, even 1 caught on 14 October 1972, possessed full gorgets.

Selasphorus scintilla, Scintillant Hummingbird (vagrant).—On 7 July 1975 I observed an individual of this tiny species feeding in a field of *Rubus rosaeafolia* (Rosaceae) in the WF-RF zone, and 2 individuals were netted on 10 July. Slud (1964) mentions no records of this mid-elevation species from the northwestern cordilleras.

I especially wish to thank the people of Monteverde for allowing and indeed encouraging these studies on their land. I am also grateful to F. G. Stiles for copious comments on the manuscript, and to W. H. Buskirk and G. V. N. Powell for use of their field notes. Field work was supported by an Andrew D. White (Cornell University) Fellowship, a Cornell Graduate Fellowship, an NSF grant to the Section of Ecology and Systematics at

Cornell, and a grant from J. S. Dunning.—PETER FEINSINGER, *Dept. of Zoology, Univ. of Florida, Gainesville, 32611. Accepted 1 Oct. 1975.*

Nest-site differences between Red-headed and Red-bellied woodpeckers in South Carolina.—Red-headed (*Melanerpes erythrocephalus*) and Red-bellied (*M. carolinus*) woodpeckers are potential competitors for nest-sites over much of their range. Parameters serving to lessen competition between them have been discussed by Reller (Am. Midl. Nat. 88:270–290, 1972) for Illinois and by Jackson (Condor 78:67–76, 1976) for Kansas. Reller states that "All Red-heads observed nested in trunks of dead trees. Red-bellies, on the other hand, favored dead limbs in live trees for nest sites," her observations having been made in oak-maple-hickory woodlands. Jackson (op. cit.), studying the 2 species under differing ecological conditions, noted that while both species preferred to nest in dead trees, 50% of which were elms, the Red-headeds preferred nest trees with open spaces around them and Red-bellieds, ones located in woodlands. Other differences were that Red-headeds, in contrast to Red-bellieds, preferred dead limbs with no bark and ones with a crack in which to make entrance holes. The aim of this report is to describe nest-site differences under still other conditions, namely those of the coastal plain in South Carolina.

Observations were made at a quail shooting plantation in Luray in April and May 1973 to 1975. Pairs of Red-bellieds and of Red-headeds were more or less intermixed in terrain where strips of loblolly pines (*Pinus taeda*), along with scattered oaks and other deciduous trees alternated with open fields. As shown in Table 1 the Red-bellied occupied holes carved originally by Red-cockaded Woodpeckers (*Picoides borealis*) in living pines or excavated ones of their own in pines that had recently died. The outstanding feature of these latter was that they still retained bark and branches. Pairs of Red-headeds, in contrast, excavated or occupied pines dead for some years. These were well-weathered, had almost no bark, and had only broken limbs remaining. Many, having lost their tops, were no more than stubs. One exceptional dead pine fell between the categories. It had, oddly enough, a pair of Red-bellieds trying to nest in an old hole made by Red-bellieds

TABLE 1

NEST TREES OCCUPIED BY RED-HEADED AND RED-BELLIED WOODPECKERS EARLY IN THE BREEDING SEASON ON A PLANTATION IN SOUTH CAROLINA

Location of Nest Hole (completed or being excavated)	No. of Pairs	
	Red-headed	Red-bellied
Hole of Red-cockaded, living	1	6*
Recently dead pines	0	8
Old dead pines	10	0
Old pine stubs	13	0
Deciduous tree; dead trunk or limb	0	2
TOTALS	24	16

* One of the pines had died within the previous year.

the year before, 3 m from the ground; 4 m higher up a pair of Red-headeds were trying to start an excavation in the face of much harassing from other Red-headeds (Kilham, Auk, in press).

Trees chosen by the 2 species differed also in that those used by Red-headeds usually contained numbers of old holes from previous years. As a result of this latter situation, Red-headeds on the plantation shared stubs in one case with Starlings (*Sturnus vulgaris*), once with Common Flickers (*Colaptes auratus*), and once with a flying squirrel (*Glaucomys volans*). It thus seemed that Red-headeds may be more prone to share nest trees with other species, an observation concurred in by Reller (pers. comm.) although she cites an exception (op. cit.). Jackson (op. cit.) in contrast, found that Red-bellieds characteristically nested in trees with more than one hole in Kansas. These discrepancies among observers are of interest in indicating that nest-site preferences can vary with underlying ecologic conditions. A main finding that seems to emerge is that wherever studied, whether in Illinois, Kansas, or in South Carolina, Red-headeds and Red-bellieds do exhibit differences in their choices of nest sites.

Another parameter serving to lessen interspecific competition it would seem, is time of onset of breeding seasons; Red-headeds, being irregularly migratory and nesting later than the resident Red-bellieds (Jackson, op. cit.) and Kilham (Auk 75:318–329, 1958; Wilson Bull. 70:347–358, 1959).—LAWRENCE KILHAM, *Dept. of Microbiology, Dartmouth Medical School, Hanover, NH 03755. Accepted 8 Dec. 1975.*

Ground foraging and rapid molt in the Chuck-will's-widow.—In a detailed study of the annual molt of the Chuck-will's-widow (*Caprimulgus carolinensis*) Rohwer (Auk 88:485–519, 1971) inferred that some individuals might be missing so many feathers in late stages of the molt that they would have trouble flying. When growing primaries 8 and 9, Chuck-will's-widows lose all 10 of their rectrices, more or less simultaneously, and are missing up to ¼ of the primary surface of each wing (all at the critical tip), as well as nearly ¼ of the secondary surface area. At this same time the rictal bristles are also lost simultaneously.

Rohwer (*op. cit.*) felt it unlikely that Chuck-will's-widows in such an intensive molt could forage aerially but little more could be said of the matter at that time, partly because of the also suggestive fact that only a single specimen molting either primary 8 or 9 had been preserved. This was a bird shot by Sutton (Bull. Okla. Ornithol. Soc. 2:9–11, 1969) at the Oklahoma Biological Station. Students had flushed it from an earthen ledge near the bottom of a deep erosion gully tangled with shrubs, vines, roots, and dead branches. It was flushed again from the same area when Sutton collected it. He reported finding the area strewn with feathers, and was able to find 9 of the 10 molted rectrices, many remiges and a great number of smaller feathers.

Mengel (Wilson Bull. 88:351–353, 1976) recently collected the second known specimen in late stages of the molt. His bird was flushed 4 times before it was shot; he reported its flight as "direct and somewhat slow and labored," a striking descriptive contrast to the normally buoyant flight of a Chuck-will's-widow. The most remarkable fact concerning Mengel's specimen was that it was virtually emaciated, weighing only 86.7 g, a value 27.5% below the normal summer weight of 119.6 g (mean of 12 specimens). Sutton's (*op. cit.*) specimen was normal in weight (117.1 g).

The question raised by Rohwer's report on the intensity of the molt in its late stages and by the specimens taken by Sutton and Mengel is "How do Chuck-will's-widows forage in this period of intensive molt?" One possibility, suggested both by the many feathers found at the secluded resting site of Sutton's specimen and by the emaciated condition of Mengel's specimen, is that they forage very little. Another possibility is that they forage terrestrially. In watching Chuck-will's-widows walking about on roads swallowing pebbles, Jenkinson and Mengel (Condor 72:236–237, 1970) give the impression that they might easily forage on the ground. An extensive search of the literature, however, reveals no information on ground foraging by Chuck-will's-widows; thus, we report the following observations.

On the evening of 23 June, 1974, in a residential suburb of Fort Myers, Lee Co., Florida, Butler repeatedly observed a Chuck-will's-widow capturing squirrel tree frogs (*Hyla squirella*) from a black-top road surface. The incident occurred in the light cast by a street lamp where the frogs were plentiful, presumably attracted to insects. On several occasions the bird alighted on the road near its intended prey and then captured a frog unaided by wings or feet and swallowed it. Once the initial attack was evaded by a timely series of leaps, but the bird again flew close to the frog and captured it. Similarly, in 1972 Clifford G. Richardson (pers. comm. to Butler) observed a Chuck-will's-widow capturing frogs beneath a street light near his home on Pine Island, Lee Co., Florida.

These observations of Chuck-will's-widows foraging on frogs are significant, not so much because they add an unknown food item to the species' diet, but because they prove ground feeding to be a fact. An apparent difficulty with the ground feeding hypothesis is the very short legs of Chuck-will's-widows; but this may be resolved by the fact that both Sutton's and Mengel's specimens could, indeed, fly. Thus, while individuals in the most intense stages of the molt might be incapable of the sort of maneuvers required to capture flying insects, they could, perhaps, move to points of prey concentration where ground feeding, such as that reported here, might pay. Furthermore, terrestrial foraging would likely be facilitated by the absence of the rictal bristles, thus explaining their simultaneous replacement.—SIEVERT ROHWER, *Dept. of Zoology and Washington State Museum, Univ. of Washington, Seattle 98195*, and JAMES BUTLER, *College of Forest Resources, Univ. of Washington, Seattle 98195.* *Accepted 8 Dec. 1975.*

Feeding responses of fall migrants to prolonged inclement weather.—September 1975 was unusually cold in northwestern Ohio. A light frost on 14 September was the earliest ever recorded, and temperatures remained 3 to 6°C below normal each day thereafter until October. The migration peak for many passerines occurred between 23 and 27 September during a period of heavy cloud cover, gusty winds, frequent rain, and cool temperatures (range 8–16°C). Our home in a wooded area near Toledo, Ohio is surrounded by fruit-bearing shrubs including yews (*Taxus* sp.) and Tartarian honeysuckle (*Lonicera* sp.). During the fall migration many frugivorous species feed at these shrubs; between 23–27 September these species were joined by birds not normally noted for frugivory.

The minimum number of normally non-frugivorous birds eating fruit and the fruits selected (H = honeysuckle, Y = yew) were as follows: flycatcher (*Empidonax* sp.), 1(H); Tennessee Warbler (*Vermivora peregrina*), 1(H); Magnolia Warbler (*Dendroica magnolia*), 1(H); Bay-breasted Warbler (*D. castanea*), 4(Y); Blackpoll Warbler (*D. striata*), 1(Y); Ovenbird (*Sieurus aurocapillus*), 1(Y). In addition, a Ruby-crowned Kinglet (*Regulus calendula*), 2 immature Chestnut-sided Warblers (*D. pensylvanica*) and a male American Redstart (*Setophaga ruticilla*) investigated both yews and honeysuckles but were not actually observed eating berries.

By 27 September the bushes were nearly stripped of ripe berries. On that day the migrants turned to foraging in atypical fashion on or near the ground. One Ruby-crowned Kinglet, 2 Magnolia Warblers, 1 female Black-throated Blue Warbler (*D. caerulescens*), 1 immature Yellow-rumped Warbler (*D. coronata*) and 3 Bay-breasted Warblers crept through the lawn, apparently plucking tiny arthropods off the undersides of grass blades and violet leaves. Simultaneously 2 female or young American Redstarts were observed plucking grass seeds (*Setaria* and *Digitaria*) from their stalks while 10 other American Redstarts foraged clumsily within 2 m of the ground on the trunks of large cottonwoods (*Populus deltoides*) and pin oaks (*Quercus palustris*).

Apparently the species listed above rarely practice frugivory in North America. Bent (1942, 1953, U. S. Natl. Mus. Bull. 179, 203) comments on their food habits as follows: Least Flycatcher (*Empidonax minimus*), fruits 2% of diet or less; Ruby-crowned Kinglet, "6% of stomach contents . . . were fruits and seeds" (in California); Tennessee Warbler, "berries in small quantities; . . . punctured grapes"; Chestnut-sided Warbler, "a few seeds and berries when hard-pressed," and Audubon saw them eating grass seeds in a May snow; Bay-breasted Warbler, no actual records ("perhaps a little fruit"); Blackpoll Warbler, "a few seeds and berries in the fall"; Ovenbird, "a few seeds and small wild fruits"; and American Redstart, "berries and seeds on rare occasions," although Wetmore found that in Puerto Rico wintering American Redstarts consumed "100% animal food."

The most likely explanation for our observations is that the unusually early onset of cool temperatures prematurely reduced populations of arboreal arthropods that normally comprise the major portion of the diet of fall migrant warblers, kinglets, and flycatchers. Our mosquito population offered circumstantial evidence to support that idea. Mosquitos were insufferable before 14 September, numerous until 21 September, and declined very rapidly thereafter until virtually none could be found by the 27th. Beginning on 23 September the birds turned to eating berries, which could be procured with low energy expenditures. They resorted to atypical (and therefore probably energetically costly) foraging for arthropods on the ground and on tree trunks only when fruits were no longer available.—ELLIOT J. TRAMER AND FLORA E. TRAMER, *Dept. of Biology, Univ. of Toledo, Toledo, OH 43606.* *Accepted 11 Dec. 1975.*

Southbound migration of shorebirds from the Gulf of St. Lawrence.—In a previous study, McNeil (L'Oiseau et R.F.O. 40:185–302, 1970) has shown that most North American shorebird species departing from northeastern Venezuela in northward spring migration have enough energy reserves to reach the southern United States by a non-stop flight over the Caribbean Sea (lower part of route B in Fig. 1). Flight-range capabilities average some 2240 km. Then most shorebirds must reach their breeding grounds by flying either along the Atlantic coast or through the Mississippi flyway.

However, for most species, the fall migration route seems to differ from that used in spring. Many literature references suggest that in fall migration several North American shorebird species deviate in a southeasterly direction. This explains their presence in greater numbers in fall than in spring on the Canadian Atlantic coasts, and their occurrence in fall, but almost total absence in spring over the Atlantic (e.g. in Bermuda: See McNeil 1970; McNeil, Can. J. Zool. 47:525–536, 1969).

Furthermore, some species of shorebirds have higher flight energy reserves for fall migration south from the Gulf of St. Lawrence than for spring migration north from northern South America (McNeil and Cadieux, Naturaliste Can. 99:589–605, 1972; Berthiaume, M.Sc. thesis, Univ. of Montreal, 1974). They have enough reserves to fly

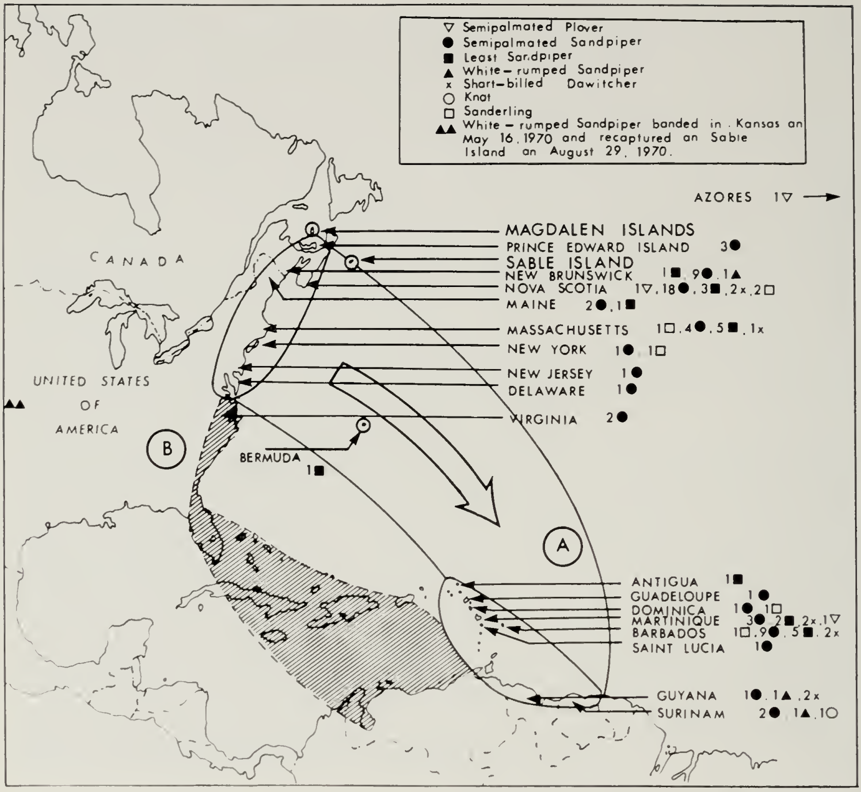

FIG. 1. Dispersal of banded color-marked shorebirds away from the Magdalen and Sable islands in the falls of 1970, 1971 and 1972. The arrow represents the over-sea route (A) apparently used by several species of North American shorebirds in southbound migration from the Canadian Atlantic and New England coasts to the Lesser Antilles and northern South America. The hatched area represents the alternative southbound route (B).

non-stop over the Atlantic in fall from Nova Scotia and the New England states to the Lesser Antilles and northern South America (Route A in Fig. 1).

Thus, knowing the flight-range capabilities of shorebirds passing through the Canadian Atlantic provinces on southward migration, we undertook an intensive program of marking and recovery of shorebirds to verify whether or not they would use the migration route described above.

Two localities were selected for the capture and marking of fall migrating shorebirds: the Magdalen Islands and Sable Island (Fig. 1). The archipelago of the Magdalen Islands is located in the Gulf of St. Lawrence, between 47°14′ and 47°39′ N and 61°23′ and 61°01′ W, about 290 km from Gaspé, 110 km from Prince Edward Island and 90 km from Cape Breton Island. Sable Island lies 160 km east of the Nova Scotia coast. Intensive bird-banding activities were undertaken on these islands from 1970 to 1972 (in 1972,

TABLE 1

NUMBERS OF SHOREBIRDS CAPTURED AND RELEASED IN 1969, 1970, 1971, AND 1972

	Magdalen Islands				Sable Island		
Species	1969	1970	1971	1972	1970	1971	Total
Semipalmated Plover (*Charadrius semipalmatus*)	7	149	176	203	81	65	681
Killdeer (*Charadrius vociferus*)		1	1	1			3
American Golden Plover (*Pluvialis dominica*)				3	2	2	7
Black-bellied Plover (*Pluvialis squatarola*)		1	4	4	29	41	79
Ruddy Turnstone (*Arenaria interpres*)		3	2	6	20	11	42
Common Snipe (*Capella gallinago*)		28	17	15			60
Whimbrel (*Numenius phaeopus*)					1	1	2
Spotted Sandpiper (*Actitis macularia*)		5	8	7	7	1	28
Solitary Sandpiper (*Tringa solitaria*)			7	5			12
Willet (*Catoptrophorus semipalmatus*)						1	1
Greater Yellowlegs (*Tringa melanoleucus*)	1	6	12	22	16	4	61
Lesser Yellowlegs (*Tringa flavipes*)		16	13	8	23	25	85
Knot (*Calidris canutus*)					11	7	18
Pectoral Sandpiper (*Calidris melanotos*)		5	5	54	3	2	69
White-rumped Sandpiper (*Calidris fuscicollis*)	7	291	505	593	62	135	1593
Least Sandpiper (*Calidris minutilla*)	73	755	1036	703	129	50	2746
Dunlin (*Calidris alpina*)		4	4	6			14
Short-billed Dowitcher (*Limnodromus griseus*)	1	46	164	99	20	38	368
Stilt Sandpiper (*Micropalama himantopus*)			1		1	1	3
Semipalmated Sandpiper (*Calidris pusillus*)	139	2124	2917	2894	694	198	8966
Sanderling (*Calidris alba*)		6	4	3	108	123	244
Total	228	3440	4876	4626	1207	705	15,082

Magdalen Islands only). Some 228 birds were marked on the Magdalen Islands in 1969 when experimental capture and marking techniques were tested. The banding activities on Sable Islands were carried on by Jean Burton (Ph.D. thesis, Univ. of Montreal, 1974). Capture and color-marking techniques have already been described in detail (McNeil and Burton, Carib. J. Sci. 13:257–278, 1973).

Collaboration for reporting sightings of color-marked shorebirds and/or band recoveries was requested from over 250 bird watchers and members of bird clubs and other regional natural history associations. The geographical distribution of collaborators covers the Canadian Atlantic provinces, the New England states, New York, New Jersey, Delaware, Maryland, Virginia, North Carolina, Florida, Bermuda, the Greater and Lesser Antilles, and northern South America.

The results obtained from 1969 to 1971 and already published (McNeil and Burton 1973) are here completed by further data obtained in 1972. A total of 15,082 birds representing 21 species were captured, banded and color-marked from 1969 to 1972 (Table 1). Eight species were sighted or recovered away from the banding locations in the fall of 1970, 1971 and 1972 (Fig. 1): Semipalmated Plover (*Charadrius semipalmatus*), Black-bellied Plover (*Pluvialis squatarola*), Knot (*Calidris canutus*), White-rumped Sandpiper (*Calidris fuscicollis*), Least Sandpiper (*Calidris minutilla*), Short-billed Dowitcher (*Limnodromus griseus*), Semipalmated Sandpiper (*Calidris pusilla*), and Sanderling (*Calidris alba*). A total of 11 birds was reported in 1970 as compared to 61 in 1971 and 28 in 1972. The higher number of recoveries in 1971 as compared to 1970 was obtained because of an increased number of birds color-marked (5581 as compared with 4647; Table 1), but also because of a higher number of bird watchers informed about our color-marking and recapture program.

The percentage of sightings and/or band recoveries away from banding locations is much higher in 1971 and 1972 than in 1970; there were none in 1969 because bird watchers were not advised about the project that year. The increased recoveries and/or sightings in 1971 and 1972 are likely related to the use of leg streamers. Shorebirds observed in 1973 and 1974 are considered as being color-marked in 1972.

The 100 color-marked individuals sighted or recovered away from the banding locations during the fall migration were in 2 areas 3200 km apart: a northern area including Prince Edward Island, New Brunswick, Nova Scotia, and the New England states south to Virginia; a southern area including the Lesser Antilles, Guyana and Surinam (Fig. 1). In addition, 1 Least Sandpiper was sighted in Bermuda and one Semipalmated Plover was recaptured at the Azores.

The 7 additional observations that were obtained during other months of the year are: 1 Black-bellied Plover at sea, 480 km S of Nova Scotia on 22 May 1972; 1 Least Sandpiper in North Carolina on 28 April 1972; 1 Semipalmated Sandpiper in New Jersey on 22 May 1973, 1 at Churchill, Manitoba, on 10 June 1973, and another 1 in New York on 7 June 1974; and 1 Sanderling in Florida on 31 May 1972.

The conclusions drawn from our previous studies (McNeil 1970, McNeil and Cadieux 1972, McNeil and Burton 1973) are maintained and reinforced by the 1972 results. While a great number of the species mentioned above appear to migrate mainly by an off-shore route to reach South America, most birds must complete their journey to the breeding grounds by passing across the Caribbean (lower part of route B in Fig. 1), then through the interior of the United States (Mississippi Valley) or along the Atlantic coast.

This study was supported by a National Research Council of Canada research grant to Raymond McNeil and a scholarship to Jean Burton. The project was partly financed during 1971 by a contract from the Canadian Wildlife Service (No. WE-71-72-38). We are indebted to Ian A. McLaren of Dalhousie University for accommodation offered to Jean

Burton on Sable Island. We thank several students and others who helped with the field work on the Magdalen Islands. Finally, we thank the amateur and professional ornithologists who reported observations or recoveries of our marked shorebirds; without their collaboration, most of these results would have not been obtained. We are grateful to Marlène Valcin and France Guimont for helping with preparation of the manuscript.—
RAYMOND MCNEIL and JEAN BURTON, *Centre de Recherches écologiques de Montréal, 4101 est, rue Sherbrooke, Montréal, Québec, H1X 2B2, Canada.* *Accepted 14 April 1976.*

Flocking and foraging behavior of Brown Jays in northeastern Mexico.—The flocking and foraging behavior of the Brown Jay (*Psilorhinus morio*) was studied from 29 December 1975 to 9 January 1976. Observations were made in a climax evergreen forest along the Rio Corona and the Rio Pilon, Tamaulipas, and a tropical deciduous forest at El Salto, San Luis Potosi, Mexico.

Brown Jays live in family groups (Sutton and Pettingill, Wilson Bull. 54:213–214, 1942; Brown, Am. Zool. 14:63–80, 1974). At all 3 study sites, the Brown Jay was the first bird species seen or heard each morning. The daily activity of the family groups began about 30 min before sunrise with a seemingly spontaneous burst of calling and rapid flight through the canopy. These flights were interrupted by short (5 sec to 2 min) intervals of complete silence during which the jays hopped about, poked at one another, and preened, but did not forage. These activity patterns were similar to the morning "rallying" as described for a Piñon Jay (*Gymnorhinus cyanocephalus*) flock by Balda et al. (Auk 94:in press), who felt that these activities may serve to attract group members and play a role in social cohesiveness.

Foraging began after the initial rallying of a Brown Jay group, with groups ($n = 9$) ranging from 8 to 15 individuals. Adults and juveniles, distinguishable by bill color (Skutch, Auk 52:257–273, 1935; Selander, Auk 76:385–417, 1959), separated by mid-morning. Significant differences in group size, reflecting this break-up (Fig. 1), were shown using Duncan's New Multiple Range Test (Steel and Torrie, Principles and Procedures of Statistics, McGraw-Hill, Inc., N.Y., 1960). Morning (08:00) and evening (18:00) group sizes were significantly different from the mid-morning size ($P < .05$), and highly significant from later (12:00, 14:00 and 16:00) group sizes ($P < .01$).

During late mornings and afternoons, single adults were observed foraging, preening, and resting quietly. When disturbed by human activity, the adults either seemed to ignore the disturbance, or moved silently away. The juveniles, however, were never observed alone, but would remain in 1 or 2 groups (4–6 individuals), flocking throughout the day. Between periods of foraging and general body maintenance, the juvenile Brown Jays would move through the canopy loudly calling. As sunset approached, the adults and juveniles rejoined; this is reflected in the increase in group size (Fig. 1). Pre- and post-roosting activities were similar, with loud calling (by all members) and a diminishing number of flights as night approached and roost sites were selected. All group members roosted in the canopy of the same or adjacent trees.

By spending the morning and evening with the more experienced adults, the juveniles may be greatly increasing their survival chances by direct observance of adult behavior. In the absence of adults, these juvenile groups may afford increased predator protection and foraging success in contrast to a juvenile foraging alone. This may imply a greater dependence on learning in Brown Jays as compared to jays that do not remain with their parents for extended periods, such as the Blue (*Cyanocitta cristata*) and Steller's (*C. stelleri*) jays (Brown op. cit.). Cully and Ligon (Auk 93:116–125, 1976) considered

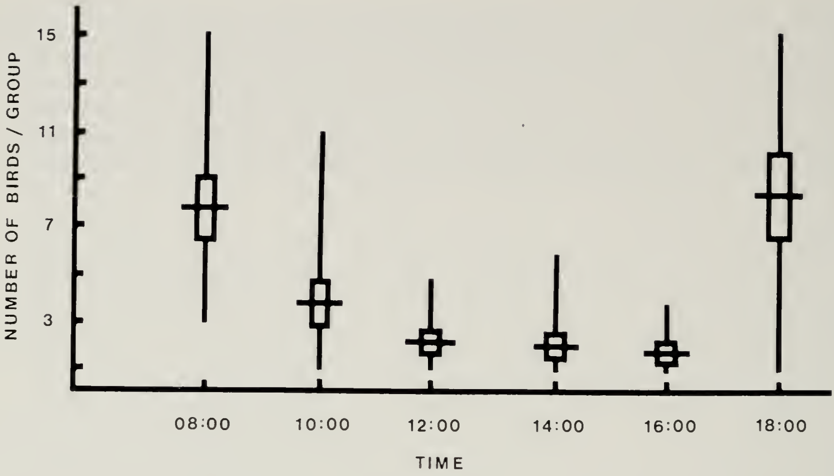

Fig. 1. Number of Brown Jays per group at selected daily time periods at Rio Corona, El Salto, and Rio Pilon, Mexico, with range, mean, and 1 standard error (bar) on either side of the mean (number of groups = 51).

this while studying the Mexican Jay (*Aphelocoma ultramarina*). Brown (op. cit.) suggests that Brown Jays raise a single brood per year and have a high nesting success. Further, the high nesting success of Brown Jays may result from the presence of juvenile nest helpers. Woolfenden (Auk 92:1–15, 1975) found that nest helpers enhance the reproductive efforts of breeding Florida Scrub Jays (*Aphelocoma c. coerulescens*), whose social system resembles that of the Brown Jay. In the non-breeding season the separation of adults and juveniles for part of the day may minimize competition for available food resources or may be an indication of the juveniles' lack of foraging efficiency and thus their need to feed longer than adults. Communal roosting and morning and evening rallying would serve to maintain the social structure of the group during the non-breeding season.

Certain data on foraging behavior were recorded for 61 Brown Jays. Only 6.5% of their daily activity was on the ground, and then only of short duration for capturing a food item. Foraging height at El Salto and the Rio Pilon averaged 75–80% of tree height ($\bar{x}$ tree height = 13.3 m, n = 32; and $\bar{x}$ = 11.9, n = 29, respectively; no detailed notes on foraging heights were taken at the Rio Corona). No significant correlation was found between foraging height and air temperature, humidity, cloud cover, or wind speed and direction. However, foraging height declined significantly as the day progressed at both El Salto ($r = -.551$, $P < .01$, $n = 32$) and the Rio Pilon ($r = -.583$, $P < .01$, $n = 29$). Upon morning arousal the canopy roosting Brown Jays would be able to directly use the sun's warmth by remaining in the tree tops and/or be better able to locate food. Although we found no direct correlation between foraging height and temperature, the importance of temperature cannot be discounted as these were recorded beneath, not above nor in the canopy. Therefore, as the day progressed and the sun rose higher, the jays may have been forced down into the shaded areas beneath the canopy either to avoid thermal stress, or in response to movement of their food supply. Pearson (Condor 73:46–55, 1971) noted such a downward movement during mid-day by much of the avian community in a tropical dry forest of Peru, and attributed these to high temperatures and/or insect movement. If Brown Jays are not responding to heat or insect movement, their downward shift in height may be a result of a movement to a preferred foraging zone after initial canopy rallying.

We wish to thank E. Shanley and P. Cantle for field assistance. K. A. Arnold, N. Silvy, S. Beasom, and W. A. Brown read earlier drafts of the manuscript.—MICHAEL L. MORRISON AND R. DOUGLAS SLACK, *Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, 77843.* *Accepted 16 Aug. 1976.*

Do more birds produce fewer young? A comment on Mayfield's measure of nest success.—Fretwell (Populations in a Seasonal Environment, Princeton Univ. Press, Princeton, NJ, 1972) has considered the effect of nest density on nesting success of Field Sparrows (*Spizella pusilla*). He used the method of Mayfield (Wilson Bull. 73:255–261, 1961) to calculate a daily mortality rate and from this the overall nest survival rate. Fretwell concluded that the nesting success rate decreases as density increases. A closer look at the data, pictured in Fretwell's Figure 44, suggests that not only does the survival rate decrease with increasing density but, in fact, the decrease in survival rate is actually so great that at higher densities the larger total number of breeding adults would produce a lower total number of young than would a smaller number of less crowded adults. The data given are not sufficient to draw this conclusion explicitly and Fretwell does not do so, but it is implicit in his schematic Figure 45 which shows overall nest survival decreasing very rapidly as nest density increases.

It is theoretically possible that more birds might produce fewer young but this seems sufficiently improbable to require an examination of the method used to estimate nesting success. Examination shows that Mayfield's method of estimating nesting success may be biased if not all nests have the same chance of success. This bias will be negligible for low or moderate nest mortality but for high nest mortality it may substantially exaggerate nest mortality.

Mayfield's measure of nesting success was designed to eliminate the bias in earlier methods of estimating nesting success. In using Mayfield's method, first a daily nest mortality rate, p, is estimated by dividing the number of nest failures by the number of nest-days at risk. Then the overall survival rate is calculated to be $(1 - p)^n$, where n is the nest lifetime. Mayfield's method assumes that the risk is the same for all nests and for all days. If, in fact, different nests have different probabilities of surviving then Mayfield's method will produce a biased estimate of the nesting success rate. In general, the estimated success rate will tend to be less than the actual success rate if the nests differ.

There is some evidence that nests may actually differ in survival probability. Nice (Trans. Linn. Soc. N. Y. 4:1–247, 1937) in her work on Song Sparrows (*Melospiza melodia*) observed that well-concealed nests are less likely to be destroyed than badly-concealed nests. Baptista (Auk 89:879–882, 1972) conjectured that the parasitism of White-crowned Sparrows (*Zonotrichia leucophrys*) by Brown-headed Cowbirds (*Molothrus ater*) that he observed in San Francisco may have been due to the suboptimum habitat which didn't offer the White-crowns adequate cover. Krebs (Ecology 52:2–22, 1971) observed that Great Tits (*Parus major*) nesting in hedgerows had less success than birds nesting in woodlands.

The bias in Mayfield's procedure when nests have different survival probabilities may be illustrated in a simple example. Assume that a nesting population consists of birds of

TABLE 1

THE EFFECTS OF BIAS IN MAYFIELD'S MEASURE OF NEST SUCCESS IF NESTING SUCCESS RATES ARE VERY DIFFERENT

Proportion of "young" α	Number of "young" N_y	Number of "adults" N_a	Success Rate per nest		Total number of Successful Nests	
			True S_1	Apparent S_2	True	Apparent
.000	0	100	.668	.668	66.8	66.8
.500	100	100	.340	.282	67.9	56.5
.667	200	100	.230	.162	69.1	48.5
.750	300	100	.176	.109	70.2	43.6
.800	400	100	.143	.082	71.4	40.8

2 types. Let proportion α of the nests be of one type, say of young birds nesting for the first time, which produce nests all of which have the same daily risk p_y. Let the remaining proportion $1-\alpha$ of the nests be of another type, say of experienced adults, which produce nests all of which have the same daily risk p_a. Then the actual nesting success rate will be $\alpha(1-p_y)^n + (1-\alpha)(1-p_a)^n$.

Assume that nests are observed daily from the time the eggs are laid. Then Mayfield's method will produce an estimate of overall nesting success which will be approximately $(1-p)^n$, where

$$p = \frac{\alpha(1-q_y{}^n) + (1-\alpha)(1-q_a{}^n)}{\alpha(1-q_y{}^n)/p_y + (1-\alpha)(1-q_a{}^n)/p_a} \tag{1}$$

where $q_y = 1 - p_y$ and $q_a = 1 - p_a$. A derivation of (1) is given in Appendix 1.

A few calculations will show the effect of the bias if nesting success rates are very different. Let $n = 20$, $p_y = .2$, $p_a = .02$, let S_1 denote the true success rate and let S_2 denote the apparent success rate using p as calculated in (1). Assume that there are a fixed number of "adult" birds' nests, $N_a = 100$, and different numbers of "young" birds' nests, $N_y = 0, 100, 200, 300$, or 400. Then we can find the "true" total number of successful nests and the "apparent" number of successful nests (Table 1). Here $\alpha = N_y/(N_y + N_a)$.

These calculations show that it is possible that an increasing population of breeding birds might produce an increasing (although here only slowly increasing) number of young while the apparent number of young produced might decrease quite sharply. In the example considered here there are a fixed number of "adult" birds likely to be successful whose success rate is unaffected by density. The increase in the number of nesting birds is due solely to an increase in the number of "young" birds whose nests are subject to high risk.

The reason that Mayfield's method produces a biased estimate of nesting success if different nests have different daily mortality rates is that the nests which are at greater risk are not only more likely to be destroyed, but if they are destroyed it will tend to occur earlier than for the nests at less risk. Thus the nests with greater chance of failing will contribute less than their share to the number of nest days.

The bias in estimating nesting success due to differences in success rate from nest to nest will be negligible if the rates are not very different or if the success rates are high.

The bias will only be significant if risks are high and are quite different from nest to nest. This would be the case, however, if the effect of increasing nesting density was not to increase the risk of all nests uniformly but was rather to increase the number of nests that were at greater risk.

The question of whether nests are all at the same risk is an important one and it could be tested. If the daily risk is the same for all nests and all days then the number of days each nest is at risk will have a "censored" geometric distribution. That is, the number of days at risk will have a geometric distribution except that since a nest cannot be at risk more than the normal nest lifetime, n days, all the probability that would otherwise be assigned to values greater than n will be concentrated at n. The observed distribution of the number of days each nest is at risk may be compared with this expected distribution and a chi-squared test performed. This test is described in Appendix 2.

Appendix 1. Derivation of (1):

$$p = \frac{\alpha(1-q_y{}^n) + (1-\alpha)(1-q_a{}^n)}{\alpha(1-q_y{}^n)/p_y + (1-\alpha)(1-q_a{}^n)/p_a}.$$

The estimate p is the ratio of the number of nest failures to the number of days at risk. The numerator of (1) is the probability that a randomly chosen nest will fail since proportion α of the nests are of "young" birds and each such nest has probability $q_y{}^n$ of succeeding, where q_y is the daily survival rate. The failure rate for "young" bird nests is $(1-q_y{}^n)$ and the failure rate for "adult" bird nests is $(1-q_a{}^n)$. Proportion $1-\alpha$ of the birds are "adults."

The denominator of (1) is the expected number of days at risk for a randomly chosen nest. If X is the number of days that a "young" bird's nest is at risk then $P(X \geqslant k) = q_y{}^{k-1}$ for $k = 1, 2, \ldots, n$. To find the expected number of days at risk we find $EX = \sum_{k=1}^{n} P(X \geqslant k) = (1-q_y{}^n)/p_y$. Similarly, for "adult" birds the expected number of days at risk is $(1-q_a{}^n)/p_a$. Proportion α of the nests are of "young" birds and proportion $1-\alpha$ are of "adult" birds.

For large numbers of nests the estimated value of p will be close to that given by (1). For small numbers of nests the estimated value may be larger or smaller than that given by (1) but it will tend to be larger.

Appendix 2. Testing for homogeneity of nest mortality. If nests are observed daily from the time laying is completed the assertion that daily risk is the same for all nests and all days may be tested by finding the expected frequency of nests that survive exactly until the k*th* day (are at risk for k days): Npq^{k-1} for $k = 1, 2, \ldots, n-1$ and Nq^{n-1} for $k = n$, where N is the number of nests observed, p is the daily risk estimated by Mayfield's method and $q = 1 - p$. These expected frequencies may be compared with the observed frequencies using a chi-squared test where the number of degrees of freedom is two less than the number of categories (of numbers of days at risk) used.—RICHARD F. GREEN, *Dept. of Statistics, Univ. of California, Riverside 92521. Accepted 17 Dec. 1975.*

Mortality of nestling Mississippi Kites by ants.—While studying aspects of the breeding and population biology of the Mississippi Kite (*Ictinia mississippiensis*) in the Great Plains (Parker, Ph.D. thesis, Univ. Kansas, Lawrence, 1974), I encountered mortality of nestlings due to the action of ants of the genus *Monomorium*, either *M. minimum*, the little brown ant, or *M. pharaonis*, the pharaoh ant. The former is a well-established exotic, the latter is native to North America. Both are omnivorous, common, and found in association with man (Swan and Papp, The Common Insects of North America, Harper and Row, N. Y., 1972). One affected kite nest was part of a colony of 5 in a large shelterbelt in Greer County, Oklahoma. It was 3 m up in one tree of a row of osage orange (*Maclura pomifera*) and originally contained 2 eggs. On 23 June 1970 I found 1 pipped egg and a very small nestling (1 day old or less). The latter was covered with scores of the small, biting ants, had blood on its legs, was weak, and died within 30 min. The ants were moving to and from the nest in columns extending up the trunk and had been present on my previous visits, but were not then numerous in the nest. Although an adult kite was on the nest the next day, the second egg was gone 4 days later.

Ants also were abundant at a second unsuccessful nest in an osage orange and attacked 2 nestlings in a third nest in a small oak (*Quercus* sp.) in one of the many small groves of trees in the "shinnery" prairie near Roll, Roger Mills Co., Oklahoma. The heads or entire bodies of scores of ants covered the nestlings (about 11 and 13 days old) on 9 July 1973. Both had patches of bare, irritated skin, were swollen around the eyes and mouth and on the feet and wings, and were listless. The older was normal in weight, but the younger was extremely underweight. Ten days later only the older nestling remained; it is likely that the ants at least contributed to the death of the younger.

Because only the heads of some ants remained attached to the bodies of the latter nestlings, I assume they were preening themselves or each other, or were preened by the adults. The newly-hatched nestling was unable to preen itself and was very recently damp from hatching. Thus it was less able to withstand the stresses imposed by the ants and probably was more attractive to them because of its damp condition. Newly-hatched young of any bird species would succumb more quickly to ants than older nestlings, but species normally eating small, ground insects might eat ants in the nest, thus protecting their young. However, ants are too small to be eaten as normal fare by Mississippi Kites and were probably not viewed as food by the adults.

Only 3 nests of the more than 400 I examined were affected by ants, so the total impact of the ants on reproductive success was minor. However, the activity of the ants is unusual, and this sort of mortality has rarely been reported, except when attributed to the imported fire ant (*Solenopsis saevissima*) (Coon and Fleet, Environment 12:28–39, 1970). However, Kroll et al. (Wilson Bull. 85:478–479, 1973) observed predation by native fire ants (*Solenopsis geminata*) on nestling Barn Swallows (*Hirundo rustica*).

Robert Hoffmann, James Cope, and Robert Mengel commented helpfully on the manuscript. Research was supported by an NSF Traineeship and Museum of Natural History Grant from the University of Kansas, a Chapman Memorial Fund Grant, and a grant from the Eastern Bird Banding Association. Charles Michener and George Byers identified the ants.—JAMES W. PARKER, *Museum of Natural History, Univ. of Kansas, Lawrence, 66045.* (Present Address: *Dept. of Biology, State Univ. College, Fredonia, NY 14063.*) *Accepted 8 Dec. 1975.*

ORNITHOLOGICAL NEWS

ANNUAL MEETING OF THE WILSON ORNITHOLOGICAL SOCIETY

Make sure you have your registration submitted for the 58th annual meeting of the Wilson Ornithological Society which will be held on the campus at Mississippi State University from 19–22 May 1977. There will be a full program of scientific papers in addition to a symposium on woodpeckers. Bring the whole family because the local committee has planned a variety of activities in addition to the scientific part of the meeting. Some of these activities include visits to antebellum homes, the Herschede Hall Clock Company, the Cobb Institute of Archaeology, and Noxubee National Wildlife Refuge. The field trips will be culminated by an all day canoe trip down the Tombigbee River. For those Yankee birders who would like to add some southern species to their life list, the local committee has given an unconditional guarantee for producing nesting Red-cockaded Woodpeckers, Black Vultures and others. For further information please contact Jerome A. Jackson, chairman of the local committee, P. O. Box Z, Mississippi State, MS 39762.

ANIMAL BEHAVIOR SOCIETY MEETING

During October 1977 the Memorial University of Newfoundland will host the Northeastern Regional Meeting of the Animal Behavior Society. The Society is encouraging attendance of ornithologists and animal behaviorists. For further information concerning the meeting, please contact Dr. William Montevecchi, Department of Psychology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1C 5S7.

GREATER SANDHILL CRANE SYMPOSIUM

The Indiana Chapter of the Wildlife Society in cooperation with Indiana Division of Fish and Wildlife and Indiana Conservation Council, Inc. will sponsor a symposium on the status of the Greater Sandhill Crane. The symposium will be held 24–26 October 1977 at the Howard Johnson Motel, Michigan City, Indiana, and Jasper-Pulaski Fish and Wildlife Area. (During late October 1976 over 12,000 cranes were concentrated on this area.) For additional information and/or inclusion on mailing list contact: Duane Shroufe, Division of Fish and Wildlife, 607 State Office Building, Indianapolis, IN 46204.

CONTINENTAL COLOR-MARKING FOR THE PURPLE MARTIN

Although several thousand Purple Martins (*Progne subis*) have been banded, very little is known or understood about their dispersal and migration from the breeding and wintering areas. Even recovery records leave many important questions unanswered. What is the postbreeding dispersal pattern? Where do breeding and hatching year individuals stage and roost prior to and during migration? Where do martins from each state or province winter and does their migration route differ? How widely do birds from each state or province disperse after the winter?

A concentrated effort to color-mark martins on a continental scale and a coordinated observation effort has been planned by Jerome A. Jackson and M. Kathleen Klimkiewicz and should help answer many of these questions.

Each state, group of states, or province will be assigned a two-color plastic leg band combination. Leg and/or wing markers may be used at a later time (both are presently being used on a small-scale experimental basis in Ontario and Maryland).

All color bands will be ordered from the same source in order to standardize colors. Only nestlings and/or breeding adults will be color-marked at the present time because roosts often consist of individuals from several states.

All banders and subpermittees are encouraged to participate in this project. Detailed directions and the continental color-marking plan will be sent to interested individuals. The source for the plastic color leg bands and a key to age and sex for adults will be sent to banders who plan to participate. A capture technique for adults is also available upon request.

All inquiries should be sent to: Kathy Klimkiewicz, Biologist, Bird Banding Laboratory, Laurel, Maryland 20811.

COLOR-BANDED SEMIPALMATED AND LEAST SANDPIPERS

Last year the Surinam Forest Service color-banded nearly 3300 Semipalmated and Least sandpipers, resulting in 14 spring and summer sightings and recoveries from the United States and Canada. In 1977 again large numbers of these species will be color-banded along the Surinam coast. As in 1976, birds will be banded above the tarsus ("knee") with a standard aluminum band and 2 ORANGE plastic bands of about the same size as the aluminum band. We again ask birders to look out for these birds and to send reports of observations to Arie L. Spaans, Surinam Forest Service, P.O. Box 436, Paramaribo, Surinam, South America. Please, report species, date and location of observation, the position of the aluminum and color-bands—left or right leg, and, if more than 1 band is on a leg, which band is above, which below, and which in the middle (some birds have all 3 bands on one leg)—and number of color-banded birds involved.

BALD EAGLE LITERATURE WANTED

The National Wildlife Federation's Raptor Information Center is creating a computer-based, working (i.e. keyworded) bibliography on the Bald Eagle. An attempt is being made to include all existing literature, both published and unpublished. Information on extant bibliographies and sources of unpublished literature (reports, theses, dissertations, etc.) is especially being sought. If you have pertinent articles that you wish to be included, please send them to: Dr. Jeff Lincer, Director, Raptor Information Center, National Wildlife Federation, 1412–16th Street, N.W., Washington, D.C. 20036.

GEORGE MIKSCH SUTTON COLOR PLATE FUND

We acknowledge with thanks the contribution of Dr. George Miksch Sutton which has made possible the publication of the color plate in this issuse and color plates in most other issues of *The Wilson Bulletin* in the past three years.

ORNITHOLOGICAL LITERATURE

HANDBOOK OF NORTH AMERICAN BIRDS VOLS. 2 & 3 (WATERFOWL). Edited by Ralph S. Palmer, illus. by R. M. Mengel & C. H. Nelson. Yale Univ. Press, New Haven, Connecticut, 1976: 1081 pp., 8 color plates, 53 range maps, 103 uncaptioned line-drawings. $60 the set—These volumes form the second part of the "Handbook of North American Birds" of which Volume 1 (Loons through Flamingos) appeared in 1962. The editor remarks that the Anatidae are already the best known avian family, so it is not surprising that there are over 1000 pages of closely-set type and nearly 2000 references. The aim has been to enable the reader to "determine what a bird of either sex, or any annual increment to the population, looks like and is doing at any time of year." The volumes deal with 18 genera and 64 species, 6 of which (the Cuban Whistling Duck, Red-breasted Goose, Ruddy Shelduck, Common Shelduck, Garganey, and Spotbill) rate only about a page, and a few others (such as Whooper Swan, Barnacle Goose, Mottled Duck, Baikal Teal, Falcated Duck, and Bahama Pintail) are not given very lengthy treatments, usually because they are accidental or at the edge of their range in North America.

Twenty-nine authors, in addition to the editor, wrote the text. This does not claim to deal thoroughly with such topics as agricultural damage, habitat improvement, hunting, aviculture, domestication, parasites, disease, lead and pesticide poisoning, navigation, internal anatomy, or genetics. Instead, plumages are very fully covered, and distribution, migration routes, banding recoveries, voice, display, breeding biology, food, and hybrids are considered in detail.

The taxonomic arrangement is that of Delacour's Waterfowl of the World (1954–59) rather than of Johnsgard's Handbook of Waterfowl Behavior (1965), so that the dabbling ducks are preceded by the shelducks and followed by the eiders, and the perching ducks come between the scaup and the scoters. At the specific level Palmer has, however, altered Delacour's classification somewhat. The Whooper and Trumpeter swans are treated as separate species, while the Whistler and Bewick's swan are amalgamated into the "Tundra Swan." The Canada Goose is split into 8 trinomials, 4 fewer than Delacour (*leucopareia* is included with *asiatica*, *parvipes* with *taverneri*, *fulva* with *occidentalis*, and *maxima*, which was only rediscovered in the 1960's after having been extinct for most of this century, has again been lost, this time into *moffitti*). There are 7 rather than 5 subspecies of the Common Eider, and the Mottled Duck and the Mexican Duck are given specific status instead of their more usual position as races of the Mallard.

With so painstaking a textual treatment of plumage, it is surprising that there are not colored illustrations of all species. There are about 100 line drawings by Robert Mengel and 5 color plates depicting plumages of white and blue phases of the Lesser Snow Goose, North American Wood Duck, Oldsquaw, Common Eider, and Masked and Ruddy duck. Almost all Mengel's illustrations are based, apparently, on layouts prepared by the editor with emphasis on Palmer's own photographs. They are both useful and decorative, and often catch the magic of waterfowl delightfully. Equally charming are the 3 color plates by Coleen Nelson of the young of 32 species, done from life. The range maps are good (although I should have liked the large river systems marked in), and well adapted to the particular species being dealt with. Parts of Asia are figured if necessary, and Greenland is included in its entirety.

How good is the detail? On the whole, it is extremely useful, especially the coverage of Russian and Icelandic literature. There is, for all that, tendency to say "more interesting data can be found in. . . ." or "for some information on habits see. . . .". Sometimes an author and date seem to have been added to Palmer's text as a publication came to hand, without much effort being made to abstract the information it contained. I want to know the bases on which it was decided that the Whooper and Trumpeter are not conspecific—the "fact" is repeated in one form or another 4 times—while the Bewick's and Whistler can be lumped. I find a statement such as "Witherby is still very useful, aside from serious errors in 'Description'," unhelpful. *What* errors exactly?

Typographical slip-ups are few and unimportant (there is, however, a mistake in the key to the Redhead map). Errors of fact also seem infrequent; however, it is not true that all 3 *Cairina* "do well" in captivity: captive White-winged Wood Duck only started breeding regularly in 1971, and Hartlaub's Duck has proved almost as difficult. Nor are 2 *Mergus* species believed extinct. It is stated that the male Fulvous Whistling Duck averages slightly larger than the female, but neither the weights nor measurements given bear this out. Similarly, the Mute Swan egg weights from Rhode Island don't really agree well with the Old World figures, although Palmer says that they do. It wasn't the Brown Duck that Milton Weller described as having hardened skin at the corner of the gape to protect it while eating spiny isopods, but the Auckland Islands Flightless Teal.

It is clear that these volumes will be contrasted with the recently published *Waterfowl of North America* by Paul Johnsgard, and the revision of Kortright's *Ducks, Geese and Swans of North America* by Frank Bellrose. In terms of straight information, Palmer stands the comparison well. His volumes are nearly twice as long (and twice as expensive), although a great part of the extra information is in the Description section—plumages are *exceedingly* well covered. Bellrose has produced a book with almost as many facts, which less often loses the intrinsic fascination of its subject. Johnsgard's book is the easiest of the 3 to read and has the most attractive layout, but has decidedly less coverage of the recent literature. Palmer does not give the impression (which Johnsgard and Bellrose do) of being a field biologist who understands waterfowl: he is basically a compiler. Geese and swans are said to sometimes post "sentinels" around the flock; does Palmer really believe that? The detail is often there, but it is not always evaluated. The taxonomic sequence that he has adopted, for instance, means that some evolutionary interest is lost or muddled.

Are the volumes easy to use? Unfortunately, not particularly. There are too many abbreviations for rapid comprehension, and yet there *are* repetitions of information that, if eliminated, could have given the space to spell place names in full. The layout is poor, and headings of sections on, for example, plumages or subspecies are much too timid for clarity. For body weight, grams or kilograms are used alongside (and translated into) pounds or ounces, and even into tenths of a pound and tenths of an ounce, and yet body lengths, egg dimensions, and weights of day-old young are given only in metric units. So why not, in a scientific work, where space is short, give the original published figure and translate into standard metric only if it isn't in that form already?

In summary then: these are 2 expensive and rather dull volumes with a wealth of useful detail and numerous references. For having assembled it with so few errors, Palmer and his collaborators are to be thanked and congratulated; at times the project must have seemed a monumental burden.—Janet Kear.

Avian Biology, Vol 5. By Donald S. Farner & James R. King (eds.). Academic Press, New York and London, 1975: xxii + 523 pp., many charts, graphs, and drawings. $49.50—This concludes a treatise reviewing established ideas and recent advances in avian biology that was initiated with the publication of volume 1 in 1971. Many of the important findings discussed in this final volume were discovered since the publication of the first 3 volumes in the series. Volume 5 contains 7 contributed chapters: Mechanics of Flight (C. J. Pennycuick), Control and Metabolic Physiology of Migration (P. Berthold), Orientation and Navigation of Migratory Birds (S. Emlen), Circadian and Circannual Rhythms in Birds (E. Gwinner), Vocal Behavior in Birds (F. Nottebohm), Incubation (R. Drent), and Zoogeography (F. Vuilleumier). The last 3 topics have nothing to do with the previous 4, and I cannot see why the topics were grouped in this manner. The vocal behavior of birds and avian incubation would have been more appropriate in volume 3 with the chapters on reproduction and behavior in birds. The zoogeography chapter would have been appropriate in volume 1. As in the previous 4 volumes the quality of the contributions is generally good, but some fall a bit below average while others are well above average.

Pennycuick's chapter is by far the most technical and is in part a review of his model of the mechanics of flight published in 1969 (Ibis 111:525–556) and a discussion of Tucker's suggested modifications (J. Exp. Biol. 58:689–709, 1973). The second half of Pennycuick's chapter examines the mechanics of gliding and soaring, and has a brief closing discourse on the loss of flight. The chapter is relatively hard reading, undoubtedly the product of the 71 equations in the paper. I am still pondering the differences in Figs. 2 and 3; although the legends are different the figures appear identical. It is unfortunate that Pennycuick did not have the chance to include a recent paper by Crawford Greenewalt on the flight of birds (Trans. Am. Phil. Soc. 65: 1–67, 1975). This paper is well written and is an excellent complement to Pennycuick's contribution. I cannot understand why Berger and Hart's chapter on the physiology and energetics of flight in volume 4 of *Avian Biology* is not referenced by Pennycuick. This omission shows a lack of communication on the part of the contributors that the editors should have discouraged.

Berthold's chapter is an exhaustive literature review on migratory restlessness (*Zugunruhe*) in birds and its environmental and physiological control. Some attention is paid to migration in the field, but the emphasis is on cage studies. In the section on climate, weather, and food supply (pp. 82–83) there is an unfortunate perpetuation of terms that I had hoped were well on their way to oblivion (e.g., instinct migrants, typical migrants, and rush migrants). A more rigorous ecological and evolutionary treatment of migration would have markedly enhanced the subsequent sections on control and metabolism. Although Berthold does a good job reviewing the available information through 1971, there is no reference to works later than 1972. In an effort to correct this problem, almost 4 pages of additional references are listed at the end of the regular bibliography but are not discussed in the text. Because of the many references in Berthold's chapter, there is a tendency toward abbreviated critical comment and limited synthesis. It might have been better to have had fewer references and more analysis of the recent information. Many of the older references have already been treated by Farner in *Recent Studies in Avian Biology*, 1955, and in *Grundriss der Vogelzugskunde* edited by E. Schuz, 1971. The review of migration physiology is in general well done, but there is a lack of integration among physiology, ecology, and evolution. Berthold knows a great deal about the physiological control mechanisms of bird migration, and I would have valued more discussion of the adaptiveness or ecological determinants of the various mechanisms.

Emlen's chapter is in my estimation the best in the volume if not in the entire series. His treatment is so up-to-date that some of the material reviewed in detail was published after volume 5 was published! The material is presented in a readable style and is very comprehensive. I am, however, surprised that Bellrose's paper on the evolution of orientation mechanisms (*Animal Orientation and Navigation*, NASA SP-262, pp. 223–257, 1972) was not included in the review. Emlen's philosophy of orientation research is well stated; he believes that those investigators searching for *the* mechanism of bird orientation are misguided. The evidence suggests overwhelmingly that many orientation cues are used by migrating birds. Emlen examines displacement experiments with free-flying birds and caged migrants and concludes that it is too soon to look for generalizations about the navigational capabilities of birds. He suggests that a whole array of navigational strategies may exist. The section on direction-finding cues is quite complete and contains the latest information on the possible use of geomagnetism. However, the subject of reverse migration is not covered; this is unfortunate because the implications of this phenomenon on orientation mechanisms may be quite important. The many questions Emlen raises in this review will undoubtedly stimulate research for many years to come. This chapter complements the recent paper by Keeton (*Advances in the Study of Behavior*, 5:47–132, Academic Press, 1974) on homing in birds, and both provide the best reviews available on bird orientation and navigation.

The contribution by Gwinner on circadian rhythms is quite thorough and covers most of the literature through 1974 with at least one "in preparation" citation for 1975. Gwinner examines the properties of circadian and circannual rhythms under constant conditions, covers their entrainment, and concludes with a discussion of their adaptive functions. Circannual rhythms were first demonstrated in birds by Merkel (*Proc. 13th Int. Ornithol. Congr.* 13:950–959, 1963), and since then many studies have confirmed that birds in a constant photoperiod go through their annual cycles with a periodicity of about a year. These rhythms have been shown to be adaptive: e.g., the length of time a caged bird shows migratory restlessness in the fall is related to the distance it must travel to reach its wintering ground. Although Gwinner does not include references to the bird papers in a recent book edited by E. T. Pengelley (*Circannual Rhythms*, Academic Press, 1974), his review is by far the most comprehensive on the subject of circannual rhythms.

In the chapter by Nottebohm not only is the adaptive significance of call and song structure discussed, as one would expect, but the anatomy and phylogeny of song development are also reviewed in a very readable style. Nottebohm emphasizes the need to follow descriptive accounts of vocal repertoires with statistical treatment of signaling context and consequences, and he urges study of the correlation between social systems and vocal repertoires.

Drent's chapter on incubation ably covers length of incubation period, the brood patch, physical optima for development, the parent as an incubator, hatching, and energetics of incubation. His emphasis is on the field approach. The chapter is an inventory of problems and phenomena rather than an exhaustive compendium of facts about incubation. It is well written, and the numerous graphics are exceptionally well done. In the section "the parent as an incubator" Drent covers the regulation of incubation temperature, egg turning, the adaptiveness of the nest, nest tending in the Megapodes, and antipredator behavior. He then summarizes these interrelated topics in a final discourse on the organization of incubation behavior. I believe this is Drent's most successful section, but his review of the energetics of incubation, the final section in the chapter, covers some of the newest information to come out of research on incubation.

He concludes that parental costs of incubation probably have upper limits of 20–25% of productive energy. Once again, 1975 "in preparation" citations in the reference section attest to the completeness of Drent's up-to-date review of incubation, but the omission of Ricklefs' review (*Avian Energetics*, Nuttall Ornithol. Club, No. 15:152–297, 1974) because of its late publication date is unfortunate.

In the final chapter Vuilleumier reviews the current status of research in zoogeography. The fresh approach currently underway in recent work is immediately recognizable. New understanding in community and population ecology with reference to dispersal, invasion, competition, adaptation, and extinction has had a tremendous impact. This, coupled with the theory of plate tectonics and the acceptance of continental drift, has injected new vitality into the study of zoogeography. It is refreshing to read of r and K selection, equilibrium values, and extinction rates in a chapter devoted to zoogeography. Vuilleumier, however, emphasizes that the break from more traditional zoogeography is only a beginning, and empirical studies are badly needed. His review will, I hope, provide the necessary impetus to get these studies underway. In an effort to make his review up-to-date Vuilleumier has included at the end of the reference section 7 additional references that were probably added when the galley proofs for his chapter were in hand.

No review would be complete without some cursory attention to errors. I found no glaring factual errors, but some minor ones were noticeable. For instance, in Pennycuick's chapter the Parrott reference should be 1971, not 1970, and in Berthold's review the term "isepeptises" on page 82 should probably be isopiestices or isobars. In Emlen's contribution those references from the *Proceedings of a Conference on the Biological Aspects of the Bird/Aircraft Collision Problem* (Able 1974b, Emlen 1974, Williams et al. 1974) contain several errors. In all those citations "Clemsen, North Carolina" should be Clemson, South Carolina, and whereas the Able and Emlen references correctly identify the Air Force Office of Scientific Research, the Williams et al. reference has Naval Office of Scientific Research. Although the latter errors were very noticeable to me because I edited these Proceedings, I wonder how many other errors, less obvious to me, are contained in the lists of references. These, however, are small points and should not detract from the overall significance of the contributions and the success of the volume. I feel it is the best of the series, and it is definitely the most expensive—approximately ten cents a page!—SIDNEY A. GAUTHREAUX, JR.

AVIAN PHYSIOLOGY: Symposia of the Zoological Society of London, No. 35. Edited by Malcolm Peaker. Academic Press, London and New York, 1975: 377 pp. $25.50—The editor invited papers from those "working primarily on domesticated species...," but this should not turn away the ornithologist for over half of the chapters are comparative in scope, and the rest are concerned with basic physiological problems.

In "Recent advances in digestive physiology of the fowl," K. J. Hill and P. J. Strachan begin with a brief review, then discuss their research on birds with re-estrant fistulae. "Motor activity of the digestive tract," "ingesta flow along the duodenum," and "interrelationships between crop and gizzard" are the subtopics.

M. J. Purves points out the general paucity of quantitative knowledge about "the control of the avian cardiovascular system" compared with mammals. Several gaps are identified where "important evidence . . . still requires to be obtained" especially response to exercise. He examines cardiovascular control during rest, in diving, in flight, and with regard to environmental temperature.

Of the 3 purposes (gas exchange, temperature regulation, and vocalization), the first is emphasized by Knut Schmidt-Nielsen in "Recent advances in avian respiration." Body size is seen to exert a major influence on rates of oxygen consumption. A brief section on anatomy is followed by "breathing and ventilation," again related to body size. The unique avian lung-air sac system is discussed lucidly in sections on gas flow and exchange, followed by oxygen carrying capacities of avian blood. The aerodynamic control of airflow remains an unsolved aspect of resting avian respiration; virtually nothing is known about gas flow during exercise and flight.

The next chapter, "Flight energetics," is by Vance Tucker, whose contributions in experimentation and theory establish him as a foremost ornithologist of our time. The level of intellectual effort required to cope with 21 equations and a half-page table of symbols is higher than for the descriptive prose of most ornithological works, but the great potential for understanding the physical basis of natural history patterns should be sufficient motivation.

"The theory" and Fig. 1 very lucidly set out the components of a bird's metabolic rate, so that anyone can visualize the power terms in equation 1. Equation 2 is reached on faith or via the derivations in the appendix to Tucker (1974). The assumptions involved are such that one cannot see at a glance where $P_{o_{in,\ par,\ pr}}$ went as components of eqn. 2 and what happened to $P_{i_{r.h}}$. Coefficients in eqn. 5 and 6 differ slightly from the same basal power relationship given on p. 35 of the previous chapter. Otherwise, the good logic is apparent and I could proceed intuitively, qualitatively to the reward. "Cost of transport," "Approximation equations," and "Energy budgets" bring us to the threshold of interpretation of migratory and time-allocation behavior. Tucker frankly acknowledges the limitations of the theory in applications to local activity vs. extended flight. This serves to remind us how over-simplified and tenuous are our "energy budgets." If the reduction of natural history to equations seems esthetically lacking, ponder how the bird "knows" or integrates information on profiles of winds aloft, or solves P_i/wV in order to pick the optimum altitude and effort. This is awe-inspiring!

In "Thermal homeostasis in birds," S. A. Richards points out that "few experiments have been designed specifically for the difficult task of separating the two possible components" of peripheral and central temperature receptors. Perhaps the temperature sensors should be in the deep-body, brain, and spinal regions, and heat-flux rather than temperature-sensors should be in the periphery. Richards describes emerging patterns, but carefully points out the limitations of methods and the interpretation of results. Central integration is not based solely upon hypothalamic input, but on a weighing such that the hypothalamus had 60 to 80% of the votes, at least in controlling panting. Especially interesting is the work on hypothalamic control of feather position index. The existence of non-shivering thermogenesis is neither disproven nor established.

"Renal and cloacal transport of salt and water," is, because of many recent reviews, limited by E. Skadhauge to recent observations. These include renal concentrating abilities of Western Australian birds' excretion of electrolytes, water, and nitrogen, cloacal resorption and interaction of renal and cloacal function, and the relationship between the concentrations of saline drinking water and renal concentrating ability. Skadhauge found an interesting correlation between weight-specific metabolic rate and maximum salinity of drinking fluid for water balance. A small bird such as the Zebra Finch can form a maximum urine concentration of 1000 mOsm, but fluids of about 1440 mOsm can constitute 10% of their water turnover, the difference being made up by metabolic water.

M. Peaker discusses "Recent advances in the physiology of the salt glands" as follows: "The primary stimulus" (increase in plasma tonicity, but not necessarily in osmolality), "Location of the receptors" (most likely "on or near the luminal wall of the major blood vessels near the heart or the heart itself"), "The secretory reflex," and "secretion and blood flow." Salt glands are of interest not only in regard to homeostasis, but for the insight they can furnish regarding the basic functioning of cells and organs, the control of blood flow to secretory organs, and the coevolution of an organ and the mechanisms controlling the blood flow rates, which are the highest measured in any organ. From such flow the salt glands can remove up to 80% of the chloride, 57% of the sodium, and 21% of the water. The % increase in plasma sodium concentration needed to stimulate salt-gland secretion is inversely related to body mass.

In "Prolactin and adaptation," D. M. Ensor discusses the complex effects of environmental factors and blood composition on prolactin release and the effects of prolactin on nasal-gland function, food and water intake, fattening and fat utilization, water balance, and urine output.

Five chapters on reproductive physiology follow. R. K. Murton ("Ecological adaptation in avian reproductive physiology," pp. 151–152), Lofts ("Environmental control of reproduction," p. 189) and Follett and Davies ("Photoperiodicity and the neuroendocrine control of reproduction in birds," p. 207) agree that daily photoperiod serves (1) to entrain a circadian oscillation and (2) to induce the photoperiodic gonad-stimulating response when light falls within the photoinductible phase of that circadian rhythm. These are interesting accounts of ingenious attempts to understand the physiological clock and its linkage from long photoperiods outside to gonads' trophin secretion within. These papers must have provided stimulating exchange of current knowledge when presented originally. However, the editor could have produced a more effective review for those not attending by appointing 1 spokesman to integrate the information from 7 species and 3 chapters.

P. E. Lake reviews "Gamete production and the fertile period with particular reference to domesticated birds." The fertile period (prolonged survival of spermatozoa from insemination until fertilization or potential fertilization is said to have been "studied closely" and "to vary distinctly between species; the reasons for the inter-specific differences are not clear." He did not consider that duration of fertile period is a unit of physiological time, which may be strongly influenced or scaled to body size.

A symposium provides the opportunity for cross-fertilization of ideas and techniques. The influence of body size was noted in previous chapters. The potential for allometry in reproductive studies can be seen if one runs logarithmic regressions of fertile period as a function of body size in Lake's Table 1, p. 236. There are differences not only correlated with size but with order. Anseriformes have shorter spermatozoan fertile periods than Galliformes. Mean duration of galliform fertile periods $= 1.09\ \mathrm{m}^{0.335}$ ($p < 0.001$), where m = body mass in g (representative body weights from other sources; original references which I was able to consult list no weights of sperm-donors or recipients). Considering the limited sample size, the exponent is roughly similar to those relating breath and heart cycle durations to body mass in birds. This relationship seems worthy of further examination.

Two chapters deal with the influence of hormones on nesting behavior, the authors reviewing their own experiments, using 2 species with long histories of adaptation to captivity and thus amenable to experimentation without undue alarm. In "The dual role of daylength in controlling canary reproduction," R. A. Hinde and E. Steel review their interesting experiments on the influence of photoperiod on nest-building in response to estrogen. This is followed by "The physiological basis of a behavior pattern in the domestic hen" by D. G. M. Wood-Gush and A. B. Gilbert. They established that the post-ovulatory follicle plays a major role in nesting behavior such as nest examination.

Injection of estrodiol benzonate and progestrone restores normal behavior after ovariectomy.

Having considered the control of reproduction and reproductive behavior, we proceed to the products, the nestlings and eggs. R. J. O'Conner reviews "Growth and metabolism in nestling passerines." A derivation from "Fourier's Law" of heat loss attempts to relate the development of homeothermy to "the decrease in surface-volume ratio and hence the reduction of the heat lost from each gram of heat producing tissue." The attempt goes awry when power functions of body weight are substituted for some but not all of the weight-dependent terms in the equation:

$$d\,Q_L/dt = W^{2/3}/r\ (T_B - T_A)$$

where $d\,Q_L/dt$ is rate of heat loss with time, W is nestling weight, r is specific insulation, and T_B and T_A are body and air temperature, respectively. However, it can be derived from Lasiewski et al. (Comp. Biochem. Physiol. 23:797–813, 1967) and Herreid and Kessel (Comp. Biochem. Physiol. 21:405–414, 1967) that the specific insulation (per unit surface area) is proportional to $W^{1/6}$. Thus, $d\,Q_L/dt$ is proportional to $W^{1/2}$ at T_A below thermoneutrality, as Kendeigh (Auk 86:13–25, 1969) has demonstrated empirically for adult birds.

Whether one includes the allometry of r and sees heat loss rate as a function of $W^{1/2}$ or uses $W^{1/3}$ as in the text, there is still a positive allometry of heat loss, *i.e.* the larger the nestling, the greater the total heat loss, and for that matter, the larger the nestling, the more surface area it has for heat loss. These facts invalidate the conclusion: "The simple change in surface-volume ratio inherent in a heavier body weight thus provides the simplest explanation of the observed pattern of metabolism in blue tits" (p. 301). Thus, increased metabolic-capacity, directly and through "Q_{10}-effect" as T_B is maintained higher, and increased insulation, must be the foundations for homeothermy. This dead-end digression should not distract the reader from the virtues of O'Conner's painstaking measurements and interesting data on growth in weight, plumage, and metabolism of the Blue Tit, House Martin, and House Sparrow.

We may take aspects of the natural history of birds, such as the formation of eggshells, for granted and never stop to wonder how they work. K. Simkiss reviews just how marvelously complex and incompletely understood are the calcium metabolism and regulation in "Calcium and avian reproduction," considering 8 current questions in the understanding of calcium metabolism. The subject is of interest not only in regard to this essential stage in perpetuation of birds, but as a system for basic cellular research. He concludes that "the control of avian calcium metabolism remains largely mysterious" but has pin-pointed research opportunity and provided new awe for egg-laying.

In "Pesticides and eggshell formation," A. S. Cooke contributes a valuable inquiry into eggshell thinning, comparing the effects of calcium-deficiency and sulfanilamide-treatment (chickens), DDT-treatment (ducks) and examination of shells collected beneath a heron rookery. Thinning seems to be caused both by reduction in availability of components and by normal deposition rates but premature termination. Cooke points out that these preliminary investigations must be followed up by detailed study of a single species, in both lab and field.

A symposium cannot produce a complete textbook on avian physiology but the ornithologist desiring a current knowledge of how the bird functions should have this volume. The physical quality of the volume is good, with flat glare-free paper. I found only 2 typographical errors. If more birders were sufficiently interested in the objects of their life-lists to make an informative work like this sell widely, perhaps the price could be less.—WILLIAM A. CALDER III.

Avifauna of Northwestern Colombia, South America. By Jürgen Haffer. Bonner Zoologische Monographien, No. 7, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, 1975: 182 pp., paper, 7 plates, 51 text figs., 8 tables. Price 35 DM.—This would appear to be the latest installment by the author in a series of repetitively overlapping analyses of Pleistocene refugia and the subsequent dispersal of their avian populations. In the introductory portion he deals "with general aspects of the ecology and zoogeography of the avifauna of northwestern Colombia as they relate toward elucidating the relationships of this forest fauna with other trans-Andean faunas and with the Amazonian fauna." The second portion presents the results of his fieldwork from 1958 to 1967: "I summarize the information obtained and give a complete list of birds that I encountered. I specially emphasize the secondary contact zones of parapatric species and hybridizing subspecies. . . ." The format and contents quoted above differ little from that by the author in an earlier paper (Haffer, Am. Mus. Novitates, 1967, no. 2294:1–2).

The introductory portion has the greater significance as it synthesizes the secondary-contact itemizations which are scattered individually through the unevenly annotated list that is the second portion. On the positive side, the author clearly delineates his "core areas" and "suture zones." He names the endemic species in each of 8 distributional centers, amounting to a total of 195 in the forested lowlands of his entire trans-Andean "province." Any species that is not one of the 195 trans-Andean endemics the reader must assume to be cis-Andean as he is given no alternative.

On the negative side, the reader has no way of knowing which other birds—i.e. the great majority of the avifauna, including the bulk of the trans-Andean and most of the cis-Andean species—occur in or between any or all of the author's distributional centers. For one thing, the information is mostly not there. For another thing, the author's use of "trans-Andean" and "cis-Andean," "forest" and "nonforest," even "humid" and "dry" and "lowland" versus presumably cloud-forest highland, terms which must be understood in combination, can be confusing and contradictory.

Take, for example, the explanatory footnote on the opening page: "The tropical lowlands and their faunas west of the Andes and in Middle America are designated as 'trans-Andean' or 'Pacific', and those east of the Andes as 'cis-Andean' or 'Amazonian'." Only later does the reader realize that "trans-Andean" includes northern Colombia and Venezuela north of the Orinoco into Guyana, that "west of the Andes" may or may not include "north of the Andes," and that in Middle America, "Pacific" means primarily "Caribbean." He should keep in mind that a trans-Andean avifauna includes cis-Andean species; often it is not evident whether "trans-Andean" is intended in a restricted or in an unlimited sense.

A trans-Andean species, we learn, is at least specifically distant, while a cis-Andean species is either undifferentiated from or is at most subspecifically, distinct from a representative Amazonian population. This definition allows the cis-Andean element a short evolutionary life in which to remain what it is before transmuting into something trans-Andean. Nevertheless the cis-Andean element dominates the trans-Andean element by a ratio of from 1.3:1 to 2:1 (following the author's figures), while many trans-Andean endemics are not easily distinguishable at the specific level from cis-Andean representatives (p. 36). A paradoxical consequence is that in the cases of disagreement over the specific status of forms that are trans-Andean geographically, genetically they must be simultaneously trans-Andean to one authority and cis-Andean to the other. The author supplies no instance in which his 195 endemics may not have evolved from cis-Andean representatives.

Another consequence is that the reader is left to decide unaided the status of a contingent of Middle American species (e.g. *Trogon melanocephalus*, *Piculus simplex*, *Celeus castaneus*, *Piprites griseiceps*) belonging to South American genera that the author does not mention. By definition they cannot be cis-Andean, yet they are not listed among the trans-Andean. Similarly, the author does not include, for example, the Cathartidae, 2 members of which frequent forest, in a list of numbers of neotropical lowland forest birds (Table 3), perhaps because he tacitly considers them North American? The reader is ignorant not only of the specific composition of the trans-Andean avifauna in toto or per refugium but also of the species which the author for unstated reasons may or may not have included in his numerical totals.

This may be the place to quote his view, shared by many, that "the faunal relationships of the densely forested Caribbean slope of Panamá lie with the humid Pacific lowlands of northwestern South America," a peculiarity that is equally conspicuous in the case of the herpetofauna (p. 67). Unfortunately, the faunal resemblance formula the author chose to select (Table 6) shows western Panama to be much closer to Caribbean Costa Rica than to central and eastern Panama and as close to southeastern Mexico as to the Chocó lowlands on the Pacific side of Colombia. Central Panama and eastern Panama are both closer to the Cauca-Magdalena region at the drier northern end of the Andes than to the Chocó lowlands on the wetter Pacific side.

An illuminating comparison could perhaps have been attempted, whether by the reader or by the author, of the Chocó and the Caribbean Costa Rican centers. The author assigns them respective forest-bird totals of 247 and 239, with 112 trans-Andean species included in the former and 104 in the latter, while the number of cis-Andean species, 135, is the same in both. Only 58 of the trans-Andean species are held in common; no figure is given for the cis-Andean species. The opportunity to analyze the replacement of large numbers of presumed ecological counterparts on a virtual one-to-one basis has been lost simply because of the lack of species lists.

In regard to "forest" and "nonforest," the author includes as forest birds a number of species—e.g. *Laterallus albigularis*, *Jacana*, *Amazilia tzacatl*, *Synallaxis brachyura* and *S. erythrothorax*, *Geothlypis semiflava*—that I for one would not. Species the author lists here as forest birds he previously considered nonforest (Haffer, Hornero 10:315–333, 1967). Some examples are *Todirostrum sylvia*, *Thamnophilus doliatus*, *Galbula ruficauda*, *Basileuterus rivularis*. The trans-Andean *Ortalis garrula-cinereiceps* complex, used by the author to illustrate speciation in Amazonian forest birds (Haffer, Science 165 (3889), 1969), he now specifies as nonforest on p. 67 but includes in a table of forest birds in secondary contact on p. 58. The reader need not face these gratuitous conceptual difficulties as he cannot, in any event, reconstitute the avifaunas in Tables 2, 3, and 6.

As to "humid" and "dry," the author states (p. 30): "We are here concerned exclusively with an analysis of the avifauna of the trans-Andean humid lowland forests (Dry, Moist, Wet and Pluvial Forest in the Holdridge classification). . . ." Thus he sees fit to lump Holdridge's Dry Forest with Holdridge's humid to very wet forests, a largely unshared view. He does so, however, for the northern Colombian and western Venezuelan but not for the Middle American portions of his trans-Andean lowlands. Incidentally, the author uses the life-zone terminology and the numerical rainfall limits of Holdridge, yet Holdridge is not cited in the author's very long list of References.

Table 1 illustrates the author's interpretation of the ecological distribution of 131 selected species in northern Colombia in dry forest on the east, moist forest in the center, and wet forest in the west. This table and the accompanying text effectively mislead the reader early in his excursion into "trans-Andea." The reader can hardly avoid the erroneous inference that the species which range throughout the Chocó wet forests, thence varying distances eastward into moist forest and sometimes into dry forest, are all Pacific or trans-Andean; the species that range primarily in dry forest and varying distances in moist forest, rarely reaching the Chocó wet forests, are all cis-Andean, though it may occur to him later in retrospect that a number may be "dry" trans-Andean, an apparent contradiction in terms the author's use of which makes it difficult to resolve.

Another result of his use of the Holdridge terminology without appreciating the concepts is that, whatever may be the author's idea of "lowland," it is not that of Holdridge, who defines it by biotemperature values which, except perhaps in local pockets, do not reach the lower limits of the atmospheric manifestation known as "cloud forest." A number of the author's tropical lowland species—e.g. *Bangsia arcaei*, *Popelairia conversii*, *Procnias carunculata*—are really subtropical inhabitants of his Caribbean Costa Rican distributional center (see Slud, Bull. Am. Mus. Nat. Hist. 128, 1964). Another species, *Euphonia anneae*, which is there subtropical, has also been found in the lowlands of eastern Panama. Thus the reader may wonder how the author may distribute other species which occur in the humid, sometimes in the "dry," lowlands in South America and only under very humid, mountainous conditions in Central America.

Finally, the wary reader should, among other items, take note that in Table 3 the heading "Caribbean Middle America" should be "Caribbean Costa Rica" and the use of "sympatric" for species known from areas the size of Surinam or southeastern Colombia is a misconception of the term; in Table 6, "southwestern Mexico" should be "southeastern Mexico," while "Guatemala" and the "Urabá region," included in Table 2, are omitted here; in Table 8, the 2 species of *Oncostoma* and 1 of the forms of *Geothlypis semiflava* are entered incorrectly.—PAUL SLUD.

THE BOOK OF BIRDS. FIVE CENTURIES OF BIRD ILLUSTRATION. By A. M. Lysaght. Phaidon Press, London, 1975: 208 pp., 142 illustrations (40 in color). $55.00.—A not infrequent dilemma for book reviewers in a specialized field such as ornithology, in which many of the authors are likely to be known personally to the reviewer, is whether or not to include "inside information" in a review, facts pertinent to some aspect of the publication that are not evident to other readers. This book is a case in point.

Averil Lysaght is a good friend, and I was privileged to examine an advance copy of her book at her home in London. I drew up for her benefit, at that time, a list of typographical errors, misidentifications, and other matters, so that nothing I may say in this review will come as a surprise to her. But I also had the benefit of a first-hand account of the problems she encountered in the course of getting out "The Book of Birds." The first thing that needs to be said is that the utterly banal title was imposed upon her by the publisher—the subtitle (which appears on the title page but not on the binding or the dust jacket) is a more precise indication of the subject matter. After the publisher was committed to this project, with advance contracts, a deadline, and half a dozen color blocks already made, the original author withdrew. Dr. Lysaght was persuaded to take on the job, with much encouragement and assistance from Derek Goodwin of the British Museum (Natural History) and Gavin Bridson of the Linnean Society (London). The pressure to meet deadlines was such that the publisher actually told the author that she need not see proofs after she had handed in the typescript!

In view of these and other items recounted to me about the history of this book, its beauty and the obvious care and scholarship evidenced in the text, are even more impressive. As the subtitle indicates, it is basically a survey of bird illustration, up to the late 19th Century. Ironically, the oldest painting reproduced, from a 12th Century Chinese scroll in the British Museum Department of Oriental Antiquities, a Finch-billed Bulbul (*Spizixos semitorques*) perched and singing among flowers, is one of the most meticulously accurate renditions in the book. Many of the best-selling bird artists of today have less understanding of the proportions, scalation, and mechanics of a bird's legs and feet than did the anonymous painter of this bulbul (possibly the Emperor Hui-tsung, 1082–1135).

The book opens with a 22-page introduction, a rapid survey of man's interest in birds from the most ancient times, gradually focusing on bird portrayal in particular. The emphasis at first is on birds in mythology and superstition, including the use of birds in ancient *materia medica.* There are such delightful tidbits as "Excrement of the cormorant mixed with lard was used [in ancient China] in the treatment of red noses resulting from too much wine." And how frustrating to be told only that "in Turkey, erotic cults concerned with geese are still extant"!

The text (introduction, notes to the plates, bibliography, index) is printed on a handsome dull-finished heavy gray paper, whereas the plates are on a white, faintly glossy stock. The margins are huge—the page measures 10½" by 14", but the type bed for the introduction is only 6" by 11½", printed toward the outer edge of the page. On the plate captions, the right margins are not justified. In a less expensive book, such design decisions might be considered extravagant, but the price of this book could scarcely have been significantly reduced had the 22 introductory pages been reduced by expansion of the type bed. And the visual effect is indeed striking.

The plates are arranged in rough chronological order, but with many exceptions, probably a concession to layout design and to the mixture of color and black-and-white printing. Reproduction of the color plates, printed in Holland, seems excellent. Each caption includes the English and scientific names of the bird or birds portrayed (if identifiable), bibliographic details of the original (if an unpublished work, the library or collection in which the original is housed), the medium and size of the original, and a variable miscellany about the artist, the author of the book in which a plate was first published, something about the bird, and various historical notes. Dr. Lysaght is not an ornithologist, but a specialist in the history of science, especially of the scientific and exploratory expeditions of the 18th and 19th centuries. This has meant that a few ornithological inaccuracies and misidentifications have slipped into the book, but for this small price we are rewarded with information and anecdotes from a field of scholarship virtually unknown to most modern ornithologists.

Identification of the rather crudely drawn birds in old woodcuts and engravings is sometimes almost impossible, and at other times uncertain. I believe "The Little Horn Owl" of plate 64 is probably a Scops Owl (*Otus scops*) rather than a Short-eared Owl (*Asio flammeus*) as identified in the caption, whereas the "Scops Owl" of plate 132 is definitely a Long-eared Owl (*Asio otus*). On plate 104, only figure 1 is a manakin of the genus *Chiroxiphia*; figure 2, which one might deduce from the text of the caption to be a female manakin, appears to me to be a White-headed Marsh-Tyrant (*Arundinicola leucocephala*). The text for plate 127 is a mixture of facts about the Imperial Woodpecker (*Campephilus imperialis*) and the portrayed Ivory-billed Woodpecker (*C. principalis*). Contrary to the statement accompanying plate 140, it is the New World and not the Old World vultures that have a well developed olfactory sense. I found fewer than half a dozen typographical errors, and 3 or 4 obsolete scientific names.

Most of the expected ornithological artists are represented—Gould, Wolf, Audubon, Catesby, Bewick, etc.—and there are unexpectedly beautiful or charming portraits by lesser known or even anonymous artists. One's respect for 16th Century science is enhanced by a 1555 engraving by one Pierre Belon, homologizing the skeletons of man and bird. An odd color drawing by J. D. Meyer of Nuremburg (1713–1754) shows a pair of Blue Tits (*Parus caeruleus*) at the top of the plate and their skeletons, in the identical poses, at the bottom; the skeletons are done in far better detail than are the live birds. One could go on and on, listing the striking and the unexpected (the rather hackneyed Audubon Blue Jay, featured on the dust jacket, was not Dr. Lysaght's choice but was one of the few plates imposed on her by the publisher).

The somewhat overwhelming price of this book will unfortunately label it as a luxury item. Do not be misled by its oversize format and high price—it is emphatically *not* one of the virtually interchangeable and superfluous "coffee-table books" that have flooded the market in recent years (at least half having originated in England, which seems odd in view of the straitened British economy of the 1970's). Dr. Lysaght's book fills admirably an unoccupied niche in ornithological literature. Any reader with an interest in avian iconography might well begin dropping hints to any affluent relatives about a suitable birthday present.—Kenneth C. Parkes.

(N.B.—As of January 1977, this book appeared on at least one list of publisher's overstocks, at less than half the original list price. This is a bargain worth hunting for.)

Identification Guide to European Passerines, 2nd (revised) edition. By Lars Svensson, illus. by the author. *Naturhistoriska Riksmuseet*, S 104 05 Stockholm 50, Sweden, 1975: 184 pp., ca. 160 line drawings. Price not given.—This compact (10 × 19 cm) identification guide by one of Europe's most noted ornithologists will be of use to a strictly limited number of people in the United States. It covers 180 species and 35 subspecies of European passerines and is primarily intended to present ageing and sexing characters for fledged birds in the hand. It is thus of little value for field ornithology but covers all the likely species a bird bander or museum worker might encounter.

The first 10 pages of "directions for use" and 15 pages of "general techniques for ageing and sexing" present a detailed explanation and discussion of the different methods used in the "systematic list" of species that follows. These introductory pages require careful reading if one is not familiar with the symbols and abbreviations used in the first edition of this book; however, all methods are fully explained and the practical problems discussed. The author follows the nomenclature of C. Vaurie, "*The Birds of the Palaearctic Fauna*," Passeriformes (1959), and he presents characters to identify the species (in difficult cases), the age, and the sex, where possible on external characters. There is also a summary of the molt regime, and wing lengths with sample sizes are usually given. Nearly every species description is accompanied by one or more text figures illustrating particular points of difference. A comprehensive 9 p. of important references are followed by an index of scientific names only.

Three controversial methods are perhaps worth singling out from an otherwise good presentation. Firstly, Svensson elects to number primary feathers ascendantly from wing tip towards the body, while most modern molt studies employ the descendant order, i.e. that in which the feathers are usually replaced. Secondly, he gives the impression that a live bird should be held with its head towards the bander's wrist during measurements, whereas most North American and British banders prefer an alternate grip with the head held between the first 2 fingers and the body in the palm of the hand. Finally, the tail shape character used in ageing some birds, e.g. genus *Turdus*, may be even more difficult in practice than the author states. Apart from these, and a few minor errors, the overall impression is of an excellent specialist reference work embodying all the most recent information on ageing and sexing from a wide range of European sources. North American banders are doubtless eagerly awaiting a similarly complete and modern reference for nearctic passerines.—TREVOR L. LLOYD-EVANS.

STATE LAWS AS THEY PERTAIN TO SCIENTIFIC COLLECTING PERMITS. By M. Houston McGaugh and Hugh H. Genoways. Museology No. 2, 1976: 81 pp. Order from the Museum Shop, The Museum, Texas Tech University, Lubbock, TX 79409. $2.00—For each state as well as Puerto Rico and the Virgin Islands, the laws pertaining to collecting animals and plants are given, along with lists of protected species and game animals. The addresses of relevant state agencies are given so that one may write for further information or permit applications. These state laws are in addition to federal requirements, which the collector must also take into account when planning research.—R. J. R.

A GUIDE TO THE BIRDS OF PANAMA. By Robert S. Ridgely, illus. by John A. Gwynne, Jr. Princeton University Press, Princeton, N.J., 1976: xv + 394 pp., 32 color plates, many black-and-white drawings. $15.00.—Although smaller than the state of South Carolina, the Republic of Panama has a remarkably large avifauna of some 883 species, mainly because of its geographical location as an area of overlap between North and South American faunas. This book is a one-volume compendium of information useful both as a field guide and general reference. The author gives full credit and appreciation to Eugene Eisenmann, who encouraged him to write the book, and provided extensive field notes that Ridgely has incorporated into his text. Following a foreword by Alexander Wetmore and an introduction, there are chapters on Climate, Migration and Local Movements, Conservation, and on the Plan of the Book. The main text consists of species accounts organized by family. For each species there is a concise description, and sections on similar species, status and distribution, habits, and range. This is followed by an appendix listing and briefly describing additional species of southern Middle America that are not known to occur in Panama. A second appendix tells where to find birds in Panama, and includes such useful information as where it is safe to drink the water. The book ends with a bibliography and an index.

The color plates by Gwynne are conveniently grouped in the center of the book, and are a major contribution to the volume. The paintings are attractive, and the birds appear lifelike. These plates should be of great value in field identification, though it is obvious that some groups, such as the hummingbirds, woodcreepers, and flycatchers will pose special problems to the inexperienced observer because of the many similar species in each group.

Measuring about 16 × 23 cm the book is a bit large to carry easily in the field, yet from the amount of information included and the efficient, compact design of the book, it is clear that there is no wasted space. Students of tropical American ornithology will welcome this attractive addition to the literature of the area.—ROBERT J. RAIKOW.

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The Wilson Bulletin

Suggestions to Authors

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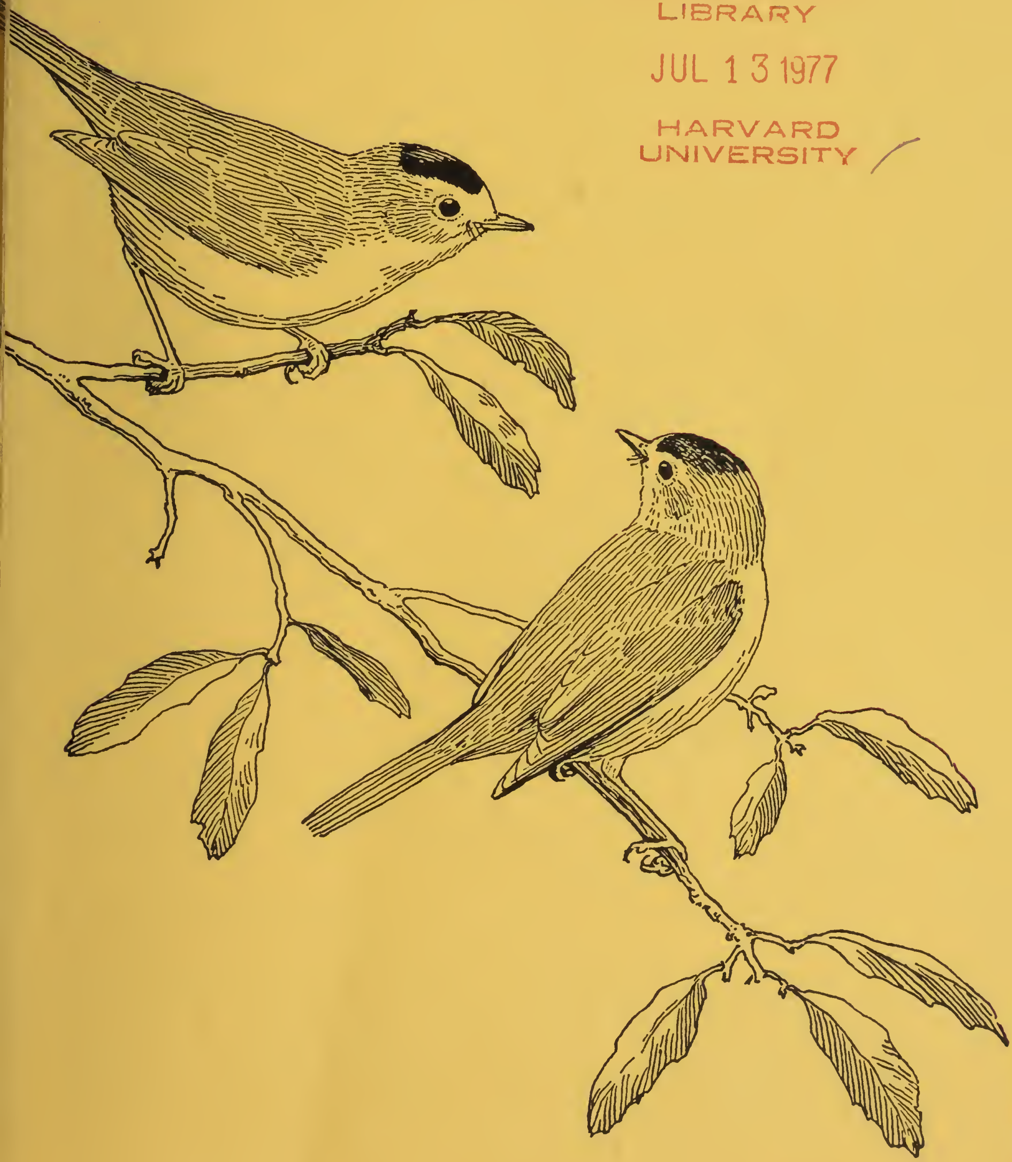

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Immature (above) and adult (below) Oahu 'Elepaio, *Chasiempis sandwichensis gayi.* Painting by Doug Pratt.

THE WILSON BULLETIN

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THE BREEDING BIOLOGY OF THE OAHU ‘ELEPAIO

Sheila Conant

The monotypic genus *Chasiempis* (Muscicapidae) is endemic to the Hawaiian archipelago, and represented by 3 subspecies: *Chasiempis sandwichensis sclateri* on Kauai, *C. s. gayi* on Oahu, and *C. s. sandwichensis* on Hawaii. Commonly called the ‘Elepaio, *Chasiempis* is believed to be related to the genus *Monarcha* (Mayr 1943, Amadon 1950), and to be of Melanesian origin by way of Polynesia or Micronesia (Baker 1951). *C. s. gayi* (see frontispiece) was described by Wilson (1891), and is endemic to the island of Oahu.

Despite its wide distribution and relative abundance, this bird has received little attention from field ornithologists. Photographs of the nest and eggs of *C. s. sandwichensis* and of the nest, eggs, and young of *C. s. sclateri* have been published only recently (Berger 1969, 1972).

METHODS AND STUDY AREA

Breeding biology data on the Oahu ‘Elepaio were gathered by field observation beginning in November 1965 and ending in May 1968. Brief observations of the Kauai ‘Elepaio were made for 3 days in April 1967, 10 days in June 1967, and 7 days in July 1975. From October 1972 to August 1973, and for about 1 week per month from July 1974 to March 1975 I collected data on the Hawaii ‘Elepaio while conducting field studies of avian communities on the east flank of Mauna Loa on the island of Hawaii. Although this paper reports primarily the results of my studies of the Oahu population, I have drawn upon observations of the other 2 subspecies to add to my discussion of some topics. Specific information on a particular subspecies will be identified as such.

The main study area consisted of about 70 ha on the northeast side of Manoa Valley on the island of Oahu, and I made occasional trips to other areas. The vegetation of the study area was mesic forest with grassy clearings. Most plants in the area were introduced species.

I recorded song and call-notes with 2 portable tape recorders and 2 types of microphones: a Nagra III with an Electrovoice 655 microphone and a Uher 4000L with a 514 microphone. To determine song patterns in relation to sex and phase of the breeding season I recorded the number of songs given by each member of a pair during the same hours of the day in each breeding season phase for a total of about 30 h. I also recorded the number of songs and nest material additions by the members of pairs for about 25 h during the first week of construction of several nests. Plumage, behavior, and egg-laying permited me to sex the birds while data were recorded.

Only 3 birds were banded and color-banded during the study: 1 bird in immature plumage caught in a mist net in November 1966 and 2 nestlings in May 1967. A total of 32 nests were found, 11 of which were collected and measured. Fifty-three eggs in 26 clutches were observed, though none was measured. A small, moveable mirror attached to a length of pipe was used to observe the contents of some inaccessible nests. In nests accessible by using ladders and by climbing trees, I marked 12 eggs as they were laid.

DIET AND FEEDING BEHAVIOR

Although ‘Elepaio forage at all canopy levels in the forest, (Perkins 1903, MacCaughey 1919, this study) they were most often seen in the lower story. During 33.3 min of feeding behavior observations of the Hawaii ‘Elepaio, birds spent 23.7 min feeding between 0 and 3 m in the canopy, 8.3 min between 3 and 6 m, and 1.3 min above 6 m. MacCaughey (1919) and Richardson and Bowles (1964) mentioned the association of ‘Elepaio with various plant species, but Perkins (1903) felt, and I concur, that ‘Elepaio are opportunistic feeders, that is, they are most likely to be found where insect densities are highest, regardless of the plant species involved. MacCaughey (1919) and the Hawaii Audubon Society (1967—probably based on MacCaughey 1919) reported nectar feeding, but Munro (1944) and I never saw ‘Elepaio eat anything other than animal material, especially insects. After examining stomach contents and observing feeding behavior, Perkins (1903) reported that ‘Elepaio fed on a variety of insects as well as arachnids, chilopods, diplopods, and some molluscs.

DISTRIBUTION AND MOVEMENTS

The ‘Elepaio is sedentary (Henshaw 1902b), and was reported by MacCaughey (1919) to have the widest altitudinal range of any native forest bird. This is probably still true of all 3 subspecies, although since 1968 I have noticed that densities, though not range, of the Oahu ‘Elepaio have decreased. The ‘Elepaio can still be found in the backs of most valleys and on ridges on Oahu, but, whereas 8 years ago one would hear or see several pairs on a 5 or 6 km ridge trail, only one, sometimes none, will appear today. The ‘Elepaio’s adaptability to a wide variety of foods (Perkins 1903), habitats, elevations, and weather conditions (MacCaughey 1919, Richardson and Bowles 1964, Berger 1972:112, 114) is undoubtedly responsible for the success of the species and its wide distribution in comparison to other native forest birds. Henshaw (1902a) predicted that it would persist in substantial numbers after other endemic passerines were rare or extinct.

During the non-breeding season ‘Elepaio remained in or near the same area

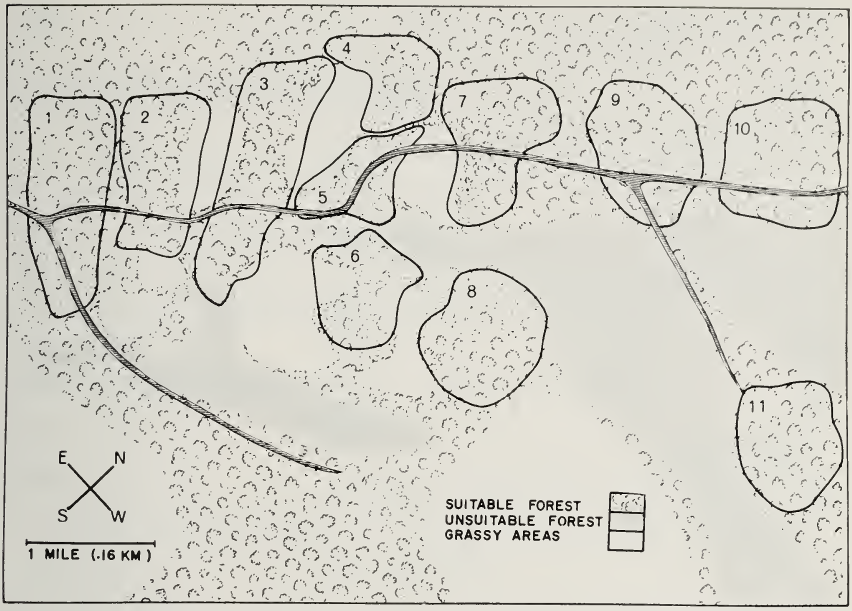

FIG. 1. Territories occupied by breeding pairs of 'Elepaio in Manoa Valley, island of Oahu, Hawaii.

as their breeding or hatching territory the entire year, but I don't know if they always defended territories. From July through December the birds traveled in pairs or family groups, presumably depending on whether or not any young had survived from the previous breeding season. These small flocks disintegrated as males established breeding territories (Fig. 1) by singing in late December or in January. The 2 nestlings banded in May 1967 and their parents exhibited this pattern of behavior. The nestlings hatched and one (the second was not seen after July 1967) remained in or near territory 6 with its parents after the 1967 breeding season. In January 1968 the banded bird established territory 5, pairing with an adult female (pair 5-68—number of pair combines territory number and year of breeding). The presumed parents of this bird (6-67 and 6-68) reestablished their former territory, and bred there. Pair 5-68 renested 3 times. After the destruction of the 4th nest, the banded male did not renest, but remained in territory 5, and his mate was not seen again.

VOCALIZATIONS

According to Henshaw (1902a), the 'Elepaio's name is the Hawaiian transliteration of its primary song, a short, melodious whistle. Perkins (1903)

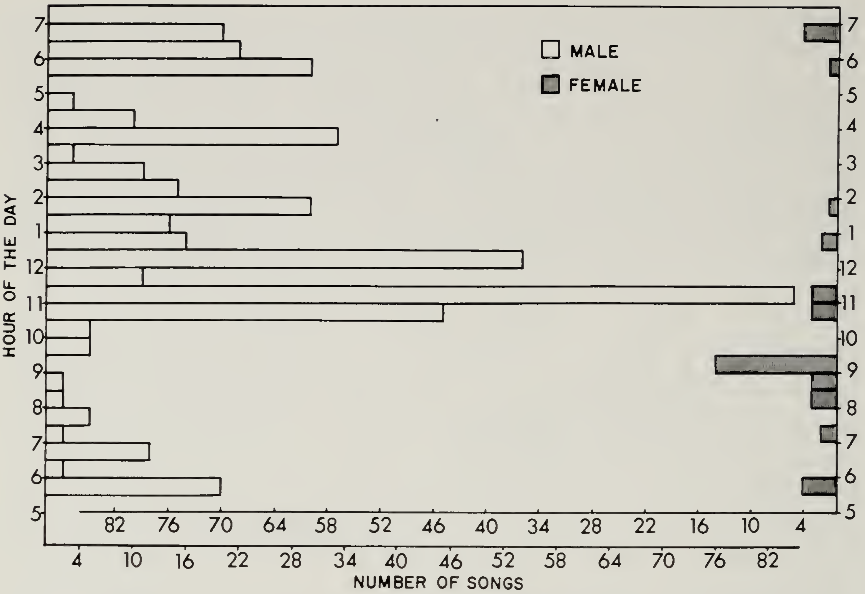

FIG. 2. Number of songs given by both sexes during each hour of the day, during the first week of nest building.

observed that birds often broke into song after intense chatter. I have heard 4 types of vocalizations: chip, chatter, song, and the alarm call. The most common vocalization heard was chatter, which ranged widely in pitch, frequency, and volume. Chatter often preceded songs, which were usually uttered in series of threes. Chatter, unaccompanied by song, was frequent as the birds moved about feeding. Frequent, loud, and excited chatter indicated mild alarm. The alarm call, a short raspy cry, was given by adults and young only when the birds were extremely disturbed, as when the young in the nest were handled or photographed. A high-pitched, soft chatter served as a food-begging call given by nestlings and fledglings, and was similar to the vocalizations of a female indicating readiness for copulation. While feeding and moving about, 'Elepaio often uttered a single, low-pitched chip, apparently as a contact note, maintaining flock or pair contiguity. This chip was also given immediately before birds exchanged places on the nest to incubate or brood, although the male often sang instead. Repeated chips appeared to function as alert notes when a bird was mildly excited or disturbed.

The 'Elepaio was invariably the first bird to sing in the morning, and the last to sing in the evening. During the breeding season I determined territorial boundaries by listening to morning song periods that began before 06:00 and lasted 30 to 45 min, and evening song periods that began at about

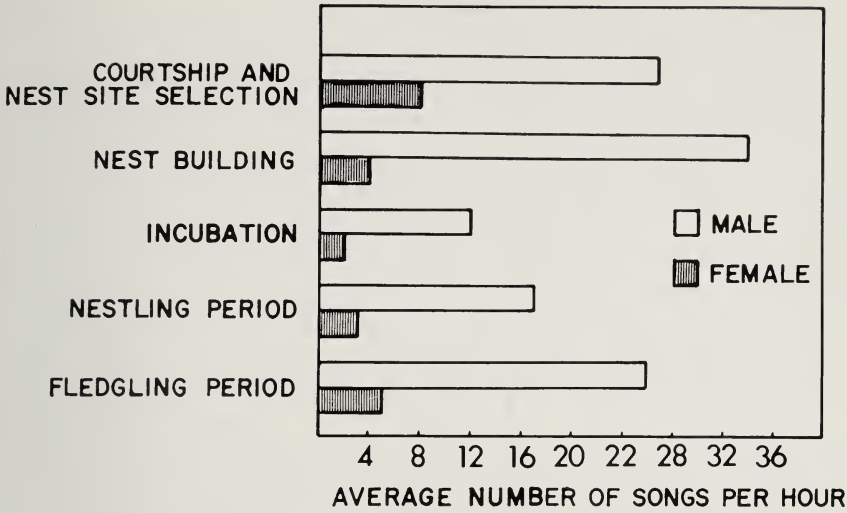

FIG. 3. Average hourly frequencies of songs during the different phases of the breeding cycle.

18:00 and lasted about 20 min. After the morning song period, singing was rather infrequent, except during nest construction. At this time both birds, especially the male, sang frequently throughout the day. Fig. 2 illustrates the average number of songs given by both sexes during a day of nest building. Fig. 3 shows the hourly frequencies of song by both sexes during each phase of the breeding season. During incubation singing was infrequent, except that males often sang once or twice during a nest exchange. The female sometimes sang on the nest in response to a long, excited series of songs and chatter given by the male, and incubating males often responded by singing to the song or chatter of a mate or of an ‘Elepaio in an adjacent territory. The frequency of singing by the parents increased after the young hatched and until they became independent.

When the birds were not breeding, song was rare. Although I did not record daily song frequency during the non-breeding season, I noted that morning and evening singing periods decreased in duration and song frequency in June, increasing again in December each year.

‘Elepaio responded to tape recordings of chatter with chattering and, occasionally, with singing, especially during the breeding season.

TERRITORY AND NESTING HABITAT

‘Elepaio territory should be considered Type A territory (Berger 1961), that is, courtship, copulation, nesting, and feeding occurred within the territory. Territory was defined by the male, although the female's movements, as she was followed by her singing mate, apparently influenced the location of boundaries. This was especially true in cases where the pair had remained together since the last breeding season. Territorial defense, primarily by song, was shared by both sexes, although the male was slightly more ambitious in defense. Territorial encounters usually resulted in pursuit, the defender chasing the intruder chattering excitedly. I observed such territorial encounters more often in the Hawaii ʻElepaio than in the Oahu ʻElepaio. Red-billed Leiothrix (*Leiothrix lutea*) and Japanese White-eye (*Zosterops japonica*) were silently chased from the area within about 8 m of the nest itself, but other species were usually ignored. I saw birds of these species remove material from ʻElepaio nests twice and once, respectively. Seale (1900) found that ʻElepaio often chased larger birds from feeding grounds, and MacCaughey (1919) reported that ʻElepaio engaged in intraspecific chasing that was both territorial and sexual in nature. ʻElepaio were quite disturbed at human intervention into their territory, particularly near the nest. Several times while nest 3 was being photographed with eggs or young in it, the male attacked the photographer, scratching face and arms with its claws, chattering, giving the alarm call, and fluffing its feathers. The female chattered and fluffed her feathers on these occasions.

Fig. 1 illustrates 11 territories occupied by the breeding pairs studied. It shows habitat type and size of each territory. The size of the territory varied from 1.2 to 2.9 ha, averaging 2.0 ha. C. van Riper (pers. comm.) reported territory size of 17 pairs of Hawaii ʻElepaio to range from 0.65 to 1.46 ha averaging 1.08 ha. This difference between average territory sizes may be related to the fact that his work was done in a sparse, savanna-like, dry forest, in contrast to the dense mesic forest of the present study. The shape of the territory appeared to be influenced by the distribution of clearings and unsuitable nesting habitat. Territories included small clearings (< 50 m^2), but never encompassed larger clearings, which provided a natural boundary between pairs (Fig. 1: territories 3, 4, and 5). The same reasoning applied to unsuitable nesting habitat, that is, either *Eucalyptus* sp. or paper bark (*Melaleuca leucadendron*) forest in the study area.

Suitable ʻElepaio nesting habitat consisted of dense, mesic forest with thick undercover. The forest was a mixture of several trees: Java plum (*Eugenia cumini*), kukui (*Aleurites moluccana*), fiddlewood (*Citharexylum spinosum*) and guava (*Psidium guajava*). Undercover included a variety of shrubs and grasses: thimbleberry (*Rubus rosaefolius*), ti plant (*Cordyline terminalis*), and palm grass (*Setaria palmifolia*), as well as tree saplings. This description of habitat applies only to the study area—ʻElepaio habitat varied throughout Oahu.

COURTSHIP AND COPULATION

Courtship began in January, consisting mainly of singing and chasing. As the male established the territory he attracted a female by singing, or repeated pair formation behavior with his mate of the previous year. In the initial phase of pair formation, 2 birds began associating regularly. Later, patterns of vocal interchange became apparent. This started with chipping, and led to loud, frequent, excited chatter, after which one of the pair sang, the other usually responding by singing. As these singing bouts became more frequent, the birds chased each other in a series of short, swift flights. This chasing was the most characteristic part of courtship, was usually initiated by the male, and was always accompanied by excited chatter and usually by song. Chasing bouts lasted from 20–30 sec to several min, sometimes with short feeding breaks.

The single copulation I observed occurred at 07:20 in the morning about 30–60 min before the female of pair 6-67 laid her second egg in nest 8. As the pair was feeding, the female began low-pitched, excited chatter. After about 30 sec of chattering, to which the male responded in like fashion, the female began to follow him as he hopped from branch to branch. She crouched each time she perched, spreading and quivering her wings and lowering her tail. The male eventually mounted. Mounting and copulation took about 5 sec. After copulation both birds chattered briefly, and the male sang twice. They resumed feeding until I left at 08:00. When the nest, which had contained 1 egg at 08:00, was checked at 08:35, it had 2 eggs in it. The single copulation I observed in the Hawaii 'Elepaio suggested that the behavior patterns of the 2 subspecies are essentially the same.

NEST SITE AND NEST CONSTRUCTION

Nest site selection.—After pairing, the birds began to examine prospective nest sites. The female perched in tree forks or on lateral branches among supporting branches. At each stop she chipped or chattered, and exhibited the nest-molding movement (described below) that both birds used later during nest construction to shape the nest cup. During this time the male usually remained within a few meters of his mate, feeding and answering her vocalizations with similar ones. Occasionally he sang and the female answered with song or chatter. When she began the nest molding movement, singing and chattering became very intense and lasted up to 10 min. After the site had apparently been chosen, the pair repeatedly returned to it and exhibited this same behavior. The ultimate point in this nest site selection pattern was the beginning of nest construction by the female.

Nest construction.—Nests were placed in forks or on lateral branches. The former type of placement was the most common: of the 32 nests observed 27

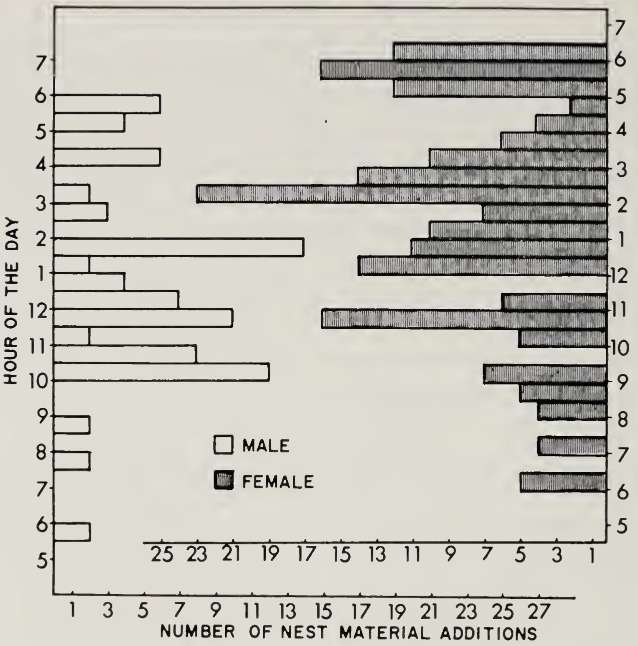

Fig. 4. Number of additions of nest material by both sexes during each hour of the day, during the first week of nest building.

were in forks. Nest height, the distance from the bottom of the nest to the ground directly below the nest, varied considerably. Heights ranged from 2.8 m to 15 m, averaging 7.6 m. Henshaw (1902a) stated that the 'Elepaio habitually nested low. He recorded one nest at less than 0.6 m, but noted that this was unusually low. According to Perkins (1903) nests were placed at heights of 1.8 to 12.2 m.

The nest was built by both sexes, although the female did most of the construction. During the first week of nest building both sexes added material frequently throughout the day. Fig. 4 shows the number of additions of nest material by both sexes during the day. An 'Elepaio often chipped as it worked material into the nest, sometimes singing on the nest or on a perch nearby after the addition. This behavior was especially characteristic of the male, and accounted for the ease with which I often found nests under construction.

'Elepaio used large amounts of spider web and some spider egg cases in the nest. This material strengthened the nest without lending rigidity to it. Web was added with a wiping motion of the head, which served to smooth and shape the outside of the nest. When the nest was nearly complete, the

Table 1

Species of Trees Used as Nest Sites by *Chasiempis sandwichensis gayi*

Species of Tree	Number of Nests in Each Species
Aleurites moluccana (kukui)	4
Citharexylum spinosum (fiddlewood)	7
Eugenia cumini (Java plum)	13
Grevillea robusta (silk oak)	1
Macadamia ternifolia (macadamia)	1
Mangifera indica (mango)	1
Psidium guajava (guava)	5

bird perched in the nest cup, stretched its head out over the edge and used the bill to smooth the entire surface of the nest. The birds shaped the nest cup by sitting in it, erecting the body plumage, and pushing against the surface of the material while shaking the entire body.

Generally the birds did not seem disturbed when I was observing nest building at a distance; however, pair 5-68 deserted nest 27, which was under construction, on the day I spent 2 hours photographing the birds with a strobe light at about 4 m distance.

Most nest construction was complete in a week, although the first egg was usually not laid until about 2 weeks after construction had begun. Small amounts of spider web, lichen, and fine lining material were added during the second week of construction. If the first nest of the season for a pair of 'Elepaio were destroyed or deserted and several days of heavy rains and high winds delayed the construction of a new nest, the new nest was completed and the new clutch laid within 17 days of the date of destruction. In mild weather the time taken to complete the clutch of a renesting was about 11 or 12 days.

The 32 'Elepaio nests I found occurred in 7 species of trees (Table 1). Java plum was the tree most often used as a nest site. All nest trees were introduced species. An analysis of nest 30 revealed that it was composed primarily of the bark of the paper bark tree and the leaves of a grass. The territory from which this nest was taken, territory 5 (Fig. 1), was adjacent to a stand of paper bark trees. The outside of the nest was partly covered with lichen, a liverwort, and the "pulu" (soft, glossy "wool" on the bases of the fronds) of the tree fern (*Cibotium* sp.). The nest was lined with fine rootlets, possibly of a grass, and animal hair. C. van Riper (1977) also found animal hair in Hawaii 'Elepaio nests. I have found leaf skeletons in some nests.

Nest measurements.—Nine of the 11 nests measured had been built in forks, 2 on lateral branches. Average dimensions were: total width, 7.2 cm; total depth, 7.8 cm; cup width 4.6 cm; cup depth, 4.1 cm; wall thickness 1.3 cm. Of previous workers, Bryan (1905) recorded the greatest variations in nest size; he also found more nests placed in upright forks than on lateral branches. Nests reported by Bryan (1905) averaged 7.6 cm in width and height with a cup depth and width of 4.6 cm.

LAYING AND INCUBATION

Eggs and egg laying.—Of the 16 *C. s. gayi* clutches I observed, 15 contained 2 eggs, nest 29 had 3 eggs. Two *C. s. sclateri* clutches I observed had 2 eggs. I have recorded three 2-egg clutches for the Hawaii 'Elepaio and observed 5 pairs of this subspecies feeding 2 young each. Eddinger found eight 2-egg and one 3-egg clutches, and Berger observed 2 pairs feeding 2 young each of the Kauai subspecies (Berger 1972:111). According to Perkins (1903) and MacCaughey (1919) a 2-egg clutch was usual, but Henshaw (1902a) recorded one 3-egg clutch.

The first egg laid in nest 32 was destroyed on the day it was laid, and I broke one of the eggs in nest 14 on the day the second egg was laid. Both pairs of birds began incubating and no more eggs were laid, although the pair at nest 14 deserted (for no obvious reason) 4 days after the second egg was laid. This indicated that 'Elepaio are determinate layers.

The eggs were white with reddish-brown spots concentrated at the larger end (Fig. 5). No eggs were measured in this study, but Newton (1897) reported length to range from 2.1 to 2.2 cm and diameter to be from 1.5 to 1.6 cm. Eddinger measured 2 Kauai 'Elepaio eggs at 2.04 × 1.52 and 2.05 × 1.53 cm (Berger 1972:111). Rothschild (1893–1900) obviously erred in reporting that eggs measured 1.25 by 1.11 in. Such egg dimensions would be truly remarkable for a 16.4 cm passerine bird. Unfortunately this mistake was carried over at least once (MacCaughey 1919).

Eggs were laid on consecutive days, 2 to 3 days after the birds had stopped adding material to the nest. I recorded the approximate time of laying of the first egg in 2 clutches and the exact time of laying of the second egg in 6 clutches. All these eggs were laid between 06:30 and 08:30. The first egg in nest 5 was laid before 07:30 on 20 April 1966, and the second egg between 06:38 and 06:45 on 21 April 1966; thus, the interval between layings was close to 24 h. The earliest observed clutch of a season was completed on 18 February 1966, the latest on 9 May 1966. The median date of completion was 23 March for 12 clutches recorded over 3 years.

The clutch of nest 5 was the latest clutch laid in any year. This nest was deserted apparently because the male, which had begun to molt, did not

FIG. 5. The clutch of nest 5.

incubate. After several days of incubating by herself, the female deserted. Both eggs were fertile. The male came regularly to the nest, as if to incubate, remaining the entire time the female was gone, but did not sit on the eggs. Nest desertion by this pair was probably due to the physiological changes manifested by a decrease in reproductive behavior—to be expected as the breeding season drew to a close.

Incubation.—The first egg in nest 16 was laid on 6 April 1967, the second on the following day. The eggs had not hatched by 08:00 21 April 1967, but were hatched by 17:00 23 April 1967. Thus, the incubation period, as defined by Nice (1953), was between 14 and 16 days. Eddinger recorded the incubation period at 3 Kauai ‘Elepaio nests as 18 days (Berger 1972:111). More incubation period data are needed to clarify the reasons for this subspecific variation, if, indeed it is real. Incubation began immediately after the second egg was laid, and females spent the night on the nest only after laying the second egg. Occasionally a female sat on the nest for short periods, less than a total of 1 h, on the day the first egg was laid. Males and females incubated in shifts, and the eggs were covered almost constantly. Single attentive periods varied from 2 to 44 min. The average attentive period of males was

FIG. 6. ‘Elepaio nestlings at nest 29, approximately 10 days old.

12 min, for females 18 min. For the first 3 days of incubation the attentive periods averaged less than 14 min, but after this became longer. Throughout the incubation period the eggs were incubated 96% of the total time (6 h, 26 min) I observed nests. In most cases, when one bird replaced the other, the eggs were uncovered less than 30 sec. On 3 occasions I saw males of 2 different pairs feed their incubating mates.

CARE OF THE YOUNG

At hatching the nestlings had dark pink skin with a sparse covering of black down on the head and dorsal body surface. The gape was orange, the rictus cream. Fig. 6 is a photograph of the 3 nestlings at nest 28 when they were about 10 days old. When the young were ready to leave the nest their wing, back, and head feathers were dark brown at the base and ochreous at the ends. The underparts were buffy white, and the short tail feathers were dark brown. Fecal sacs of nestlings were white with brownish-black tips. The fledgling’s head was brown and underparts whitish. There were black down feathers scattered about the head and body (Fig. 7).

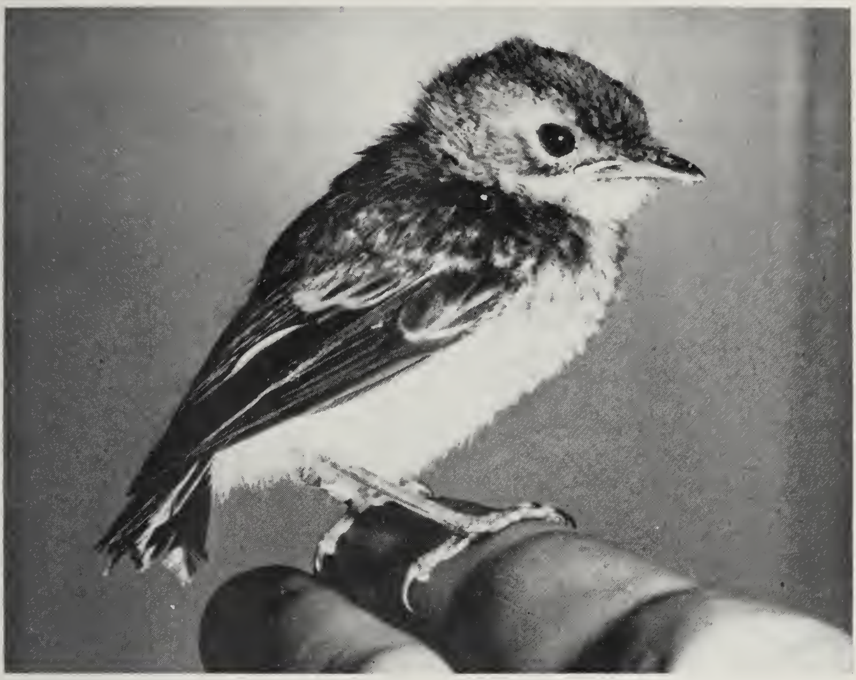

FIG. 7. ‘Elepaio fledgling, approximately 28 days old.

Both parents brooded and fed the young. I observed a pair brooding their day-old nestling for 5 h, 5 min. The nestling was brooded 96% of this time, and the average attentive periods were 18 min for the female and 10 min for the male. During this time the nestling was fed 5 times and the parents brought food to the nest an additional 5 times, but did not feed the nestling, apparently because it did not gape. The male fed his mate 4 times when she was brooding. The nestling died when it was 3 days old, but the adults continued to brood, although the attentive periods rapidly became shorter. Feeding attempts continued until the nestling was missing from the nest 2 days after it died. The 2 nestlings in nest 16 hatched on 21 April 1967 and left the nest on 6 May 1967. The nestling period, as defined by Berger (1961), was 16 days.

During a 69 min period, pair 6-68 at nest 16 fed their two 9-day-old young 23 times at intervals of less than 4 min, and removed 4 fecal sacs. At nest 29, the parents fed 3 young, approximately 10 days old, about 10 times per hour per nestling during 6 h of observation. At each feeding the adults waited, and if a fecal sac was ejected they picked it up, flew away immediately, and swallowed it; they removed about 3 fecal sacs per hour. In 2 other

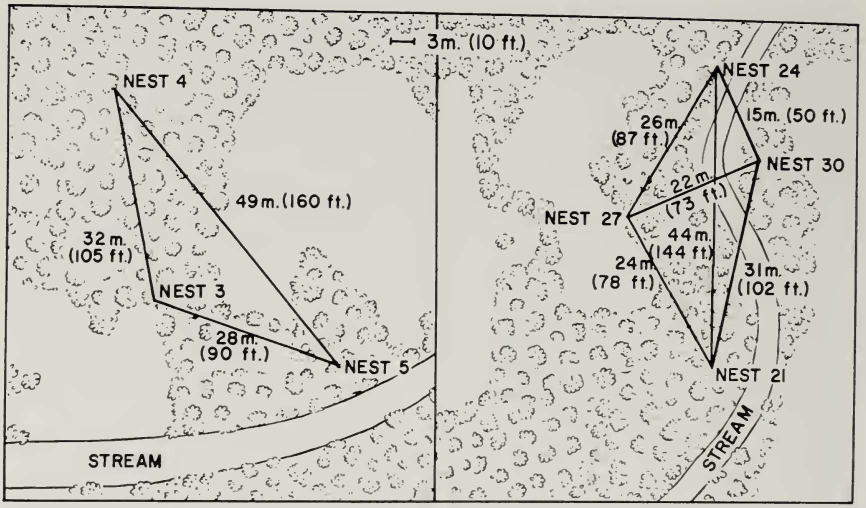

FIG. 8. Diagram of habitat and distance relationships among nestings of pair 1-66 and 5-68. Nests 3, 4, and 5 are those of pair 1-66.

instances I observed 2 adults feed a fledgling 9 times during a 30 min period, and a different pair feed a fledgling once every 7 min for about an hour.

The only previous mention of care of eggs or young was by Rothschild (1893–1900). His collector, Palmer, found a nest on which he collected an adult male that was incubating. Palmer also saw both parents feeding their young.

RENESTING AND NESTING SUCCESS

Most of the pairs I studied renested at least once, first nests having been unsuccessful. In 1966 pair 1-66 renested twice and in 1968 pair 5-68 renested 3 times. Fig. 8 illustrates habitat and distance relationships for the nests of these 2 pairs. Nest dimensions of renestings were similar to those of first nestings, but height, nest habitat, and time taken to build varied.

Because it took a total of about 6 weeks from the beginning of nest construction until the young fledged, and because nesting occurred from February to May, it would have been possible for one pair to raise 2 broods in one season under ideal conditions. Pair 10-68 was feeding fledgings on 4 April 1968, and a pair in territory 10, possibly the same pair, was feeding 2 newly fledged young on 16 May 1968. This suggests that the same pair raised 2 broods in one season.

The total nesting success for 27 nests with 53 eggs was 13%, while hatching success was 29%, and nestling mortality 42%. The figure for hatching success takes into account both infertility and egg destruction. Clearly the egg stage was the most vulnerable: 34 of 53 eggs observed were destroyed before hatching. Rats, which I observed frequently in the study area both before and after dark, may have preyed upon eggs and young.

The low percentages for hatching and nesting success and nestling mortality may not be typical of the entire species. The Oahu ‘Elepaio I studied nested in slender-stemmed trees that bent freely in the wind. The period of high winds and heavy rains, which usually occurred in March, destroyed many nests each year. If the birds had nested in the sturdy native ‘ohi‘a tree, as they often do in areas where native forest remains intact, fewer nests may have lost eggs or young due to tipping by the wind. In Kokee State Park on Kauai, where ‘ohi‘a is in abundance, nesting success seemed to be greater, in that nearly every pair of adult ‘Elepaio I observed was feeding fledglings in June 1967. Four of the 6 ‘Elepaio nests I found at Kokee were in ‘ohi‘a, and Berger (1972) reported that most Kauai ‘Elepaio nests observed were in ‘ohi‘a.

LENGTH OF THE BREEDING SEASON

No author has specified a time duration for the breeding season, although various authors have given all of the months from January through June as breeding months (Bryan and Seale 1901, Bryan 1905, MacCaughey 1919, Richardson and Bowles 1964). There is evidence indicating that each subspecies begins nesting at different times (Berger 1972). In this study, the breeding season of *C. s. gayi* was from mid-January to mid-June. Courtship activities began in mid-January, although males sometimes began territorial singing during the last week of December. Nesting began during the first week of February and continued until May; the last observed young of the season became independent in June.

AGE AT BREEDING

‘Elepaio breed in their first year. A male hatched in nest 16 on 21 April 1967 was banded on 1 May 1967. He began building a nest in territory 5 on 7 February 1968, after forming pair 5-68 with an adult female. The female completed her first clutch of the year on 21 February 1968 in nest 21. This pair renested 3 times without success, and the female completed 2 more clutches. Perkins (1893) and Bryan and Seale (1901) believed that breeding of the species in immature plumage was rare. However, Perkins (1903) reported that birds in immature plumage were breeding, and MacCaughey (1919) stated that ‘Elepaio paired and nested before assuming the adult plumage.

TAXONOMIC RELATIONSHIPS

Comparisons between aspects of the breeding biology of *Chasiempis* and that of other muscicapids (Stead 1932, Barret 1945, Jack 1949, Vaurie 1953, Oliver 1955, Storr 1958, Kirkman and Jourdain 1966) indicate that its breeding biology is similar to all 4 groups of muscicapids (whistlers, typical flycatchers, robins, and monarchs); however, the data gathered in this study indicate that the 'Elepaio probably belongs to the monarchid group, as Mayr (1943) and Amadon (1950) suggested. Specifically, the roles of the sexes in territoriality, nest building, incubation, and care of the young in the 'Elepaio are more similar to this behavior in monarchs than in whistlers, typical flycatchers, or robins. The appearance, constituents, and placement of 'Elepaio nests are similar to those of monarch nests. In addition, the color of 'Elepaio eggs and the plumage of their young most closely resemble the eggs and young of monarchs.

SUMMARY

The breeding biology of *Chasiempis sandwichensis gayi* was studied from November 1965 to May 1968 in Manoa Valley, island of Oahu, Hawaii. Birds bred monogamously from mid-January to mid-June. The phases of courtship were territory establishment, attraction of females by singing males, and chasing. The territory, which averaged 2.0 ha, was defended against other *C. s. gayi*, *Leiothrix lutea*, *and Zosterops japonica* primarily by males. Nesting habitat in the study area was a dense forest of *Eugenia cumini*, *Aleurites moluccana*, *Citharexylum spinosum*, and *Psidium guajava*; whereas, *Eucalyptus* sp. and *Melaleuca leucadendron* forests were suitable for feeding, but not for nesting. There were 4 types of vocalizations: (1) chipping, given during feeding, or by one bird before it replaced the other on the nest to incubate or brood, or as a mild alerting note; (2) chatter, a prelude to song, a low-intensity alarm note, and, in modified form, a food-begging or copulation-solicitation call; (3) song, given by both sexes; (4) the alarm call, a raspy cry, given by the parents when their young were being disturbed or by the young themselves in the same situation. Singing reached peaks of daily frequency during nest building; it was infrequent during incubation, and increased again from the time the young hatched until they were independent. It decreased after May, and resurged in December.

The nest site, selected by the female, was a tree fork or a lateral branch. Nest building, carried out by both sexes, took about 2 weeks. Nests, placed at an average height of 7.9 m were made of spider web, bark, grass leaves, leaf skeletons, lined with rootlets and animal hair, and covered with lichen and liverwort. Nest width averaged 7.2 cm, depth 7.8 cm, cup width 4.6 cm, and cup depth 4.1 cm. Nest dimensions of renestings were similar to those of first nestings, but height, nest habitat, and time taken to build varied.

Eggs were usually laid in clutches of 2, and were white with reddish-brown spots. The eggs were laid before 08:30 with an interval between layings of about 24 h. They were incubated 96% of the day and all night for at least 14 days. Both sexes incubated, brooded and fed young, and sang on the nest. Nine-day-old young were fed an average of 10 times per hour; the nestling period was 16 days.

Total nesting success was 13%; hatching success was 29%; nestling mortality was

42%. Although high winds and heavy rains were the primary causes of nest failure, predation by rats may have been a factor.

Many aspects of *C. s. gayi's* breeding biology indicate that it is related to the monarchid group of muscicapids.

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NEW LIFE MEMBER

Dr. Norman F. Sloan is a new life member of the Wilson Ornithological Society. Dr. Sloan is presently a professor in the Department of Forestry at Michigan Technological University in Houghton. His ornithological interests include avian population dynamics as they relate to biological control of forest insects; he has done considerable work with White Pelicans and also has a research interest in ravens and Peregrines. Dr. Sloan is married and has two children. In addition to belonging to several ornithological societies and other professional organizations, Dr. Sloan has been editor of Inland Bird Banding News since 1970.

LIFE HISTORY FACTORS AFFECTING THE INTRINSIC RATE OF NATURAL INCREASE OF BIRDS OF THE DECIDUOUS FOREST BIOME

Richard Brewer and Lynda Swander

The intrinsic rate of natural increase, r_m, is an important population trait indicating the capacity of a population for growing (Lotka 1925). It is, specifically, the rate of increase per head when the population is suffering no adverse effects from crowding (see Caughley and Birch 1971 for a more complete definition and Cole 1954 and Andrewartha and Birch 1954 for discussion of the concept). A high r_m results from many offspring (in birds, large clutches and multiple broods), low mortality through the reproductive ages, especially through the first reproduction, reproduction at an early age, and a long reproductive life.

MacArthur and Wilson (1967) used the terms r and K selection to designate, respectively, selection occurring in populations living in an uncrowded environment and selection in populations at their carrying capacity (that is, at K). One important contribution of the discussions of r and K selection (Cody 1966; MacArthur 1960; Pianka 1970, 1972; Southwood et al. 1974) was the realization that, contrary to the traditional view, natural selection will not necessarily tend to maximize r_m in populations which are generally at their carrying capacity.

In a series of field studies of the organization of avian communities and life histories of the constituent organisms (such as Brewer 1967 and Robins 1971) differences between communities in life history traits influencing r_m became evident. The purpose of this study was to examine, by a literature survey, life history features bearing on r_m for characteristic birds of different communities of the deciduous forest biome of eastern North America. More specifically, the purpose was to determine whether species of successional communities tended to have traits favoring a high r_m in comparison with species of presumably more stable communities, such as the climax forest.

METHODS

Three basic vegetation types, forest, forest edge, and grassland-marsh, were subdivided as follows: forest into wet, mesic, and dry; forest edge into thicket, trees-shrubs, and open trees; and grassland-marsh into grassland and marsh. Thicket is dense, low, woody growth, generally set in herbaceous vegetation; tree-shrubs is an interspersion of low, woody growth with some trees and usually patches of herbaceous vegetation; open trees is a parkland category with good-sized trees numerous but not forming a closed canopy. After preparation of lists of characteristic native species for each community, life history information was collected. Seventy-five species were used. Several other species breeding in the biome were omitted because we could not locate minimal satisfactory life history information for them. Studies from the part of the biome between about 38° and 44° N latitude were favored; findings obtained elsewhere were ignored unless there seemed reason to believe they were applicable to the middle area of the biome. Features considered were clutch size, number of broods per year, age at first reproduction, presence of non-breeding individuals, and nesting, hatching, and fledging success. For most species included we failed to locate satisfactory information on one or more topics. In cases of conflicting statements we exercised judgment, often based on our own experience with the species, to reject aberrant reports.

The species used, by community, are listed in Appendix I. A complete listing of sources of life history information has not been provided because most are the same as those cited in the various volumes of Life Histories of North American birds by A. C. Bent and in the compilations by Kendeigh (1952), Verner and Willson (1966), and Ricklefs (1969).

Most data were assembled so that significance of differences in a particular trait could be tested between communities using χ^2. In the subsequent text, stated differences are significant at the 5% level. To save space we have not included χ^2 values but the data are presented in such a way that the reader can readily calculate them for himself.

CLUTCH SIZE

Modal clutch size was determined for each species for which satisfactory data were available. For double-brooded species, the first clutch was used. When 2 clutch sizes seemed equally prevalent, the species was counted as half in one category and half in the other.

Modal clutch size in the deciduous forest biome overall is clearly 4 (Table 1) but differences existed among the communities. Confining our attention to open-nesting passerine species (to eliminate 2 obvious additional sources of variation in clutch size), number of eggs is largest in grassland where there are as many species with clutches of 5 as of 4 and smallest in mesic forest where modal size is but 3.

Comparing related birds in different communities tends to confirm the trend of smaller clutches in forest, particularly mesic forest. The 4 species of mesic forest having clutches of 3 are Red-eyed Vireo (Southern 1958), Eastern Wood Pewee (Bendire 1895, Mengel 1965), Acadian Flycatcher (Mumford 1964), and Hooded Warbler (Mengel 1965). Most vireos (Bent 1950) and small flycatchers (Walkinshaw 1966a, b) in other communities of the biome have 4-egg clutches. Other warblers of the biome have 4- or 5-egg clutches (Bent 1953).

Good comparisons within families are fewer for grassland-marsh versus other habitats. The grassland sparrows, nevertheless, seem to have 5 eggs more frequently than do sparrows of forest edge; the Bobolink (Raim 1975) and Eastern Meadowlark (Roseberry and Klimstra, 1970) have 5 eggs whereas the Northern Oriole has 4 (Bendire 1895); and the marsh wrens have larger

TABLE 1

NUMBERS OF SPECIES HAVING A GIVEN MODAL CLUTCH SIZE BY HABITAT (ALL SPECIES AND, SECOND LINE IN EACH HABITAT, OPEN-NESTING PASSERINES)

	Modal Clutch Size[1]										
Habitat	2	3	4	5	6	7	8	9	10	11	15
Mesic forest		4	2.5	2.5	1	1					
		4	2		1						
Wet forest	2		4	2						1	
			4								
Dry forest	2		4	1			1				
			3	1							
All forest	4	4	10.5	5.5	1	1	1			1	
		4	9	1	1						
Grassland		1	3.5	3.5		1					
		1	3.5	3.5		1					
Marsh		1	3	2	1		1	1	1		
			2	1							
Grassland-marsh		2	6.5	5.5	1	1	1	1	1		
		1	5.5	4.5		1					
Thicket			4								1
			4								
Trees-shrubs	1	4	6	4							
		3	6	3							
Open trees		1	4	1	2						
			4								
All forest edge	1	5	14	5	2						1
		3	14	3							
Total, all habitats	5	11	31	16	4	2	2	1	1	1	1
		8	28.5	8.5	1	1					

[1] No species had modal clutch sizes of 1, 12, 13, or 14.

clutches than do House or Carolina wrens (Bent 1948), even though the latter pair are hole-nesters.

NUMBER OF BROODS PER YEAR

The difference between forest and other habitats in the tendency toward multiple broods is striking (Table 2). Forest birds are single-brooded; the regular exceptions are the Wood Thrush (Brackbill 1958), Carolina Wren (Laskey 1948), and Acadian Flycatcher (Walkinshaw 1966c). A high proportion of grassland-marsh and forest-edge birds—probably well over half in both categories—regularly have multiple broods.

TABLE 2
NUMBER OF SPECIES WITH SINGLE OR MULTIPLE BROODS BY HABITAT[1]

Habitat	1 brood	1 brood, sometimes 2	1 brood + 1, sometimes 2	2 or more broods
Mesic forest	3	6	9	2
	2	4	6	2
Wet forest	4	2	6	1
	0	2	2	1
Dry forest	2	3	5	0
	1	2	3	0
All forest	9	11	20	3
	3	8	11	3
Grassland	1	2	3	5
	0	1	1	3
Marsh	1	4	5	3
	0	0	0	0
Grassland-marsh	2	6	8	8
	0	1	1	3
Thicket	0	1	1	4
	0	1	1	3
Trees-shrubs	3	4	7	5
	1	1	2	1
Open trees	2	0	2	4
	0	0	0	4
All forest edge	5	5	10	13
	1	2	3	8
Total, all habitats	16	22	38	24
	4	11	15	14

[1] The category "1 brood, sometimes 2" includes species in which second broods have been reported but are rare and species said to have one brood in the north and two in the south. The first line in each habitat includes all species, the second, species on which information is based on banded populations.

Most species in a family are consistent in being single- or multiple-brooded regardless of habitat; differences between communities, consequently, are mainly the result of differences in the distribution of families among the various communities. Differences within families, when they occur, generally are in the expected direction: although most warblers have only one brood, the Common Yellowthroat (thicket) has 2 (Stewart 1953); most fringillids raise more than one brood but the Rose-breasted Grosbeak (dry forest) raises only one (Forbush 1929 but cf. Rothstein 1973).

NON-BREEDING BIRDS

As Cole (1954) and Lewontin (1965) have demonstrated, the age at which reproduction begins is an extremely influential determinant of r. Although some birds are known to delay reproduction until they are 2 or more years old (Lack 1968:295–305), with a consequent low value for r, most of the birds considered here probably breed as yearlings.

The existence of "surplus" or non-breeding birds is known for several species, including birds of forest, forest edge, grassland, and marsh (e.g., Stewart and Aldrich 1951, Offutt 1965, Ficken 1962, Zimmerman 1963, 1966, Hardy 1961, Kendeigh 1941). Reliable information is not available for enough species to draw conclusions as to differences among the various habitats. Most of the surplus birds detected are males and in a few of the species considered here (such as the Red-winged Blackbird) some or most males regularly delay breeding until their second year. The failure of males to breed would not lower r_m if all females were mated. The failure of females to breed would lower r_m, and markedly if the birds which did not breed were yearlings. Although the percentages of birds of various ages which do not breed is difficult to determine, the topic is one to which more life history studies should address themselves.

For a few species, mostly not those of habitats considered here, age at first breeding is clearly density dependent, being earlier when populations are low (Lack 1968:298). For these species r_m is higher than it would appear to be when based on the age of first reproduction in stable populations.

MATING SYSTEMS

Monogamy is the rule among species of the deciduous forest biome (Table 3). Our compilations agree with Verner and Willson (1966) that regular polygyny is a feature primarily of grassland and marsh.

The influence of polygyny on r_m is not completely obvious. We may consider the situation in which a number of birds greater than the carrying capacity is available to occupy a particular area. If, as often happens, males which fail to gain a mate derive less of their food from the area than those that do (for example, by failing to maintain a territory through the whole breeding season; Ficken 1962), then polygyny will increase r_m by substituting females for males as members of the population existing on the limited resources.

This implies that polygyny might raise r_m for birds living at K but would be unlikely to do so for birds under uncrowded conditions. It has been suggested (Verner 1964, Orians 1969) that selection for polygyny occurs where resources important for nesting are patchily distributed such that polygamous

TABLE 3

NUMBER OF MONOGAMOUS AND POLYGYNOUS SPECIES BY HABITAT[1]

Habitat	Monogamous	Monogamous with exceptions	Monogamous + monogamous with exceptions	Polygynous
Mesic forest	7	2	9	0
Wet forest	3	3	6	0
Dry forest	4	1	5	0
All forest	14	6	20	0
Grassland	4	0	4	4
Marsh	1	0	1	3
Grassland-marsh	5	0	5	7
Thicket	2	2	4	0
Trees-shrubs	12	0	12	1
Open trees	3	3	6	1
All forest edge	17	5	22	2
Total, all habitats	36	11	47	9

[1] The category "Monogamous with exceptions" includes normally monogamous species for which any incident of polygyny has been reported.

females on good territories are more successful than monogamous ones on poor territories. This hypothesis of the evolution of polygyny depends on local populations being at K; at population sizes which were low relative to K, sufficient favorable habitat would be available that all males could establish themselves in suitable sites and monogamous females presumably would be more successful than polygamous ones (because of the greater participation of the male in nest building, feeding young, etc., Martin 1974).

OTHER FACTORS INFLUENCING r_m

For 2 species otherwise similar, the one producing more eggs in its first year has a higher r_m and this is true even if the other species later has an increased number of eggs so that the lifetime egg production is the same (Lewontin 1965). Some changes in number of eggs laid with age occur (Ricklefs 1973:368, van Balen 1973) but how important they are and whether there is a difference among habitats are unknown.

The pattern of survivorship of birds under uncrowded conditions is another trait influential in determining r_m but poorly known. Survival to the first breeding season is, of course, particularly important. Information on survival to fledging is available for many species and some comments on this time period are given beyond; however, the period from fledging to first nesting is difficult to study owing to its being the main time of dispersal in birds. Also, differential mortality in this period is probably of importance in population limitation; consequently, the mortality figures for stable populations will be higher than under uncrowded conditions and will be of little value for comparisons designed to evaluate r_m.

ESTIMATES OF r_m

It is worth dealing with some numerical examples to help visualize the effects of some of these life history features on r_m. Uncrowded survivorship/maternity data for a real calculation of r_m do not exist for any bird as far as we know. For the following calculations we tried to use mortality values that would be realistic for a small altricial bird in an uncrowded environment. The assumed mortality rates were 15.5% from egg-laying to hatching (15 days), 7.5% for the nestling period (10 days), 40% per annum from fledging to the age of 12 months, and 35% per annum past this age. Potential natural longevity was assumed to be 10 years.

The same survivorship schedule was used throughout. The maternity schedule was varied to include clutch sizes of 1–8 eggs and 1–3 broods per year. Egg laying was assumed to begin at 12 months of age for all birds in single-brooded species and for birds of first broods in multiple-brooded species but at 11 months for birds produced in second broods and at 10 months for third broods. Also, a one-year delay (first breeding at 24 months for single-brooded species) was examined for several clutch-brood combinations. Calculation of r was iterative, using the formula (Lotka 1925)

$$1 = \sum_{x=0}^{\infty} l_x \, m_x \, e^{-r_m x}$$

where l_x is survival rate at age x, m_x is natality rate at age x, and e is the base of natural logarithms (see Birch 1948 for additional details of calculations).

Although we believe that the survivorship-natality model and the values used are realistic, some simplifications are involved (Ricklefs 1973:394–396). We think that these do not impair the model's usefulness for examining the relative effects on r_m of the various maternity schedules.

The results (Fig. 1) suggest that r_m for mesic forest species (if represented by 1 clutch of 3 eggs per year) may be only about ¼ that of grassland species (if represented by 3 clutches of 4 eggs per year). The importance of this difference for population growth is more easily grasped when translated into population figures. If a male and a female of 2 species arrive on an island of favorable habitat and one species undergoes population growth such that

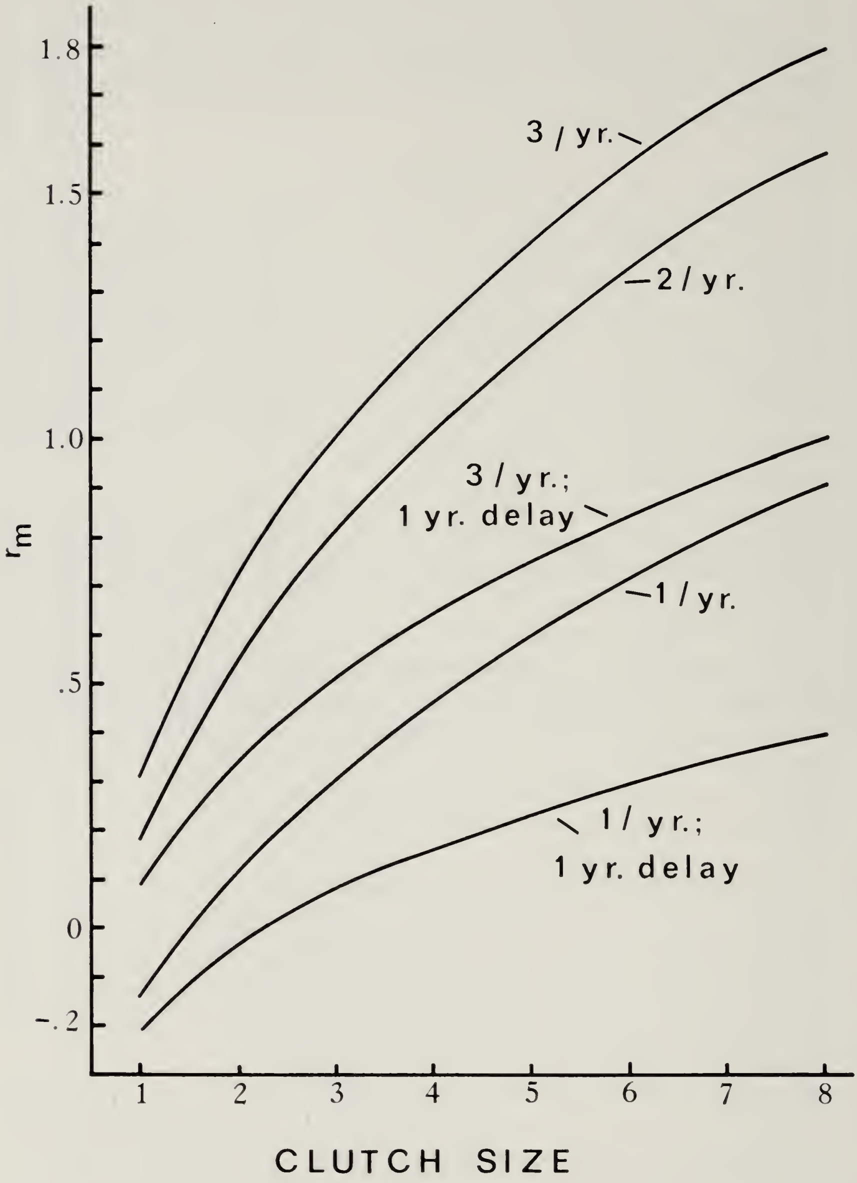

FIG. 1. Values of r_m (per head per year) for birds having clutch sizes of 1 to 8 and 1–3 broods per year (mortality schedules as described in text).

r is .3 per head per year and the other such that r is 1.2 (Fig. 1), the population size at the end of some period (t) during which the environment remains uncrowded is given by the expression for exponential population growth

$$N_t = N_o e^{rt}$$

If we take t as 3 years, then the population of the species with the r of .3 is, at the end of 3 years, 3 or 4 birds. The population of the species with the r of 1.2 is over 70 birds.

Certain other features in Fig. 1 are worth pointing out. As has been mentioned, age at first breeding is extremely important. A bird which lays a clutch of 8 eggs but delays breeding until 2 years of age has an r_m well below that of a bird which lays a clutch of 4 eggs but begins breeding at age 1 (Fig. 1). Delaying reproduction by a year reduces r_m proportionately less for small clutches than for large but only birds with considerably lower mortality than that assumed in the model could adopt a life history of delayed breeding if their clutch size was 1 or 2; r_m in both these situations is negative. Finally, the assumed survival rates are not high enough to allow a bird such as the Passenger Pigeon (which was, of course, a mesic forest species) to exist; r_m is negative for a bird laying a single 1-egg clutch per year.

If, as we believe, the estimates of r_m in Fig. 1 are in the right neighborhood, they indicate that r_m for birds is low in relation to other animals of comparable size (e.g., Leslie and Ransom 1940, Leslie 1945). The main reason is the periodic nature of avian reproduction. Birds of temperate regions have little opportunity for raising r_m by lowering age of first reproduction below one year; the opportunity does exist for some tropical species and a few have taken it (Cody 1971:468). Most tropical birds, however, breed at about one year, have some sort of annual cycle of reproduction (Immelmann 1971) and, owing particularly to their small clutches (Ricklefs 1973), probably have low values of r_m.

DISCUSSION

It has been postulated that r selection should occur in organisms of temporary or unstable ecosystems; species would be fitted to such environments if they could "(1) discover the habitat quickly, (2) reproduce rapidly to use up the resources before other, competing species could exploit the habitat, and (3) disperse in search of other new habitats as the existing one began to grow unfavorable" (Wilson and Bossert 1971:110). In stable environments (Wilson and Bossert mention climax forest, coral reefs, and caves) "no longer is it very advantageous to have a high r. It is more important for genotypes to confer competitive ability, in particular the capacity to seize and to hold a piece of the environment and to extract the energy produced by it."

TABLE 4
SUMMARY OF LIFE HISTORY TRAITS AFFECTING r_m BY HABITAT

Trait	Habitat Mesic forest	 Other forest	 Grassland marsh	 Forest edge
Clutch size	low	medium	**high**[1]	medium
Number of broods	single	single	**multiple**	**multiple**
Mating systems	monogamy	monogamy	**polygyny frequent**	polygyny infrequent
Non-breeding females, uncrowded changes in clutch size or number of broods with age	?	?	?	?

[1] Traits favoring a high r_m are shown in boldface.

Our compilations indicate that birds of forest, especially mesic forest which is generally climax, tend to have life history traits favoring a low r_m (Table 4). Birds of forest edge and, especially, grassland and marsh tend to have traits favoring a high r_m. We address, first, the question of whether forest represents a K-selecting environment and grassland, marsh, and edge, r-selecting environments and, later, the question of whether the low r_m of forest birds is, or is not, maximal.

Are breeding-bird populations at carrying capacity?—By the Clementsian criterion of potential replaceability (Clements 1916) all of the ecosystems discussed except mesic forest are successional and, in this sense, temporary. The actual period of existence of a particular stand may vary from a few years for some pioneer herbaceous communities to thousands of years for some marshes and forests. For some kinds of organisms some of these habitats may be uncrowded for a significant period after establishment but we think this is not true for birds. We know of no studies of newly created grassland showing population growth curves for any bird species unrelated to successional changes in vegetation. In studying a new alfalfa field Harrison (1974) found the same species in almost the same numbers in the first full year of its existence (following planting the preceding year) as in its second. The high dispersal powers of birds in conjunction with habitat selection presumably account for the virtually immediate occupancy at carrying capacity of newly created habitats.

We believe that the characteristic birds of all of these habitats tend to be near K. The existence of surplus birds in various life history studies and in the studies of Stewart and Aldrich (1951) and Hensley and Cope (1951) suggest K conditions. Further, in those 2 studies, the re-establishment of most species in 1950 in about the same numbers as 1949, despite the almost complete annihilation of the 1949 resident population and the failure of the plot to produce any fledglings (3 species excepted) suggest that these numbers represent carrying capacities. Experiments in which nest-boxes have been added to habitats (cited in von Haartman 1971:401–404) have produced larger breeding populations of both migratory and sedentary species.

The studies mentioned in the preceding paragraph deal mostly with forest species but surplus birds are known in marsh and forest edge (e.g. Kendeigh 1941, Nero 1956). The correlation of numbers of Red-winged Blackbirds with breeding site favorability reported by Davis and Peek (1972) suggests K conditions. As we have already pointed out, polygyny, common only in grassland and marsh, is not an adaptation to uncrowded conditions.

In the next section we present evidence that grassland species frequently do not occupy every area that seems to be suitable habitat. This may seem contradictory to the conclusion just reached but local populations and regional (or whole-species) populations must be considered separately. Birds tend to be at or near K in examples of their optimal habitat because of their tendency to occupy habitats according to their suitability (Fretwell 1972). Even if some additional field, marsh, or forest exists which could support the species, the slightly suboptimal habitat tends not to be occupied (disregarding the effects of site tenacity and sociability which are complicating factors for some species) if the regional population of the species is low (cf. Svärdson 1949, Brown 1969).

Consequences of low habitat stability in grassland and marsh.—We suggest that a feature important in selection for life history traits affecting r_m by which forest and grassland-marsh differ is stability (cf. Wilbur et al. 1974). Grasslands and marshes may show drastic differences from year to year, or even within years, even though successional changes are occurring slowly, if at all. The classic study of vegetational fluctuation (sensu Hanson and Churchill 1961) is of the Nebraska grasslands during the great drought of the 1930's (e.g. Weaver 1961). Such fluctuations presumably affect K for the bird populations, both by altering the structure of the vegetation and by changing the kinds and amounts of food. Changes of similar magnitude occur in marshes (Weller and Spatcher 1965). Vegetational fluctuations have rarely been reported for forest. This is at least partly because of the buffering effect of the greater perennial biomass of forest and possibly also a greater capacity for integrating environmental fluctuations (e.g., by leaf production being based partly on energy stored in preceding years). Ricklefs (1969) has suggested that the high starvation component of nestling mortality of birds of field and marsh indicates that the food supply in these habitats is more variable than in forest and edge.

Fluctuations in avian populations in marshes were studied by Weller and Spatcher (1965). Their study began with the marshes nearly dry and continued into a wet period in which much of the vegetation was inundated. Bird populations changed drastically; for example, Least Bittern nests at one marsh rose from 5 in 1958 to 62 in 1961 and dropped to 2 the following year (Weller and Spatcher 1965: Table 4).

Reports of fluctuations in density of grassland species are numerous. Wiens (1974:397), in a paper which develops the theme of instability in climax grassland, cited large population changes in bird numbers on a Texas grassland during drought. Most reports are not quantitative but consist of remarks about the "local and erratic" occurrence of the species, implying that not all seemingly suitable areas are occupied every year and that abundance at a given site varies greatly from year to year. Some typical citations are Barrows (1912), Pough (1946), Smith (1963), Bull (1964), and Mengel (1965) for the Dickcissel, Short-billed Marsh Wren, Grasshopper Sparrow, Henslow's Sparrow, and Lark Sparrow, respectively.

Our own observations on grassland birds and several accounts in the literature (Nero 1956, Smith 1963, Robins 1971, Potter 1972, Raim 1975) suggest a shifting pattern of occupancy, including shifts in territory locations and changes in population size, even within a breeding season. A forest-edge species for which large-scale territory shifts have been reported is the Gray Catbird (Darley et al. 1971). Comparable changes between breeding seasons and, especially, within the season are difficult to find in the literature for forest species. Populations of the more common species on a given area vary little from year to year (Brewer 1963). The whole breeding population apparently arrives within a few days and the arrival of a new male thereafter is a rare event (e.g., Hann 1937).

We suggest that grassland or marsh that remains stable tends to support populations around K. Because of habitat fluctuations altering K, populations fairly frequently find themselves overcrowded or undercrowded. The shifting pattern of occupancy of grassland birds can be best understood as movements into and out of areas as suitability changes. Areas which, in fact, show large swings in numbers with essentially no change in vegetational or other environmental conditions are usually suboptimal for the species in question, occupied mainly by the overflow, large, small, or none, from more nearly optimal areas (cf. Kluyver and Tinbergen 1953, Brewer 1963, 1967, Fretwell 1972).

We presume that the main source of additional birds, when grassland populations build up over the course of the breeding season, is from nearby areas abandoned as unsuitable; however, this may not be the only source. It is possible, for example, that some of these species have an unusually long period over which they return from winter quarters.

Although we suspect that grassland birds have evolved a more flexible system of habitat occupancy than forest birds, it is possible that forest birds if presented with habitat changes of comparable magnitude might also show a more shifting pattern. Kluyver (1951), for example, was able to cause adult Great Tits, *Parus major*, to abandon an area by plugging all the nest holes. When about half of a 10 ha spruce forest was blown down by hurricanes between breeding seasons (Cruickshank and Cadbury 1954, 1955) nesting Golden-crowned Kinglets, *Regulus satrapa*, decreased from 8 to 1; however, several spruce forest warblers showed no significant decline.

Wilson and Bossert (1971) mentioned the abilities to discover habitat quickly and to disperse in search of new areas as the existing one began to grow unfavorable as traits to be selected for in species of temporary habitats. These traits are related to a high r_m only to the degree that a high r_m favors greater or more effective dispersal. For most organisms, increasing offspring is a poor way of increasing distant dispersal. This is because the number of dispersing units, or disseminules, reaching a given distance tends to be directly proportional to the number produced (e.g., Kettle 1951, Andrewartha and Birch 1954:103). Consequently, committing the resources necessary to double production of offspring merely doubles whatever small fraction of an individual is expected to reach some distant site. Because an exponential relationship tends to exist between dispersal ability and the number of disseminules reaching a particular distance, increasing dispersal ability is a more efficient way of achieving increased dispersal.

For birds (and some other kinds of organisms; Johnston 1961, French 1971), the pattern of dispersal is complex, with more individuals reaching greater distances than would be expected. Birds as different as the Song Sparrow (Johnston 1956) and the Pied Flycatcher, *Ficedula hypoleuca*, (Berndt and Sternberg 1968) have a basically similar dispersal pattern. Murray (1967) showed that this pattern could be reproduced by a model making the assumptions that dispersal is by sub-adults, the adults returning to their previous breeding site where they are dominant to sub-adults; that the first subadult to reach an unoccupied site is dominant to subsequent arrivals; and, an important implicit assumption, that the environment is patchy such that individuals that leave the modeled habitat rarely settle on an immediately adjacent site but instead go some appreciable distance. These assumptions seem realistic for birds (Murray 1967; see also Pinowski 1965).

Murray further found that increasing survival of young to breeding age from 23% to 62% increased the number of young settling near their natal site slightly but greatly increased the number of young leaving the area. It seems possible, then, that a high production of offspring, in fact, increases dispersal. The major affect is probably increased dispersal ability as a result of intraspecific antagonism.

Although this paper deals primarily with life history traits affecting r_m, this is just one aspect of the broader question of the adjustment of life histories to ecosystems. There are too few detailed studies to judge whether birds of different habitats differ in dispersal pattern. One behavioral feature, however, that could increase dispersal ability, including the ability to leave an unfavorable area for a favorable one in the middle of the summer, exists in at least 2 grassland birds. In the Bobolink (Raim 1975) males throughout the breeding season take long flights in which they leave the breeding area; often they fly out of sight and may be gone for many minutes. Suitable areas could be found on such flights, either for switching locations in the same breeding season or for possible occupancy in a later one. Similar "distant flights" also occur in the Dickcissel (Schartz and Zimmerman 1971).

The foregoing discussion would suggest that site tenacity (except on optimal sites) ought to be low in grassland and marsh and this seems often to be the case; however, males of one of the most characteristic marsh species, the Red-winged Blackbird, are known to show strong site tenacity (Nero 1956). Davis and Peek (1972) described a situation in which the number of territorial males (apparently not individually marked) varied in one marsh only between 17 and 21 during an 8-year period that included a drought. The number of females in the same period varied from 7 to 42. Surplus females are rare or absent in the species (Orians 1969) so many of the females presumably shifted to other areas where males were occupying more favorable habitat. This suggests that polygyny is, in effect, an exceedingly flexible method of maintaining a high r_m where short-term fluctuations are common. The evolution of such a system is explainable by individual selection: females having the ability to shift would probably leave more offspring than if they remained in a deteriorating habitat; males, on the other hand, might well contribute more to the next generation if they stayed put rather than trying to establish themselves in a strange area, often in competition with other, already-established, males. These disadvantages may help to explain the higher site tenacity of male birds generally; however, except in polygynous species, the result of some males occupying territories unacceptable to females might be to leave some females unmated, lowering r_m.

Does the low r_m of forest birds represent K selection?—The alternative to K selection, in explaining the low r_m of forest birds, is that, low or not, it is the best they can do. The most common version of this idea is Lack's view of the evolution of clutch size (or what might be called the "I can scarce maintain two" hypothesis after the ancient nursery rhyme that goes [Opie and Opie 1951]: The dove says coo coo, what shall I do?/ I can scarce maintain two. pooh, pooh, says the wren, I have got ten,/ and keep them all like gentlemen). In its simplest form, this hypothesis states that "in species in which parents feed their young, clutch size corresponds to that brood-size from which the parents can, on average, raise most young, the limit being set by the amount of food which they can collect for them" (Lack 1968:307). Following Lack's line of reasoning for number of broods per season would suggest that every bird raises as many broods as it can; the single brood of forest birds results from the period in which the food supply is sufficient for raising young being too short for another brood.

There is no reason, for birds living generally under carrying capacity conditions, that clutch size or number of broods must be selected for in this way (although under r-selecting conditions they should be). Neither, however, is selection against a high r_m under K-selecting conditions inevitable. For the genotype with fewer eggs or fewer broods to have the advantage over ones with more, the first must use savings of time or energy from the decreased birthrate to enhance its changes for recruitment into the breeding population above those of the second (cf. Cody 1966; Fretwell 1969). Some of the ways in which this might be achieved would be by improved parental care that brought a larger fraction of the young through the vulnerable egg-nestling stage, by increased ability to locate appropriate territorial sites and to establish and defend territories, and by increased ability to escape death from predation, parasitism, and disease. If the low r_m of forest birds represents K selection the saving of time or energy, or its result, should be detectable in comparisons with related species of different habitats.

In comparisons not presented here we examined, first, various measures of nesting success. Nesting success is clearly higher in forest than in grassland-marsh (see Ricklefs 1969: Table 5); however, nesting success of forest-edge species is at least as good as forest species. Consequently, it is difficult to conclude that the higher success of forest species vs. grassland-marsh is the result of diversion of resources which would otherwise have been used in maintaining a high r_m.

We also compared birds of the various habitats as to egg size (relative to body size) and length of incubation and nestling periods. We detected no consistent differences in forest birds compared with their non-forest relatives. It is, however, true that differences need not be consistent from one species to another: the savings of time or energy might be used differently by different species. For example, most members of the Tyrannidae in eastern North America delay molting until they reach the wintering grounds, unlike most passerines which molt prior to fall migration. A lack of time or energy or both may tend to preclude molt prior to migration (Morehouse and Brewer 1968). We suggest that the ability of the Great Crested and Acadian flycatchers to molt prior to migration is related to their inhabiting mesic forest. (We note, further, that the other North American tyrannid which molts before migration, the Eastern Phoebe, *Sayornis phoebe*, is probably K-selected. Although it occurs in a variety of habitats, it depended for nesting, under primeval conditions, largely on rock ledges which were probably stable in terms of appearance and disappearance.)

Historical factors.—Many forest-edge species appear to have high values of r_m yet forest-edge habitats do not show obvious vegetational fluctuations and may be long-lived (Niering and Egler 1955). The forest-edge group is, of course, heterogeneous. Particular species may have life history features favoring either a high or a low r_m (e.g., Am. Goldfinch vs. Eastern Kingbird). Probably finer habitat subdivisions leading, ultimately, to a consideration of the different circumstances of every species would help to reconcile these differences (as would be true also for forest, grassland and marsh).

Additionally, historical factors may be important. The deciduous forest biome has undergone many changes during the Quaternary (Kendeigh 1974: 303–310); however, the period from around 8000 years ago until the arrival of European man was one of relative stability. In this period many forest birds must have been common and many grassland and forest-edge birds rare. Much of the habitat for forest-edge species may have been along rivers which, owing to flooding, probably was unstable. Many other suitable sites, such as areas of wind-thrown trees, must have been isolated and transient. Such conditions might have favored a high r_m.

The period from around 1650 to 1850 and a little later, in which man altered the landscape on a large scale, must have seen populations of forest-edge and grassland birds increase enormously. Whether or not local breeding populations were at K, the increasing amounts of habitat could have provided r-selecting conditions for many forest-edge and grassland species during this period. At some point, winter limitation of the size of the species populations might have become important (Fretwell 1972). It is conceivable that at least a part of the failure of some grassland species to occupy all seemingly suitable breeding sites results from limitation of total population size on the wintering grounds. At the same time total populations of forest species must have shrunk greatly. Unless large changes in competitive relations occurred, it seems unlikely that most migratory forest species have been winter-limited. This situation may, of course, be changing with the heavy destruction of natural habitats that has recently occurred in the American tropics.

SUMMARY

Forest birds, especially those of mesic forest, have life history traits favoring a lower intrinsic rate of natural increase (r_m) than do birds of grassland, marsh, or forest edge. Specifically, forest birds tend to have smaller clutches than birds of grassland or marsh; several mesic forest species typically have clutches of only three eggs. Almost no forest species are regularly double-brooded but a high percentage of grassland, marsh, and forest-edge species have two or more broods per season.

Forests can probably be thought of as K-selecting environments. Grassland and marsh probably are not, specifically because vegetational fluctuations make particular areas unpredictably uncrowded or overcrowded. Probably because of these fluctuations (and consequent changes of K) grassland birds show a more flexible pattern of occupancy, even within a breeding season, than do forest birds. Polygyny may be a particularly powerful method of maintaining a high r_m where short-term fluctuations are common.

Probably one advantage of a high production of young in unstable environments is enhanced dispersal. The main effect seems to be through increased dispersal ability because of increased intraspecific antagonism.

The low r_m of forest birds may be partly the result of natural selection diverting resources from reproduction to other traits more advantageous for organisms living continually around their carrying capacity; however, a conclusion to this effect should await a demonstration of what activities that time or energy otherwise used in reproduction is being diverted to. This demonstration may be difficult because the diversion may be to different activities in different species. The alternative explanation, that r_m in the various habitats is a reflection of the amount of available energy and the time over which it is available, deserves continued attention.

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APPENDIX I

Bird species assigned to each habitat:

Mesic Forest: *Melanerpes carolinus*, Red-bellied Woodpecker; *Picoides pubescens*, Downy Woodpecker; *Myiarchus crinitus*, Great Crested Flycatcher; *Empidonax virescens*, Acadian Flycatcher; *Contopus virens*, Eastern Wood Pewee; *Parus atricapillus*, Black-capped Chickadee; *Parus bicolor*, Tufted Titmouse; *Hylocichla mustelina*, Wood Thrush; *Vireo olivaceus*, Red-eyed Vireo; *Dendroica cerulea*, Cerulean Warbler; *Wilsonia citrina*, Hooded Warbler.

Wet Forest: *Aix sponsa*, Wood Duck; *Strix varia*, Barred Owl; *Caprimulgus carolinensis*, Chuck-will's-widow; *Thryothorus ludovicianus*, Carolina Wren; *Catharus fuscescens*, Veery; *Polioptila caerulea*, Blue-gray Gnatcatcher; *Parula americana*, Northern Parula; *Protonotaria citrea*, Prothonotary Warbler; *Setophaga ruticilla*, American Redstart.

Dry Forest: *Bubo virginianus*, Great Horned Owl; *Caprimulgus vociferus*, Whip-poor-will; *Picoides villosus*, Hairy Woodpecker; *Sitta carolinensis*, White-breasted Nuthatch; *Mniotilta varia*, Black-and-white Warbler; *Seiurus aurocapillus*, Ovenbird; *Piranga olivacea*, Scarlet Tanager; *Pheucticus ludovicianus*, Rose-breasted Grosbeak.

Grassland: *Eremophila alpestris*, Horned Lark; *Cistothorus platensis*, Short-billed Marsh Wren; *Dolichonyx oryzivorus*, Bobolink; *Sturnella magna*, Eastern Meadowlark; *Spiza americana*, Dickcissel; *Passerculus sandwichensis*, Savannah Sparrow; *Ammodramus savannarum*, Grasshopper Sparrow; *Ammodramus henslowii*, Henslow's Sparrow; *Pooecetes gramineus*, Vesper Sparrow.

Marsh: *Podilymbus podiceps*, Pied-billed Grebe; *Ixobrychus exilis*, Least Bittern; *Botaurus lentiginosus*, American Bittern; *Anas platyrhynchos*, Mallard; *Rallus limicola*, Virginia Rail; *Porzana carolina*, Sora; *Chilidonias niger*, Black Tern; *Telmatodytes palustris*, Long-billed Marsh Wren; *Agelaius phoeniceus*, Red-winged Blackbird; *Melospiza georgiana*, Swamp Sparrow.

Thicket: *Colinus virginianus*, Bobwhite; *Dumetella carolinensis*, Gray Catbird; *Geothylpis trichas*, Common Yellowthroat; *Spizella pusilla*, Field Sparrow; *Melospiza melodia*, Song Sparrow.

Trees-shrubs: *Butorides striatus*, Green Heron; *Zenaida macroura*, Mourning Dove; *Coccyzus americanus*, Yellow-billed Cuckoo; *Tyrannus tyrannus*, Eastern Kingbird; *Empidonax traillii*, Willow Flycatcher; *Cyanocitta cristata*, Blue Jay; *Toxostoma rufum*, Brown Thrasher; *Vireo griseus*, White-eyed Vireo; *Vermivora pinus*, Blue-winged Warbler; *Den-*

droica petechia, Yellow Warbler; *Dendroica pensylvanica*, Chestnut-sided Warbler; *Cardinalis cardinalis*, Cardinal; *Passerina cyanea*, Indigo Bunting; *Carduelis tristis*, American Goldfinch; *Pipilo erythrophthalmus*, Rufous-sided Towhee.

Open trees: *Coccyzus erythrophthalmus*, Black-billed Cuckoo; *Colaptes auratus*, Common Flicker; *Troglodytes aedon*, House Wren; *Turdus migratorius*, American Robin; *Sialia sialis*, Eastern Bluebird; *Vireo gilvus*, Warbling Vireo; *Icterus galbula*, Northern Oriole; *Spizella passerina*, Chipping Sparrow.

NEW LIFE MEMBER

Mr. William W. Cole, Jr. is a new life member of the Wilson Ornithological Society. Professionally Mr. Cole has been a management consultant in the materials control field, although presently he is processing manager for a centrifugal pump manufacturer. He has been an amateur ornithologist since youth and has quite an extensive library of both books and periodicals. Mr. Cole conducts an ornithological thematic stamp business on the side and for the past year and one-half has been involved in preparing the rough draft of a comprehensive catalog of bird topical stamps of the world. He is married with twin daughters and in addition to his work and catalog project he enjoys tennis and classical music.

NESTING HABITAT OF COMMON RAVENS IN VIRGINIA

Robert G. Hooper

The Common Raven (*Corvus corax*) inhabits a region 80–160 km wide extending along the Appalachian Mountains from northern Georgia to northern Pennsylvania. The raven is generally described in the regional literature as a wary species that avoids man and his activities by nesting on cliffs in remote mountainous areas at high elevations (Harlow 1922, Murray 1949, Stupka 1963:101–103, and others). A species with these characteristics could be seriously disadvantaged by intensive use of the southern Appalachians for recreation and raw materials. This study was conducted to better define the ecological latitude in which the raven exists in a portion of the southern Appalachians.

STUDY AREA AND METHODS

Study area.—The study was conducted northwest of Radford, Salem, and Lexington, and southeast of the West Virginia state line. Quartzite cliffs occur on ridges and in water gaps. Shale cliffs are usually adjacent to streams. Limestones and dolomites form bluffs on the Maury and New rivers. Valley elevations are 275–305 m on the James River and 470–538 m on the New River, while ridges rise to 1318 m above sea level. Over 85% of the study area is forest and the remainder is pasture and urban area. Mountain slopes are forested with mixtures of oaks (*Quercus* spp.) and other hardwoods. Xeric ridges are covered in Virginia, Table Mountain and pitch pine (*Pinus virginiana*, *P. pungens*, and *P. rigida*). Mesic ravines are forested with hemlock (*Tsuga canadensis*), white pine (*P. strobus*), yellow poplar (*Liriodendron tulipifera*), and other hardwoods (Braun 1967:225–242).

The 7000 km^2 study area has a population approaching 20 people per km^2. Areas of 10–25 km^2 with less than 1 person per km^2 are scattered throughout. A 2000 km^2 strip adjacent to the southeastern boundary supports over 90 people per km^2.

Ravens have inhabited the study area continuously since pre-Columbian times but no data exist on past abundance. A 518 km^2 segment of the study area had 1 active nest per 30.6 km^2 (Hooper et al. 1975). I consider this to be a moderate density based on densities in Britain of up to 1 nest per 17.1 km^2 (Ratcliffe 1962).

Methods.—I searched for raven nests during March and April of 1972 to 1974. Nest building began in late January, and most nests had eggs by 8 March. Nestlings fledged in late April and early May. From 2 to 6 visits were made to each nest site to determine if it was active and the number of young fledged. Nestlings that lacked visible sheaths on their contour feathers as the birds sat in the nest fledged in less than 7 days and were at least 35 days old. I considered birds that reached this stage of development as "fledged." Dorn (1972) found nestling periods in Wyoming to be 39–45 days.

Twenty-eight territories were found. Because birds in 13 territories used alternate nest sites in different years, 41 nest sites were found. I determined the outcome of nesting attempts in 5 territories during all 3 years, in 10 territories during 2 years, and in 9 territories in only 1 year.

TABLE 1

PRODUCTIVITY OF RAVEN NESTS IN RELATION TO ALTITUDE AND ROADS

Altitude or Distance	Total Nest Attempts	% Success	Number Fledged				Mean Number Fledged	p[a]
			1	2	3	4		
			(% Successful Nests)					
Altitude								
<580 m	19	68.4	0.0	23.1	46.2	30.8	3.08	.001
≥ 580 m	25	64.0	31.0	25.0	18.8	25.0	2.37	
Distance to Road								
$<.4$ km	23	73.9	11.8	17.6	41.2	29.4	2.88	$>.05$[b]
$\geq .4$ km	21	57.1	25.0	41.7	16.7	16.7	2.25	

[a] $P \leq .05$ was considered significant.

[b] Tabular $U = 64$ and calculated $U = 66.5$.

The Mann-Whitney U-test was used to evaluate differences among and between means (Siegel 1956). Values for U with probabilities less than .05 were considered significant.

RESULTS

Characteristics of nest sites.—Eighteen nest sites were found between 335–579 m above sea level, 12 between 580–879 m, and 11 between 880–1130 m. The lowest nest site at 335 m was just above the lowest point in the study area. Few cliffs existed above the highest site at 1130 m. Nest success was similar above and below 580 m, but significantly more young were fledged in successful attempts below 580 m than at higher altitudes (Table 1).

All but 3 nest sites were on cliffs. The use of cliff sites of a particular type of rock was roughly proportional to the abundance of that type. Quartzite, the most common cliff forming rock, composed 27 of the nest cliffs. Seven sites were on shale cliffs, 3 on limestone cliffs, and 1 on a tufa deposit. Height of nest cliffs varied from 4.9 to 38.1 m and averaged 19.7 m. Nests that were always successful during the study were no higher on cliffs than nests that always failed (Table 2). Nest ledges faced south to west at 18 sites and north to east at 10 sites. The main ridges ran northeast-southwest and most cliffs were at the ends of ridges and in water gaps. The other 10 cliff sites were on the sides of ridges.

Profiles of nest cliffs had several consistent characteristics. All cliff nests were sheltered by overhanging ledges of 2 cm to 600 cm, measured from the front of the cup. Cliffs were undercut below the nest ledge at 63.2% of the

TABLE 2
COMPARISON OF RAVEN NEST SITES THAT HAD SUCCESSFUL NEST ATTEMPTS TO SITES THAT FAILED[a]

Type of Site	Number	Mean (m)	Range (m)	p[b]
		Height of Nest Ledge		
Success	20	11.2	3.8–19.8	.32
Failure	8	9.9	5.2–18.3	
		Height of Cliff		
Success	20	19.6	4.9–38.1	.44
Failure	8	18.6	9.7–27.4	
		Distance to Road		
Success	23	513	60–1450	.26
Failure	8	865	80–2410	
		Distance to Dwelling		
Success	23	853	60–1920	.43
Failure	8	1366	320–4830	

[a] Sites with both successes and failures were not included.
[b] $P \leq .05$ was considered significant.

sites and nearly vertical at 31.6%. At 5.3% of the sites the rock face sloped away from the nest ledge. One nest was in a cavity in the side of a cliff and another was wedged in a vertical crevice. The other 36 nests were on ledges that were usually shielded by a rock buttress on one or both sides. Mean width of 13 ledges was 63.5 cm and the range 38–107 cm. Eight nests averaged 61.3 cm wide with a range of 41–91 cm. Ledges often sloped away from the cliff, and at 4 sites a small shrub helped hold the nest on the ledge. Rock faces were too steep and protected from weathering near nest ledges to support the large foliose lichens that covered more exposed surfaces. One end of a nest ledge on a limestone cliff extended beyond the overhang and the exposed portion was covered with bleeding heart (*Dicentra eximia*). This was the only instance where forbs or grasses were seen on a nest ledge.

Search of a 104 km^2 area without cliffs revealed no tree nests, but I could not be sure none existed. In a 518 km^2 area that was intensively searched, one nest was found in a Virginia pine and 2 in shortleaf pines (*Pinus echinata*).

TABLE 3
DISTRIBUTION OF RAVEN NEST CLIFFS BY HEIGHT AND DISTANCE FROM HUMAN DWELLING

Distance to Dwelling	Height of Nest Cliff			
	Number of Cliffs		Mean[a] Height (m)	Range (m)
	< 15 m	$\geqq 15$ m		
$<.8$ km	5	13	21.6	4.8–38.1
$\geq.8$ km	7	13	18.0	9.1–30.5

[a] Means were not significantly different ($p = .14$).

The nests were built by ravens that occupied 1 territory. In 1972 they attempted to build on a cliff about 50 m from the nest tree but the ledge was too steep to hold the nest. A nest of previous years was found on a cliff about 220 m from the tree nest and within 50 m of a newly constructed road. In 1973 and 1974 the birds built within 250 m of the 1972 nest, but farther from the road. These birds fledged 4 young in 1972, 3 in 1973, and 2 in 1974.

The percentage of the area that was forested within 0.8 km and 1.6 km of nest sites was obtained from 7.5-min topographic maps. I did not determine home ranges, but adult ravens on several occasions flew over 2 km from the nest. I saw 1 bird fly about 3 km from its nest. Thus 0.8 km and 1.6 km are probably within the home range of most nesting pairs. Within 0.8 km of the nests, the mean area in forest cover was 90% and the range 20–100%. The mean area in forest cover within 1.6 km of the nests was 86% and the range 28–100%.

Relation of nest sites to human activity.—Nearly as many low nest cliffs (< 15 m) were found less than 0.8 km from a dwelling as were found in more secluded locations and an equal number of taller cliffs were found in both categories (Table 3). Successful nest attempts averaged closer to roads and dwellings than unsuccessful ones, but differences were not significant (Table 2). Successful nest attempts less than 0.4 km from a road averaged more fledglings than attempts farther away, but the difference was not quite significant (Table 1).

Ravens exhibited 2 general behavior patterns when I was near their nests. In 16 territories the birds were evasive and seldom vocal. They would fly into sight then quickly disappear. Often they repeated this pattern several times but rarely flew close to the nest or intruder. Some birds would soar 400–800 m away but within sight. In 8 territories the birds appeared defensive and were vocal. A rapid "*kack-kack* . . ." was usually given. This call was given on 3 occasions when ravens near their nests were diving at Red-tailed Hawks (*Buteo jamaicensis*). A sharp single "*hark*" was given by some birds when I was at the nest. This call was given by a tame raven when deprived of food for short periods or when threatened (D. R. Chamberlain, pers. comm.). Other calls were also heard near nests but these were the prominent ones when I was in direct contact with a nest. Defensive birds flew within 50 m or less of intruders. One bird landed on the cliff 7 m above a worker and another dove within 3 m. In both cases the man could touch the nest.

Birds in a given territory usually reacted similarly during each visit. Striking changes were noted in different years in 3 territories, perhaps indicating a replacement of mates. At 2 nest sites, birds that were normally evasive to humans reacted defensively when Red-tailed Hawks flew close to the nests. Unusually defensive birds in another territory became evasive when I found a prematurely fledged nestling at the base of the cliff. Residents of homes 60, 90, and 150 m from a nest did not know of its existence, although a former resident knew the nest had been active at least since 1961. The nest was on a river bluff and the houses were on top, 50 m above the river. The ravens were probably evasive to attract so little attention from people living above them. When I found the nest in 1974 the ravens were defensive and gave the "*kack*" call until I was 200 m downstream and out of sight. Since ravens cannot defend a nest against a human, an evasive reaction seems more adaptive than a defensive one, particularly since defense advertises the presence of a nest. However, 50% of the pairs classified as defensive and 44% classified as evasive nested within 0.4 km of a road or dwelling. In one case an extremely evasive pair of ravens may have jeopardized nest success through inattention to nestlings. The nest failed in all 3 years of the study and may have been unsuccessful for 3 years prior to the study, according to observations of a local fisherman. The nest was on a 27 m cliff and was well-protected from direct human intervention. However, the cliff was 150 m from a popular trout stream and a frequently traveled road. In 14 trips by the nest site, adults were seen only twice and were evasive both times. The oldest nestling I saw was about 10 days old.

The nest most subject to human activity was on private land and the owner permitted interested groups to visit the nest for short periods. On one occasion in 1972, about 20 people were below the nest ledge and a climber rappelled to the nest. Two young were fledged that year. In 1973, a graduate student rappelled to the nest once a week throughout the nesting cycle, and 4 young were fledged. The site was not used for nesting in 1974 or 1975, although a pair of ravens frequented the cliff in January of both years. Adults at this site were evasive. At only one site did I suspect destruction of a nest by humans. The nest was on a 9.6 m cliff 40 m from a road and clearly visible to people passing in cars.

DISCUSSION

Selection of nest sites.—Cliff profile—a suitable ledge with an overhang above and steep rock face below—was one of 2 factors apparent in the selection of a particular cliff as a nest site. Similar sites have been described by others (Harlow 1922, Bent 1946, Ratcliffe 1962, White and Cade 1971). The lack of deviation from this profile in the nest sites I found is important, because cliffs with these attributes are relatively scarce in the southern Appalachians. The second factor was the proximity of other active raven nests. In a 518 km^2 segment of the study area, the mean distance to the nearest active nest was 4.3 km and the closest nests were 2.2 km apart (Hooper et al. 1975). Although scarcity of potential nest cliffs probably limit some local populations in the southern Appalachians, a surplus of suitable cliffs was available in the above-mentioned portion of the study area. Ratcliffe (1962) thought the density of nesting ravens, unless nest sites were scarce, was determined by a proximity tolerance limit of nesting pairs to each other and that the limit in a particular area was dependent upon the food supply. The regular spacing of active nests, the moderate density of nesting pairs, and the surplus of suitable nest cliffs suggest that overall food supply may have been regulating the population to a large extent in my area. But, until a surplus of potential breeders is demonstrated and other facets of the population dynamics examined, the above hypothesis lacks support.

Because tree nests were difficult to find in the heavily timbered area in which I worked, I did not adequately assess their relative value. In the 518 km^2 area previously mentioned, birds in 1 of 17 territories nested in trees. Since a surplus of cliff sites existed, there was little need to use trees. Ravens nest extensively in trees in other regions, and such sites may be more important in the southern Appalachians than my data indicate. In Pennsylvania, Harlow (1922) found cliff nests outnumbered tree nests about 8 to 1.

Altitudinal relationships.—Only 27% of the nest sites I found were over 880 m above sea level and 44% were below 580 m. Although nesting at lower altitudes is probably not a recent adaptation, specific nest locations mentioned in the regional literature were all above 880 m (Bailey 1913, Jones 1933, Hostetter 1938, Tyrrell 1945, Murray 1957). Murray (1957) mentioned a nest near a hard-surfaced road that was probably below 880 m. About 1950 a resident of Giles County found a raven nest with young at 518 m near the New River. One site at 335 m on the Maury River was active as early as 1961. Thus, nesting occurred at low altitudes in the 1950's if not sooner. The frequency of nest sites found at lower elevations could indicate an increase in the raven population.

Although the difference I found in production of fledglings at high and low altitudes was significant ($p \leqslant .001$), the biological implications are not known. A similar but non-significant relationship between altitude and productivity was reported by Allin (1968) in Wales. I probably worked at the low end of the altitudinal range of the raven in the southern Appalachians. Jones (1933) reported a nest at 1500 m in Virginia. Most sightings of ravens in the Smoky Mountains of Tennessee and North Carolina were above 1070 m (Stupka 1963). More recently, W. D. Zeedyk (pers. comm.) has sighted birds primarily at 1070–1900 m in North Carolina. Nests have been reported at these elevations (Stupka 1963; B. A. Sanders, pers. comm.). Reduced production of fledglings with increasing altitudes, particularly if the trend continues above elevations I worked, is potentially an important factor in the population dynamics of the raven in the southern Appalachians.

Stupka (1963) thought ravens were more plentiful in the Great Smoky Mountains prior to creation of the National Park when livestock was pastured at the higher elevations. The distribution of food within my study area could have been a cause of higher productivity at the lower elevations. A greater food supply probably existed in the valleys, where railroads, houses, farms, and most roads were located. Investigation of raven food habits in the study area indicated considerable foraging was done at lower altitudes (Harlow et al. 1975). Ravens nesting at higher elevations may have to spend more time hunting for food, or have to fly farther to find it. If so, the efficiency of adults feeding their nestlings would be affected, perhaps contributing to increased mortality in nestlings through starvation. That starvation is a major cause of mortality in nestlings of other corvids was shown by Holyoak (1967) for *Corvus frugilegus* and *C. corone*, and by Mishaga (1974) for *C. cryptoleucus.*

Interactions with humans.—Ravens in the southern Appalachians have a reputation of avoiding human contact by living in remote areas. However, many nested relatively close to human residences and probably relied on human activities for a substantial part of their food. Ravens were persecuted in former times (Sprunt 1956), but I believe killing of the species by man is currently of minor importance in Virginia. I found no evidence that ravens in my area caused loss of sheep as reported in the West (Larsen and Dietrich 1970). The only nuisance reports I had on ravens were on a flock that dug grubs from a golf green and on a single bird that took balls from another course. Several birds were destroyed as a result, but these were isolated incidents. Thus, there is little reason for man to molest ravens in Virginia. The apparent restriction of ravens to higher and remoter areas in other parts of the southern Appalachians suggests that persecution may still be a problem in those sections.

Hickey (1942) found that the minimum acceptable height for a Peregrine Falcon (*Falco peregrinus*) nest site was inversely related to its remoteness and directly related to the amount of molestation by man. Ratcliffe (1962) found the same relationship for the raven and Peregrine in England, but a similar one was not apparent in my data. Only 17.2% of the raven nest cliffs in England within 0.8 km of a main road or dwelling were less than 30 m tall compared to 77.8% in this study. Also, nest success in Virginia was higher and number of young fledged greater within 0.4 km of roads than farther away.

Raven nest cliffs probably have been used for centuries and occupancy of a given site may have continued as the landscape slowly changed. During years of inactivity, evidence of past nesting remained perhaps to serve, along with the general suitability of the cliff, as a stimulus to birds seeking a nest site. Of course, many former sites in the southern Appalachians are no longer in use, especially in Alabama and Kentucky where the species was extirpated (Imhof 1962, Mengel 1965), as well as throughout the region where present densities are low. Hickey (1942) thought the occupancy of a given site by Peregrines in face of human disturbance was determined by the personality of the resident birds. Personality differences in ravens were noted by Harlow (1922), Ratcliffe (1962), and Dorn (1972). The ability of ravens I studied to cope with human activity near their nest varied greatly and apparently played a role in nesting success of sites close to roads and dwellings. However, the overt reaction of ravens to humans near their nests was not apparently related to the birds' tolerance of disturbance.

Human activity, in my judgment, should be curtailed near active nests, despite the tenacity of some nesting pairs. The actual distance to restrict activity depends on the terrain and type of activity. In general, pedestrians should not be permitted within 200 m of a nest if they are visible to birds on the nest cliff, or within 100 m if they are hidden from view. Vehicular traffic as close as 100 m to a nest would not create excessive disturbance if parking areas are not provided within 200 m. However, road construction within 200 m could cause desertion. Overlooks should not be built on top of nest cliffs. Rockclimbing should be discouraged on active nest cliffs from 15 January until the nestlings fledge in late April or early May. These guidelines are more liberal than I had originally thought possible. Although a few birds may be adversely affected by humans within 200 m of the nest, I believe most will not. Unless physically harassed, many birds would accept closer contact.

SUMMARY

Common Ravens in Virginia were primarily cliff nesters. The major factors apparent in selection of a nest site were cliff profile, determined by a suitable ledge with an overhang above and steep rock face below, and the distance to other active raven nests, the closest 2.2 km and the average 4.3 km. Nest cliffs averaged 19.7 m in height. No significant difference was found between heights of successful and unsuccessful sites.

Nest cliffs close to human activity were not taller than those in remote areas. Observed proximity of roads and dwellings to nests had no significant effect on nest productivity. Nest sites were found between 335–1130 m above sea level, with 44% below 580 m. Successful nests below 580 m fledged a mean of 3.08 young compared to 2.37 at higher elevations. Starvation of nestlings, due to a loss of feeding efficiency in adults nesting at higher elevations, was suspected.

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GROWTH AND DEVELOPMENT OF KNOWN-AGE RING-BILLED GULL EMBRYOS

John P. Ryder and Lynn Somppi

This paper describes growth and development of Ring-billed Gull (*Larus delawarensis*) embryos. It provides a basis for estimating the age of eggs at previously unvisited colonies. The data also supply a way to determine, within a colony, the location of early and later nesting pairs by comparing, during the same sampling time, relative ages of eggs located in different parts of a colony.

STUDY AREA AND METHODS

There are no descriptions of embryo growth and development of Ring-billed Gulls in the literature. Dawkins et al. (1965) compared increase in body weight and development of California Gull (*L. californicus*) and Domestic Chicken (*Gallus gallus*) embryos using known-age eggs. Drent (1970), using known-age embryos plus data from Paludan (1951) and Harris (1964) formulated a logarithmic body weight curve for the Herring Gull (*L. argentatus*). Maunder and Threlfall (1972) described the growth and development of various parts of Black-legged Kittiwake (*Rissa tridactyla*) embryos. Gilbertson and Hale (1974) used Maunder and Threlfall's (1972:800) body weight curve for the Black-legged Kittiwake embryos to age those of the Herring Gull. We consider such inter-specific comparisons weak because different species do not necessarily show the same developmental characteristics at equivalent age. We decided not to use the egg flotation technique devised by Westerkov (1950) because the results vary depending on egg size and the age of the egg when incubation starts. Additionally, Schreiber (1970) noted that addled and infertile eggs of Western Gulls (*L. occidentalis*) show essentially the same flotation as viable eggs during the early stages of development.

We conducted this study in 1975 at a colony of approximately 800 pairs of Ring-billed Gulls on Granite Island (48°43′N, 88°29′W), Black Bay, northern Lake Superior, Ontario. The island is a strongly undulating granite outcrop 402 m by 201 m with a summit 30 m above the surrounding water. Soil and vegetation occur in depressions of the rock surface. Each spring Ring-billed Gulls nest in the depressions especially near the summit away from wave action and possible flooding. Dominant plants in the depressions are Kentucky bluegrass (*Poa pratensis*), rough cinquefoil (*Potentilla norvegica*), and red raspberry (*Rubus strigosus*). The remainder of the island is densely forested with balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and white birch (*Betula papyrifera*).

On 16 May we marked, with a black felt pen, 31 1-egg clutches and 5 2-egg clutches in the center and 19 1-egg clutches and 13 2-egg clutches on the periphery of the Granite Island colony to determine if equivalent age embryos showed equal development in the two areas. Central and peripheral clutches were designated respectively as those near the geometric center of the colony and those forming the outside border (Dexheimer and Southern 1974). Only nests which subsequently contained 3 eggs formed our sample so that we eliminated potential variation in development because of different clutch sizes. Our final sample was 29 central and 21 peripheral nests.

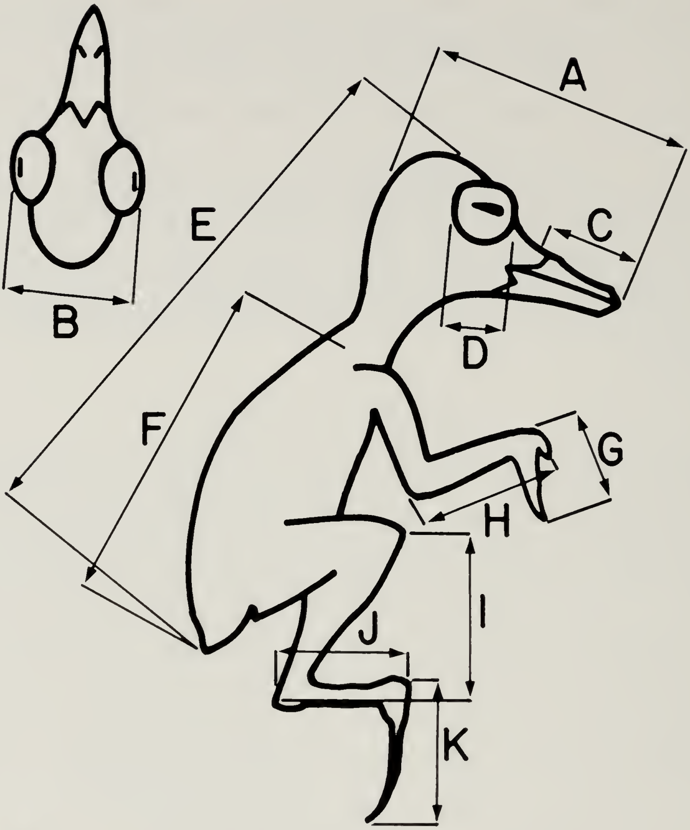

FIG. 1. Measurements of Ring-billed Gull embryos. A, head length; B, head width; C, culmen; D, eye diameter; E, total length; F, back length; G, hand; H, forearm; I, tibia; J, tarsus; K, midtoe. Modified from Maunder and Threlfall (1972).

The age of eggs found in the study nests on our first visit was determined by assuming a 1.9 day interval between laying of successive eggs in Ring-billed Gulls (Vermeer 1970: 20). For example, if a 1-egg clutch on 16 May contained 2 eggs on 17 May, we assumed the first egg was laid on 15 May. If a second egg was not in the nest on 17 May but was by 18 May, we assumed the first egg was laid on 16 May. We considered the longest egg in the 2-egg clutches marked on 16 May the first laid (Vermeer 1969, Ryder 1975). Because we assumed the 1.9 day interval between successive eggs, we aged embryos to an accuracy of ±24 h and grouped embryos according to age into 3-day intervals.

On 17 May we collected 2 clutches each from the center and periphery of the colony in which the second egg was freshly laid and 2 clutches from each area in which the third egg was fresh. From these, we determined if any development occurs in first and second eggs by the time the third egg is laid. Sampling for the remainder of the study involved taking individual first, second, and third eggs of known age from different nests in each

TABLE 1

EXTREMES IN EARLY DEVELOPMENT OF KNOWN-AGE RING-BILLED GULL EMBRYOS FROM THE CENTER AND PERIPHERY OF THE GRANITE ISLAND COLONY, 1975

Age (days)	Development	
	Center	Periphery
1	No development to blastodisc with diameter 0.66 cm.	No development.
3	Head fold stage of primitive streak to embryo with 30 somites, heart beating, area vasculosa developed.	No development to primitive streak.
5	Embryo with 18 somites to an embryo 0.82 cm in length, wing and leg buds visible.	Embryo with 14 somites to 16 somites.
6	Embryo 0.79 cm in length, slightly prominent midbrain to embryo 1.0 cm in length, leg bud 0.30 cm and wing bud 0.42 cm, choroid fissure visible.	Embryo with 23 somites to embryo 0.99 cm in length, prominent midbrain, choroid fissure visible.
7–9	Embryo 0.93–1.56 cm in length, area vasculosa 4.52 cm at sinus terminalis, body wt. 0.25–0.40 g, wing bud 0.36–0.43 cm, leg bud 0.32–0.41 cm, well defined choroid fissure.	Embryo 0.78–1.54 cm in length, area vasculosa 3.74–6.10 cm at sinus terminalis, body weight 0.30–0.50 g, wing bud 0.39–0.46 cm, leg bud 0.28–0.53 cm, well defined choroid fissure.

sampling period so that each of the eggs collected was of equal age per sampling day. Each egg removed from a nest was replaced by an unmarked one in an attempt to eliminate any growth changes in the remaining study eggs which might have resulted from reduced attentiveness by the parents because of a smaller clutch (see Beer 1965).

We opened eggs by the procedures outlined in Rugh (1962). This involved cutting around the widest diameter of the egg and emptying the entire contents into a petri dish without breaking the yolk. During the early stages of development we retained the embryo in the yolk and measured the diameter of the blastodisc and area vasculosa, number of somites, and other general developmental characteristics using a Wild M5 dissecting microscope. We removed embryos older than 6 days from the yolk and immediately weighed them to the nearest 0.1 g on a triple beam balance and measured them to 0.01 mm with vernier calipers. Embryos were preserved in 10% neutral buffered formalin. The measurements taken are illustrated in Fig. 1. Later development is defined here as that shown by an embryo 10 or more days old. By this time all of the various body parts are easily visible and can be measured accurately.

RESULTS

Early development (1–9 days).—The aging of these embryos presented problems because of considerable variation in development among embryos

TABLE 2

INTRA-CLUTCH VARIATION IN EARLY DEVELOPMENT OF RING-BILLED GULL EMBRYOS FROM THE CENTER AND PERIPHERY OF THE GRANITE ISLAND COLONY, 1975

Egg No.	Age (days)	Development	
		Center	Periphery
1	3	11 somites.	Embryonic shield stage.
2	1	No development.	No development.
1	3	Primitive streak stage.	No development.
2	1	No development.	No development.
1	5	18–19 somites; area vasculosa developing.	14 somites; initiation of area vasculosa.
2	3	7 somites; optic vesicle visible.	Head fold stage of primitive streak.
3	1	No development.	No development.
1	5	Embryo 0.82 cm in length. Limb buds visible.	16 somites, head turned.
2	3	Area vasculosa well developed. Heart visible and beating.	Head fold stage of primitive streak.
3	1	Diameter of blastodisc 0.66 cm.	No development.

of the same age. Table 1 details our results of embryos from the center and periphery of the colony to 9 days of age. Embryos from the center of the colony were slightly advanced to those of equal age from the periphery (Tables 1 and 2).

It was clear from our collections of complete clutches on 17 May that some development occurred in first and second eggs before the third egg was laid (Table 2). In all clutches the first egg showed more development than the second and the second more than the third. Similar variation in first, second, and third eggs of Herring Gulls was reported by Parsons (1972). The significance of this result is that based on the apparent differential development among eggs of a single clutch, individual eggs should be aged according to the day each was laid and not from the day on which the clutch was completed (see Drent 1970:80 and Parsons 1972:540).

Later development (10 days to hatching).—Figure 2 illustrates typical Ring-billed Gull embryos in each of the 3-day groupings. Embryos collected from the center were slightly, but not significantly ($P > 0.05$) larger than their peripheral counterparts. Consequently, we grouped all embryos from both

FIG. 2. A series of known-age Ring-billed Gull embryos, Granite Island, 1975. A, 7–9 days; B, 10–12 days; C, 13–15 days; D, 16–18 days; E, 19–21 days; F, 22–24 days; G, 25–27 days (pipping, note intact yolk sac). Embryos shown actual size.

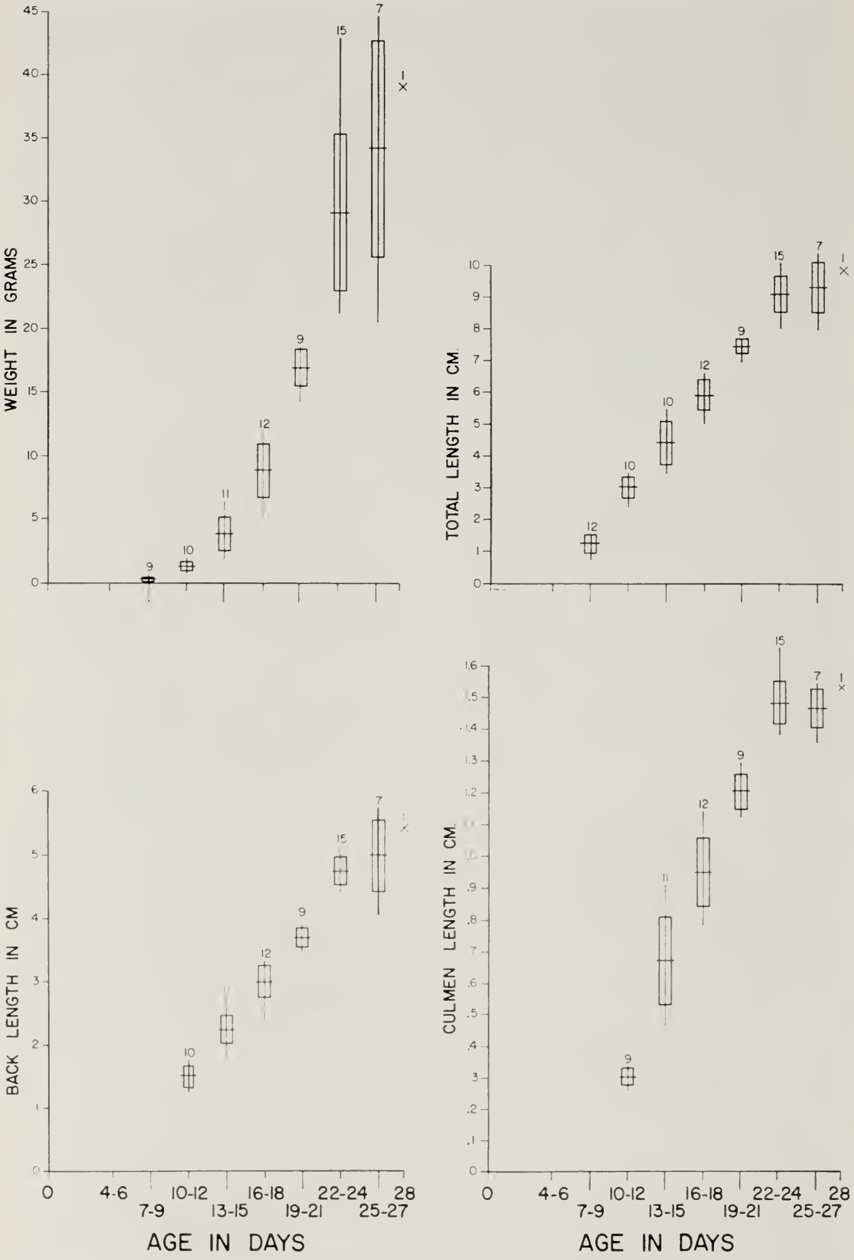

FIG. 3. Increase in weight, total length, back length, and culmen length of Ring-billed Gull embryos, Granite Island, 1975. Vertical line is range; horizontal line is mean; rectangles enclose $\overline{X} \pm 1$ SD, and number above is sample size.

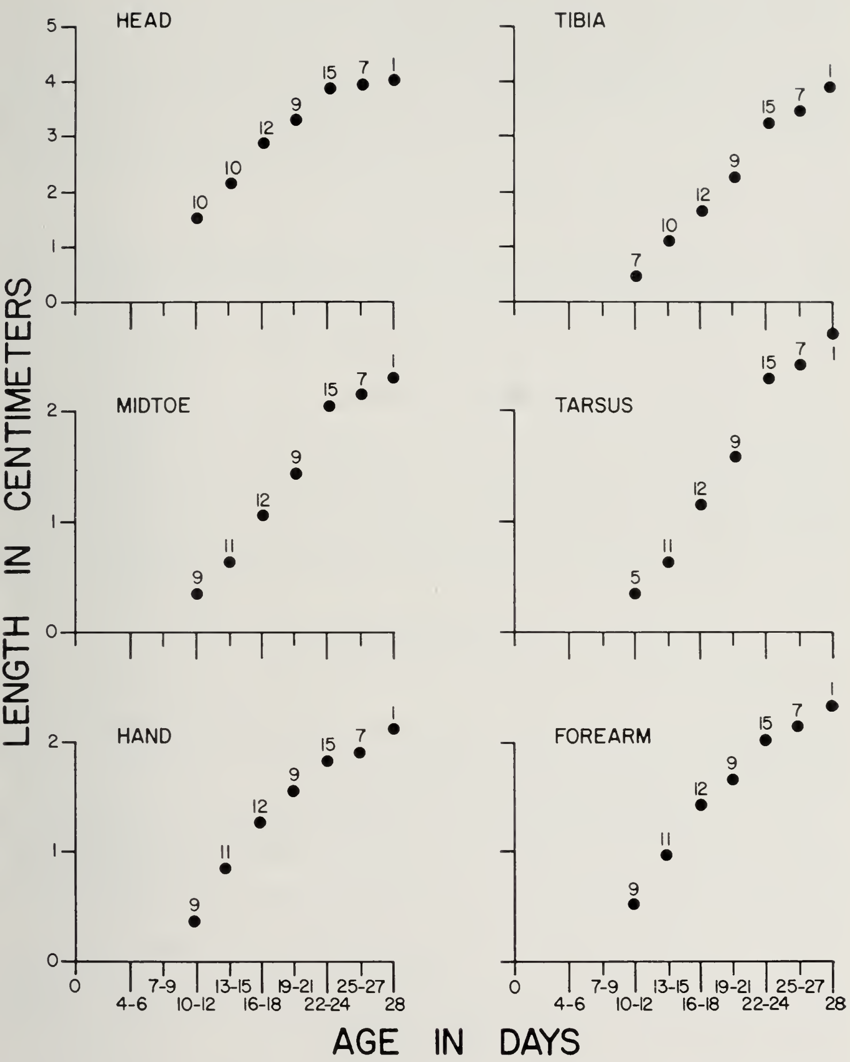

FIG. 4. Growth of body parts of Ring-billed Gull embryos, Granite Island, 1975. Number above each dot is sample size.

areas to determine aging parameters useful to the field investigator. Figure 3 shows growth in terms of body weight, total length, back length, and culmen length. No overlap at 1 standard deviation occurred in any of the age group measurements except those recorded near the end of incubation. Some of the chicks in the 22–24-day and 25–27-day groups were in the process of pipping

TABLE 3

FIELD CHART FOR AGING RING-BILLED GULL EMBRYOS

Age (days)	Characteristics
1– 3	No development through primitive streak stage to presence of somites, heart beating, blood vessels on area vasculosa.
4– 6	Embryo usually $\leqq 1.0$ cm in length; wing and leg buds appearing; midbrain becoming prominent, eye pigmented; choroid fissure visible.
7– 9	Embryo 1–2 cm in length; less than 1 g body wt.
10–12	Embryo 2–4 cm in length; 1–2 g body wt. Choroid fissure complete.
13–15	Embryo 4–5 cm in length; 2–6 g body wt.; pterylae visible; feathering on spinal and caudal tracts.
16–18	Embryo 5–7 cm in length; 6–13 g body wt. All pterylae feathered; dorsal pterylae well feathered.
19–21	Embryo 7–8 cm in length; 13–20 g body wt. All pterylae feathered; pigment appearing in upper and lower mandibles, claws, and legs.
22–24	Embryo >8 cm in length; >20 g body wt.; mandibles, claws, and feet well pigmented; yolk compacted when close to hatching.

and of similar size. The point at 28 days in Figs. 3 and 4 represents 1 peripheral embryo which, along with others, tended to take longer to start pipping compared to embryos from the center.

Figure 4 presents growth curves for various body parts. They are not as useful by themselves as an aging tool because of overlap at 1 standard deviation in most cases. However, they do provide aid to the field researcher as a supplement to data in Fig. 3.

Table 3 summarizes the results. Based on 2 easily obtained measurements, weight and length of body, one can estimate the age of an embryo to within 3 days. Supplementary information such as degree of feathering and pigmentation also aid in embryo age determination.

DISCUSSION

Data in this report provide the basic information required to age embryos of Ring-billed Gulls to within 3 days. Of interest are the statistically insignificant differences between equivalent age embryos from the center and periphery of the colony. The general lack of differences in development characteristics and size of newly hatched chicks from the 2 areas suggests the young have approximately the same chance of survival. Dexheimer and Southern

(1974) found no significant difference in fledging success between central and peripheral Ring-billed Gull chicks on an island similar to our study area where flooding posed no problem. They did find significant differences in fledging success on an island where peripheral chicks were exposed to wave action and excessive wetting causing death.

SUMMARY

Characteristics for aging Ring-billed Gull embryos to within 3 days are given. Body weight, total length, back length, and culmen length from 10 days after laying to hatching were the most accurate aging parameters. No overlap at 1 standard deviation occurred in any of the above characters in 3-day intervals.

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HABITAT PARTITIONING IN A COMMUNITY OF PASSERINE BIRDS

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Since the concept of the niche was brought into the forefront by G. E. Hutchinson (1957), many ecologists have sought to analyze niche relationships in natural communities. The quest for quantification has led to numerous field studies from which huge quantities of ecological data have been amassed, much of it concerned with birds (e.g. MacArthur 1958, Hespenheide 1971, Willson 1974). One problem in such studies is to visually synthesize relationships from complex data matrices. Several techniques have been developed to address this problem. One such technique is ordination. Briefly stated, ordination is an arrangement of units in a uni- or multi-dimensional order as opposed to a classification in which units are arranged in discrete classes (Bray and Curtis 1957). Classically, ordinations have been restricted to plant complexes but ecologically meaningful ordinations can be constructed of animal data as well (e.g. James 1971, Whitmore 1975a).

Additional operational problems are listed by Green (1971): (1) there is a practical limit to the number of environmental parameters which can be measured, and (2) many of the parameters measured are likely to be highly correlated (redundant), and some may be relatively invariate or irrelevant. The use of multivariate statistical analyses, especially those techniques which reduce the number of variables to a more easily visualized set, can help provide answers to these last 2 problems. Combining ordination with multivariate statistics can give insight into all of the above problems (e.g. James 1971, Whitmore 1975a). Once the position of the birds along environmental gradients has been established, generalizations can be made about their relationships with each other and other species.

The purpose of this study was to quantify the relationships of a community of passerine birds in an attempt to ascertain which variables are important in habitat selection, to develop an ordination along environmental gradients, and to determine the range of habitat use.

STUDY AREA AND METHODS

The Virgin River Valley is located in the southwest corner of Utah, northwest corner of Arizona, and southeast tip of Nevada at about 37°N 113°W. Lower Sonoran desert surrounds the valley on 3 sides and the Pine Valley Mountains border on the north. The Valley is an isolated oasis from the rather harsh surrounding environment and the density of birds in it is quite high. I collected data in the streamside vegetation along Santa Clara Creek to the Virgin River and along the Virgin River to Zion National Park. The area is characterized by stands of mature Fremont cottonwood (*Populus fremontii*), large clumps of tamarix (*Tamarix pentandra*), and isolated patches of sand bar willow (*Salix exigua*). Much of the river valley is heavily planted with alfalfa (*Medicago sativa*) and numerous species of fruit, nut, and ornamental trees. The rivers and streams of the area usually flow year round, though excessive removal of water for irrigation or unusually low rainfall will sometimes cause drought in August and September.

Avifaunal investigations in the valley have been primarily restricted to species accounts, most notable those of Behle (1943), Wauer and Russel (1967), and Wauer (1969). Much collecting, under the direction of W. H. Behle, has been done in the valley and surrounding areas.

Vegetational data were collected between 1 May and 30 June 1973 using a modification of the range finder circle method described by James and Shugart (1970). I measured 10 vegetational variables in a 0.04 ha circular plot around each singing, territorial male bird encountered while walking along the river. Habitats for 421 individuals of 24 species of passerine birds were measured. Table 1 lists the passerine species I encountered.

In order to determine which variables were important in species' separation, the data were subjected to stepwise discriminant analysis (Dixon 1970), a multivariate statistical technique. The underlying theory for the use of the discriminant function in ecology is discussed elsewhere (Green 1971, 1974, James 1971, Whitmore 1975a) and will not be considered here. The stepwise adaptation of the discriminant analysis allows for insertion of each variable in a stepwise manner based on its ability to achieve discrimination between species. The order of insertion determines the order of importance in group separation.

When dealing with an n-dimensional data matrix, interpretations may be more meaningful if the number of axes can be reduced to a number which can be easily visualized. Principal component analysis (PCA) can be used to accomplish such a task. PCA produces linear combinations of the original variables in such a manner as to explain progressively smaller portions of the total variance in the data. This total variance is the sum of the variances for each of the variables. The first axis is constructed so that linear combination of variables represents the greatest amount of response variance. The second axis, which is orthogonal to the first, represents the second greatest amount of variance. The third represents the third greatest amount and so on. The sum of the variance of components is the total variance. The data were subjected to PCA in order to produce an ordination along vegetational gradients.

Vegetational resource use was calculated by dividing each of the measured variables into discrete units. For example, canopy cover was divided into 10, 10% classes and the number of individuals in each species present in each class was determined. After the development of resource matrices for each of the 4 most important variables as determined by stepwise discriminant analysis, I calculated vegetational resource use values using the procedures described by Colwell and Futuyma (1971) for expanded matrices.

RESULTS

Discriminant analysis.—Results of the stepwise discriminant analysis have been presented elsewhere (Whitmore 1975a).

Prior to calculating the discriminant functions the stepwise discriminant analysis program performs a multivariate analysis of variance (MANOVA) among the species based on the measured variables. The advantage of such an analysis is that it not only accounts for the variate but also the covariate

TABLE 1

LIST OF PASSERINE SPECIES ENCOUNTERED IN THE VIRGIN RIVER VALLEY FROM 1 MAY TO 30 JUNE 1973 GIVING SYMBOLS USED IN FUTURE TABLES AND FIGURES

WK	Western Kingbird	(*Tyrannus verticalis*)
AF	Ash-throated Flycatcher	(*Myiarchus cinerascens*)
*	Black Phoebe	(*Sayornis nigricans*)
WF	Willow Flycatcher	(*Empidonax traillii*)
*	Western Flycatcher	(*Empidonax difficilis*)
*	Western Wood Pewee	(*Contopus sordidulus*)
HW	House Wren	(*Troglodytes aedon*)
BW	Bewick's Wren	(*Thryomanes bewickii*)
*	Rock Wren	(*Salpinctes obsoletus*)
BGN	Blue-gray Gnatcatcher	(*Polioptila caerulea*)
*	Phainopepla	(*Phainopepla nitens*)
WV	Warbling Vireo	(*Vireo gilvus*)
*	Orange-crowned Warbler	(*Vermivora celata*)
LW	Lucy's Warbler	(*Vermivora luciae*)
YW	Yellow Warbler	(*Dendroica petechia*)
AW	Audubon's Warbler	(*Dendroica coronata auduboni*)
YT	Common Yellowthroat	(*Geothlypis trichas*)
YBC	Yellow-breasted Chat	(*Icteria virens*)
MW	MacGillivray's Warbler	(*Oporornis tolmiei*)
WW	Wilson's Warbler	(*Wilsonia pusilla*)
*	Yellow-headed Blackbird	(*Xanthocephalus xanthocephalus*)
RWB	Red-winged Blackbird	(*Agelaius phoeniceus*)
BHC	Brown-headed Cowbird	(*Molothrus ater*)
*	Hooded Oriole	(*Icterus cucullatus*)
BO	Bullock's Oriole	(*Icterus galbula bullockii*)
*	Summer Tanager	(*Piranga rubra*)
BHG	Black-headed Grosbeak	(*Pheucticus melanocephalus*)
BG	Blue Grosbeak	(*Guiraca caerulea*)
IB	Indigo Bunting	(*Passerina cyanea*)
LB	Lazuli Bunting	(*Passerina amoena*)
*	House Finch	(*Carpodacus mexicanus*)
LG	Lesser Goldfinch	(*Spinus psaltria*)
*	Rufous-sided Towhee	(*Pipilo erythrophthalmus*)
AT	Abert's Towhee	(*Pipilo aberti*)
SS	Song Sparrow	(*Melospiza melodia*)

* Not included in analyses since the sample was less than 5.

relationships among habitat variables (Anderson and Shugart 1974). The regular assumptions required for statistical tests are needed here and are considered to be met based on the multivariate central limit theorem (Morrison 1967). A total of 276 species comparisons can be made from 24 different species; of these all but 4 were significantly different ($p < .01$). These 4

TABLE 2

CORRELATION MATRIX (r) FOR 10 VEGETATIONAL VARIABLES $N = 24$

	SPT[1]	T-7	T-15	T-22	T-30	T-38	% SD	% CC	CHM
SPT									
T-7	0.65*								
T-15	0.74*	0.83*							
T-22	0.78*	0.85*	0.90*						
T-30	0.69*	0.40*	0.59*	0.68*					
T-38	0.63*	0.21	0.34*	0.47*	0.83*				
% SD	–0.09	0.28	0.01	0.01	–0.22	–0.30			
% CC	0.78*	0.64*	0.62*	0.66*	0.61*	0.60*	–0.10		
CHM	0.85*	0.39*	0.44*	0.55	0.66*	0.74*	–0.29	–0.81*	
% GC	–0.32	–0.18	–0.30	–0.25	–0.39*	–0.33	–0.28	–0.17	–0.20

[1] See key to abbreviations of variables in Table 3.

* Significant at $p < 0.05$.

will be discussed later. It is remarkable that 10 measured variables can separate 272 of the possible 276 species pairs, especially since the environment is restricted and low in plant diversity. Whitmore (1975a) presented a 2-dimensional ordination along the first 2 discriminant function axes and compared those results with those of James (1971).

Principal component analysis.—Since PCA is usually based on a correlation matrix, it is of value to examine the correlations among the vegetational variables. As can be seen in Table 2 many of the variables are highly correlated. Values greater than 0.34 are significant ($p < .05$). James (1971) found many similar vegetational correlations in a study in Arkansas. Percent ground cover is negatively correlated with all other variables. This corresponds to going from the high biomass forested areas, cottonwood and tamarix stands, to the low biomass open areas, alfalfa and open field. The highest correlations are found among the 3 classes of middle and small sized trees, possibly corresponding to the isolated willow and tamarix stands. The 2 classes of large trees are positively correlated due to the presence of several sizes of large cottonwoods. Canopy cover and canopy height are also positively correlated. Other positive correlations occur between the number of species of trees and the number of trees in each of the size classes. Thus, tree species number per unit area is positively correlated with vegetational diversity. Shrub density is not strongly correlated with any of the other variables, indicating rather uniform distribution throughout the study area. It is, however, correlated positively with small trees, again corresponding to the clumps of willow and tamarix, and correlated negatively with the large tree variables and ground cover.

TABLE 3

SUMMARY OF THE RESULTS OF THE PRINCIPAL COMPONENT ANALYSIS OF EACH OF 10 VEGETATIONAL VARIABLES FOR 24 SPECIES OF PASSERINE BIRDS

	Correlations With Original Variables Component I	II
Number of Species of Trees (SPT)[1]	–0.65	–0.14
Number of Trees 7.6–15.2 cm DBH (T-7)	–0.54	0.42
Number of Trees 15.2–22.9 cm DBH (T-15)	–0.65	0.23
Number of Trees 22.9–30.4 cm DBH (T-22)	–0.71	0.10
Number of Trees 30.4–38.1 cm DBH (T-30)	–0.64	–0.36
Number of Trees > 38.1 cm DBH (T-38)	–0.53	–0.58
Percent Shrub Density (% SD)	0.01	0.74
Percent Canopy Cover (% CC)	–0.49	–0.22
Canopy Height in Meters (CHM)	–0.43	–0.48
Percent Ground Cover (% GC)	0.75	–0.16
Percentage of Total Variance Accounted for	56.56	16.87
Cumulative Percentage of Total Variance Accounted for	56.56	73.43

[1] Abbreviations for variables used in Tables 2 and 4.

The results of the PCA are summarized in Table 3. The first component accounts for 56.6% of the variance in the original data. Percent ground cover shows a high positive correlation with the first axis. Species of birds having high values on this axis occur where there is high ground cover. The first axis also shows negative correlations with the measured variables for trees. Therefore, this axis represents a gradient starting with the forested areas with low ground cover and proceding to open areas with high ground cover, i.e. going from cottonwood stands to alfalfa fields. The second axis, which accounts for an additional 16.9% of the variance, is correlated positively with shrub density and small trees and negatively with large trees and canopy height. This corresponds to a gradient going from areas of tall trees, if trees are present at all, with low shrub density to areas of high shrub density and no large trees. A 2-dimensional plot is presented in Fig. 1.

Species in the lower left of this ordination, e.g. Bullock's Oriole, Yellow Warbler, Audubon's Warbler, and Black-headed Grosbeak, are those associated with high canopy cover and many trees. Ground cover and shrub density are low in this area of the ordination. A species such as the Warbling Vireo would be expected to be found in areas with the same amount of canopy cover and ground cover as the Bullock's Oriole, but with increased shrub density. A group of 5 species; Yellow-breasted Chat, Red-winged Blackbird,

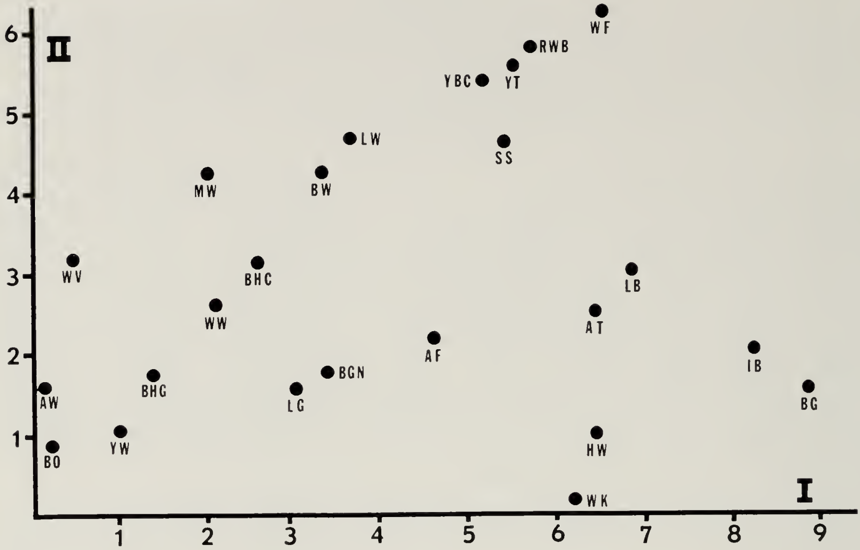

FIG. 1. Two-dimensional ordination of bird species along the first and second principal component axes. The first, horizontal, axis accounts for 56.6% of the response variance and second, vertical, axis accounts for an additional 16.9%. Increasing values on the first axis correspond to an increase in ground cover and a decrease in the numbers of trees. Increasing values on the second axis represent an increase in shrub density. Species' names are abbreviated as in Table 1.

Yellowthroat, Song Sparrow, and Willow Flycatcher, is located on the upper end of both axes. These are high shrub density species with little canopy cover and moderate ground cover in their territories. Six species cluster in the lower right corner of Fig. 1. These species are found in either open country or the alfalfa fields as evidenced by their positions on axis I. If these 6 species are considered a separate habitat guild, then a regression line ($r = .77$) can be drawn through the remaining 18. This line can be viewed as a third gradient and corresponds to going from densely forested areas with low ground cover (lower left), to dense shrub areas with moderate ground cover (upper middle). Therefore, 3 separate gradients are apparent on this 2-dimensional ordination, thus increasing its value.

In this study the addition of a third PCA axis adds little new information in that only 11.2% more variance is accounted for and there are no strong correlations with the original variables. The 4 most important variables, as determined by the stepwise discriminant program, are all accounted for by the first and second principal component axes. Therefore, discussion of

TABLE 4
SPECIES HABITAT USE VALUES OF THE 4 MOST IMPORTANT VARIABLES[1]

Species	% CC[2]	% SD	T-7	% GC
BO[3]	.208	.511	.274	.563
WK	.383	.376	.256	.393
AF	.513	.344	.303	.464
BHG	.328	.678	.626	.403
LB	.399	.310	.256	.457
BG	.245	.288	.276	.356
YW	.342	.255	.332	.310
AW	.263	.300	.379	.362
WW	.193	.440	.430	.560
IB	.317	.376	.274	.390
YT	.201	.385	.428	.399
YBC	.437	.546	.358	.378
MW	.351	.356	.364	.325
LW	.253	.413	.422	.379
AT	.416	.443	.327	.361
BHC	.372	.658	.463	.257
GHN	.378	.593	.497	.605
RWB	.392	.365	.309	.354
HW	.410	.341	.309	.331
BW	.408	.667	.523	.475
WF	.179	.271	.311	.334
LG	.391	.219	.435	.309
WV	.393	.310	.470	.436
SS	.362	.223	.435	.285

[1] Calculated by formulae in Colwell and Futuyma (1971).
[2] See key to abbreviations of variables in Table 3.
[3] See key to abbreviations of species' names in Table 1.

species' distributions along gradients constructed using PCA will be confined to the first 2 axes.

Habitat resource use.—Values for resource matrices constructed from the 4 most important variables are found in Table 4. Most of these values are less than 0.5, indicating that the species are restricted in habitat use. Those species that show consistently low values and with a low mean value for the 4 resource use determinations, may be termed habitat specialists. Included in this designation are the Blue Grosbeak, Yellow Warbler, Willow Flycatcher, Lesser Goldfinch, and Song Sparrow. Species with high resource use values, are relative habitat generalists. They include the Black-headed Grosbeak, Yellow-breasted Chat, Brown-headed Cowbird, Blue-gray Gnatcatcher, and Bewick's Wren. Some species, e.g. Bullock's Oriole, Lazuli Bunting, and Wilson's Warbler, are high in 1 variable and low in others.

DISCUSSION

Certain aspects of the ecological distribution of species in the Utah study area lend themselves to comparisons with previously published data. For this reason the following species or groups of species will be examined in more detail.

Indigo Bunting and Blue Grosbeak.—One of the 4 species' pairs that were found to be not significantly different by the MANOVA was the Indigo Bunting and the Blue Grosbeak. In a table presented by Shugart and James (1973) only moderate overlap between these species was recorded, the Blue Grosbeak being found solely in clonal persimmon field plots while the Indigo Bunting was scattered throughout several habitat types, most notably forest edges. Stewart and Kantrud (1972) found the Blue Grosbeak in the Coteau Slope of North Dakota while the Indigo Bunting was found in the Coteau Slope and Northeastern Drift Plain. In 2 types of ordinations, James (1971) found moderate separation between the species. Using the same techniques, discriminant analysis and principal component analysis, I found little separation between the species. In my study the Blue Grosbeak was one of the most restricted in habitat use (Table 4). Therefore, in the Virgin River study area their habitat use was almost indistinguishable. Even though species specific habitat differences were not detected it is reasonable to assume that the 2 might take different sized food items, based on bill size alone. In other southwestern studies (Dixon 1959, Raitt and Maze 1968, Austin 1970, Carothers et al. 1974) Indigo Buntings were not observed. Whitmore (1975b) suggests that the Indigo Bunting is new in Utah, coming from the southeast approximately 30 to 40 years ago. Perhaps as a result of interspecific competition with its congener, the Lazuli Bunting, it may be forced into a suboptimal habitat, therefore causing overlap with the Blue Grosbeak.

Bewick's Wren and Song Sparrow.—Although these species seem to require river lowlands with dense vegetation and cover (Behle 1943), as in the previous pair of species, effective partitioning may be carried out by means of different food preferences and feeding behavior. Two other pairs of birds indistinguishable in habitat preference, House Wren and Western Kingbird, and Abert's Towhee and Ash-throated Flycatcher, also differ behaviorally and in food selection.

House Wren and Bewick's Wren.—Inasmuch as Kroodsma (1973) recorded instances of competition between the House and Bewick's wrens in Oregon one might expect similar activity in the Virgin River Valley. I observed 16 House and 20 Bewick's wren territories in my study area and recorded no instances of interspecific territoriality. Behle (1943) states that the House Wren only winters in the lowlands while breeding in the mountains in Utah. This is not consistent with my observations nor those of Wauer and Carter

(1965) who stated that there are several records of the House Wren in the riparian woodland during the breeding season. Habitat use was, however, similar to that reported by Kroodsma (1973) in that the Bewick's Wren was confined to the dense thickets and House Wren occurred where shrub density decreased and grassy substrate increased. This latter point can be noted also by the positions of the species in Fig. 1. As noted in Table 4, the Bewick's Wren has one of the broadest habitat ranges of all the species measured and therefore species' overlap with it is to be expected.

Parulidae.—All 7 species of the family Parulidae observed in the Virgin River Valley fall on or very close to the regression line drawn through the 2-dimensional principal component ordination. With the exception of the chat and yellowthroat, 2 species of different size, the species seem to be evenly distributed along the gradient going from the forested areas to dense shrub zones. Warblers are not found on the gradient going to the open country. A species that Cody (1974) found to be a generalist, the Yellow Warbler, is found here to be one of the most restricted species. This could be due to the high number of warbler species in such a restricted habitat. Carothers et al. (1974) found only 3 warbler species in their study in the riparian habitat of Arizona. As evidenced by the uniform distribution of warblers along the forest-shrub gradient one might think that competition is severe. The presence of large numbers of Audubon's Warblers, the closest warbler on the ordination, could exert a competitive influence on the Yellow Warbler, but I have no direct evidence that they are affecting one another. Behle (1943) and Wauer and Carter (1965) stated that the Audubon's Warbler is an abundant migrant through the Virgin River Valley during April and May but breeds only in the conifers found at higher elevations. I observed them actively countersinging and defending territories through June. Therefore, even if these birds are non-breeding in the area, they probably affect community structure. I do not know if Audubon's Warblers ever left during the breeding season and if they did leave the effect of competitive release on the other warbler species. One explanation for the appearance of many Audubon's Warblers late in the season is that the severe winter of 1972–1973 could have delayed northward migration.

The 2 warblers most closely associated in habitat use are the Common Yellowthroat and Yellow-breasted Chat. As noted from their positions on the ordination, these species inhabit areas of dense shrubs. Both species are rather broad in their habitat use (Cody 1974; Table 4) but differ in body size and foraging behavior. The chat, the larger, feeds primarily by gleaning insects from the foliage of shrubs whereas the yellowthroat often hawks insects from exposed perches or flies to the ground to pick prey out of the grass. In spite of the closeness of the 7 warbler species in habitat use, I observed few instances of interspecific aggression.

Brown-headed Cowbird.—With the exception of the Ash-throated Flycatcher all of the 24 passerine species analyzed in this paper are known hosts of the Brown-headed Cowbird (Friedmann 1963, 1971). Since the Ash-throated's eastern congener, the Great-crested Flycatcher (*Myiarchus crinitis*) is a known host, I assume that the Ash-throated Flycatcher is also parasitized. To be effective at nest parasitism it should be advantageous for the cowbird to be broad in its range of habitat choices, thus allowing it better access to more nests. Examination of Fig. 1 shows that the Brown-headed Cowbird is centrally located in the ordination and almost equidistant from the ends of the regression gradient. Its mean habitat use value of .438 is one of the highest, indicating broad use of the 4 variables tested. James (1971) states that the Brown-headed Cowbird shows remarkable latitude in habitat use. One might conclude, therefore, that the cowbird, in order to take advantage of as many hosts as possible, is not as restricted as other species in habitat use.

Willow Flycatcher.—Of all of the species in this analysis, the Willow Flycatcher has the lowest habitat use value. This species is confined to areas of shrub density ranging from 70% to 100%. Trees of any size or species seldom occur in its defended territories. Behle (1943) listed this species as a common breeder in the streamside willows throughout the valley and cited numerous specimens collected along the Virgin River and Santa Clara Creek (including 6 collected from one site 3 km southwest of St. George, Utah). This species is now uncommon to rare. A possible explanation for this is habitat change. Christensen (1962) documented the introduction and spread of the shrub tamarix (*Tamarix pentandra*) in Utah. This colonization has taken place at the expense of the willows. The stands of streamside willow discussed by Behle are almost totally gone. In fact, one is hard pressed to find any substantial willow stands along the Santa Clara Creek. Probably tamarix does not provide a suitable nest site for the Willow Flycatcher and as a result the bird has been forced to go elsewhere. Possible evidence for this exists in that Wauer and Carter (1965) observed the species in the remaining willows at the Springdale Ponds area near the mouth of Zion Canyon. Habitat changes such as this are probably responsible for many of the differences in recent observations as compared to the older published data of Behle (1943) and Woodbury et al. (1949).

Blue-gray Gnatcatcher.—Also found near the center of the ordination is the Blue-gray Gnatcatcher. James (1971), Whitmore (1975a), and Kimberly Smith (pers. comm.) observed and discussed the wide range of habitats selected by this species. In a more definitive study, Root (1967) lists many habitats in which the Blue-gray Gnatcatcher may be found and remarks on the variability of selected sites in various areas of its geographic range. Based on the 4 most important variables, gnatcatchers in the Virgin River Valley had the broadest habitat use of any of the species in the community. My observations of the foraging behavior of this species are consistent with those of Root in that foraging was primarily confined to the foliaged portions of the available habitat, most notably the outer most foliage of large mature trees. Hawking for insects was observed, but it was mostly confined to times when gnatcatchers were flying between trees. Occasional sorties low over the alfalfa were also observed, possibly, as mentioned by Root, to catch grasshoppers.

The use of indices such as niche breadth and overlap has been discussed by Cody (1974) but one point should be re-emphasized, that of weighting. The aspect of the Colwell and Futuyma (1971) calculations that make them so valuable is that the species themselves determine the weights of each of the resource states by their positions in the habitat, i.e. their use of each state. This type of calculation effectively eliminates the misconception that each of the subdivisions of the resource matrix is equally important to the species and, therefore, provides a more meaningful interpretation of the data. However, these calculations, to date, have been confined to one resource matrix at a time. What is needed, and is currently being worked on, is an n-dimensional habitat use matrix, i.e. one that will allow simultaneous analysis of several variables. It is possible to combine several variables into one by the construction of an index, such as an importance value, but in this type of statistic much information is lost.

It is frequently reported in the literature (Wiens 1969, James 1971, Anderson and Shugart 1974) that bird species select certain parts of the habitat based on specific search images. But care should be taken in emphasizing habitat keys. Perhaps the perceptual world (niche-gestalt) described by James (1971) is an artifact of the observer, i.e. the ecologist may be recognizing distinct habitats or positions along environmental gradients, but the bird species present may not be capable of the same distinctions or their distinctions may not be equivalent to those of the observer (Vandermeer 1972).

Vandermeer argues that the ecologist will never be able to view the niche through the eyes of a bird, even though the sensory systems are similar. However, if the goal of the ecologist is, as Bronowski (1973) stated, to have the ability to visualize the future and to foresee what may happen, i.e. gain an index of predictability, then placing the species along environmental gradients offers useful insights. Acknowledging the conceptual problems involved, it is still useful to derive axes that allow the scientist to predict the behavior of a species, particularly in respect to the concept of environmental change and its impact on the community. The validity of ordination work can be tested by subsequent field observation.

SUMMARY

Habitat relationships within a community of passerine birds were examined using multivariate statistical techniques and one index of niche breadth here termed "habitat use." Four species pairs were not significantly distinct when analyzed using multivariate analysis of variance. A 2-dimensional ordination along known vegetational gradients was constructed using principal component analysis. A regression line was drawn through this ordination providing a third gradient. Habitat use analysis defined several habitat generalists, including the Blue-gray Gnatcatcher and Brown-headed Cowbird, and several habitat specialists, including the Willow Flycatcher and Blue Grosbeak. Reasons for taking care in discussing avian habitat selection were presented.

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BREEDING DISPLAYS OF THE LOUISIANA HERON

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Information on the breeding behavior of herons is for the most part not sufficiently detailed to permit comparative analysis. However, as a consequence of modern ethological research methods and theory (see, for example, Lorenz 1950, Tinbergen 1952, Hinde 1970), the behavioral patterns of numerous species of ardeids are now better understood. Meyerriecks (1960), while concentrating on the breeding behavior of the Green Heron (*Butorides virescens*), also made a preliminary study on the Great Blue Heron (*Ardea herodias*), Snowy Egret (*Egretta thula*), and Reddish Egret (*Dichromanassa rufescens*). Later, Meyerriecks (1962) synthesized what was known at that time of the breeding behavior of all North American ardeids. Blaker (1969) recently completed a detailed monograph on the breeding behavior of the Cattle Egret (*Ardeola ibis*).

The objective of this paper is to present detailed information on the breeding displays of the Louisiana Heron (*Hydranassa tricolor*). Each display is discussed with respect to its form, function, and possible evolutionary origin.

METHODS AND STUDY AREA

Most field observations on the Louisiana Heron were made on Grand Island, Barataria Bay, Louisiana, during 1972 and 1973. The predominant vegetation growing on Grand Island is black mangrove (*Avicennia nitida*) and saltmarsh cordgrass (*Spartina alterniflora*). I studied Louisiana Heron behavior for over 900 h from 2 observation blinds. Observations were made with 7× binoculars and were documented by tape recordings and photography (35 mm still and 8 mm movie). The line drawings and diagrams in the text were made from field notes or photographs.

DISPLAYS

While the displays of the Louisiana Heron have been treated in summary form by various authors (see Noble in Bent 1926, Meyerriecks 1962), a detailed description of the individual displays and the role they play in the overall reproductive cycle has not been presented. In furnishing such a description, I have adhered as closely as possible to the terminology of Meyerriecks (1960, 1962).

Agonistic Behavior

Scott (1956) defines agonistic behavior as any behavior associated with conflict or fighting. The behaviors treated in this section are grouped together because they exhibit the most obvious external signs of agonistic behavior.

Alert Posture.—In assuming an Alert Posture, a Louisiana Heron extends the head upward, holds the wings tight to the body, the neck and legs become very straight, and the body axis is oriented toward the vertical. The feathers all over the body, including the white crest plumes, are sleeked; and the head is oriented in various directions as the bird attempts to locate the disturbance. Frequently the heron utters a "*scaah*" vocalization. I did not observe tail-flipping as described for the Green Heron (Meyerriecks 1960) as a part of the alert behavior of the Louisiana Heron.

Territorial males are quick to rise to the Alert Posture at the slightest disturbance. Neighboring birds readily react to nearby herons and also assume the Alert Posture. A Louisiana Heron that has been startled while incubating or brooding exhibits this behavior and the "*scaah*" call when observing the surroundings or when returning to its nest or territory after having been driven away.

The Alert Posture, with sleeking of the feathers, holding the wings to the body, and extension of the head upwards exhibits preparatory components of taking-off and may be derived from the intention movements of flight. Meyerriecks (1960) believes the amount of neck extension reflects the degree of escape tendencies; the greater the escape tendency, the greater the extension of the neck. Often associated with the Alert Posture is repeated sleeking and partial erection of the crest and upper neck feathers. Just as the sleeking component may indicate escape tendencies (Meyerriecks 1960), the erection component may indicate aggressive tendencies. Aggressive behaviors such as the Upright display are characterized by partial erection of the crest and upper neck feathers by Louisiana Herons.

Upright display.—This aggressive display is characterized by the extension of the neck to an almost vertical position above the body, orientation of the bill horizontally, and a moderate amount of feather erection of the crest and the upper and lower neck. The Upright may be accompanied by a nasal "*aaah*" call which is probably indicative of a more aggressive behavior, since this sound also is a component of other aggressive displays (described below). The Upright is generally performed at the approach of an intruding heron or some other disturbance. Most often, a trespassing heron is intimidated by the Upright and flees or at least halts its approach. The Upright is observed in other situations. For example, a Louisiana Heron returning to the heronry exhibits the Upright when preparing to feed its nearly fledged juveniles as they approach the parent.

Forward display.—The Forward display is characterized by extreme erection of the crest, the feathers of the upper and lower neck, and the scapular aigrettes. The white crest plumes point upward almost perpendicular to the head. From a front or rear view of the head, the erected white crest plumes take on a multipronged appearance that calls attention to the head and the bill, the heron's weapon. The head and neck are extended fully upwards, with the bill held horizontal and the bends of the slightly drooped wings exposed.

The Forward display usually intimidates an intruding heron and thus ends the confrontation without further interaction. If the intruding heron continues to approach and violate the territory, the resident heron then usually attacks. In what Meyerriecks (1962) calls the Full Forward display, the mandibles are open, and the wings are fanned out to the sides with the dorsal surface facing the opponent. The extension of the wings out to the sides and the extreme feather erection greatly increases the apparent size of the heron and probably heightens the threat or intimidation effect of the display. From a crouched posture, with the neck partially retracted, the heron lunges at its opponent while emitting an "*aaah*" vocalization. At the fullest extension of the lunge, the mandibles are closed producing a snap which is audible at 3 to 5 m. If the attacking heron is on the ground, it frequently runs toward its opponent with the wings held out to the sides while giving several "*aaah*" calls. Often the attacking heron chases after the fleeing bird as far as 15 to 20 m away from the nest. In flight, the legs dangle beneath the pursuing heron, the head is held up, and the neck is coiled in an S-shaped position. Rapid forward extensions of the head occur as the heron lunges at the escaping bird.

Aerial fighting.—Highly aggressive interactions occasionally include 2 Louisiana Herons flying up from the ground or top of a bush, attaining heights of up to 15 m. During the encounter the fighting herons often give loud "*aaah*" calls as they repeatedly lunge their bill and thrash their feet at one another. The wings beat rapidly, as each heron faces its opponent. Aerial fighting between males contesting territorial boundaries is common during the courtship period.

Twig Shaking.—Twig Shaking is characteristic of unpaired male Louisiana Herons during the courtship period, and is also performed by paired males and females in conflict situations. While Twig Shaking, the heron leans forward, extends the head out and down and grasps a twig in the nest or a nearby branch. During this action the feathers of the crest and upper and lower neck regions are moderately erected. The twig is then shaken from side to side.

The intensity of Twig Shaking varies with the circumstances surrounding its performance. During more intense Twig Shaking, the nest or branch sways from the force exerted by the displaying heron. For example, an unpaired male often performs vigorous Twig Shaking during the approach of a female or a neighboring male. In less intense forms of Twig Shaking, the twig or branch is merely grasped or only slightly shaken.

Twig Shaking may be a low intensity Snap, without a prominent downward pumping motion. These displays include similar feather erection and body posture. Arguments against Twig Shaking being a Snap are as follows: (1) In the Snap a twig is only sometimes grasped. (2) The downward pump observed in the Snap is absent in Twig Shaking. (3) Twig Shaking appears to exhibit more aggressive tendencies than the Snap. Territorial males frequently Twig Shake before or during a border confrontation with a neighboring male, but they do not perform the Snap in such a situation. (4) Only unpaired male Louisiana Herons perform the Snap, while both males and females perform Twig Shaking.

The side-to-side movements that accompany Twig Shaking resemble the twig placement and rearrangement that are part of nest building behavior. This may indicate that Twig Shaking is derived from some component of nest building, though twig arrangement lacks feather erection and vigorous twig manipulation. However, Twig Shaking in the Louisiana Heron appears to be a redirected agonistic behavior vented toward an inanimate object such as a twig, or to be in the process of evolving into a "full" display. The erection of the feathers appears to indicate aggressive tendencies. Blaker (1969) speculated that Twig Shaking in the Cattle Egret is aggressive in origin and function. I observed no obvious signal function of Twig Shaking as it exists in the Louisiana Heron, and designate it as a display at this time only for comparative purposes.

Tail-flipping.—Tail-flipping, as described for the Green Heron by Meyerriecks (1960), was not observed in the Louisiana Heron.

Withdrawn Crouch.—A Louisiana Heron assumes the Withdrawn Crouch in the presence of another Louisiana Heron, especially when the first heron is being threatened or attacked by the second. In the Withdrawn Crouch, the feathers are sleeked, the legs bent, and the head and neck are tucked back onto the body so that the horizontal posture presents a relatively low profile. The bill is held either horizontal or downward, never in an upward direction or toward the opponent. This is also the case in the Green Heron (Meyerriecks 1960) and the Cattle Egret (Blaker 1969).

The Withdrawn Crouch apparently serves to reduce the aggressive tendencies of the attacker. Female Louisiana Herons usually assume the Withdrawn Crouch during their approach toward a displaying male. Darwin (1872) and Morris (1956) have pointed out that a submissive posture in overall form is often the opposite of aggressive postures in a species. Such is indeed the case with the Louisiana Heron. In the Withdrawn Crouch the heron shows intention movements (terminology of Daanje 1950) of takeoff such as feather sleeking, crouching, and tucking in the head to the body, thus indicating possible escape tendencies.

Wing Preen.—When a female Louisiana Heron approaches an unpaired male during the courtship period, the male begins rapid and intense preening. This preening differs markedly from the slow, smooth motion of normal preening. In preening performed between courtship displays, the heron droops 1 wing slightly and then runs the bill down through the primaries 1 or more times in succession (once 64.9%, twice 30.9%, 3 times 4.0%, 4 times 0.2%; N = 126 performances). Blaker (1969) describes a similar behavior of Wing Touching in the Cattle Egret. While Wing Preening is very stereotyped in form in the Louisiana Heron, I did not observe any indication of its signal function.

Agonistic display discussion.—The form and vocalizations of the agonistic displays of the Louisiana Heron are similar to other North American ardeids, especially the Reddish Egret (Meyerriecks 1960). Only twice did I observe a display corresponding to Meyerriecks' (1962) description of the Aggressive Upright Threat for the Louisiana Heron. Both instances were brief encounters and an accurate description was not made.

Snap and Stretch Displays

The Louisiana Heron appears to be unusual among North American ardeids in that it tends to perform the Snap and Stretch displays in one sequence, and for purposes of description they will be treated as a unit. Snap and Stretch displays are performed only by the male Louisiana Heron, either from the nest or less frequently, from some other site on the territory. Both displays cease after pair formation. The form and sequence of movements are as follows:

(1) In one smooth motion the male moderately erects the scapular aigrettes and the feathers of the crest, upper and lower neck, leans slightly forward, and extends the head fully outwards (Fig. 1A) and downward until the bill is perpendicular and near or below the level of the feet (Fig. 1B).

(2) The legs bend almost completely and the wings droop slightly as the body drops quickly downward. The head is thus lowered well below the nest. In its extreme downward position, the male usually grasps a branch of the mangrove and shakes it with twisting side-to-side motions of the bill (Fig. 1C). This concludes the Snap portion of the sequence.

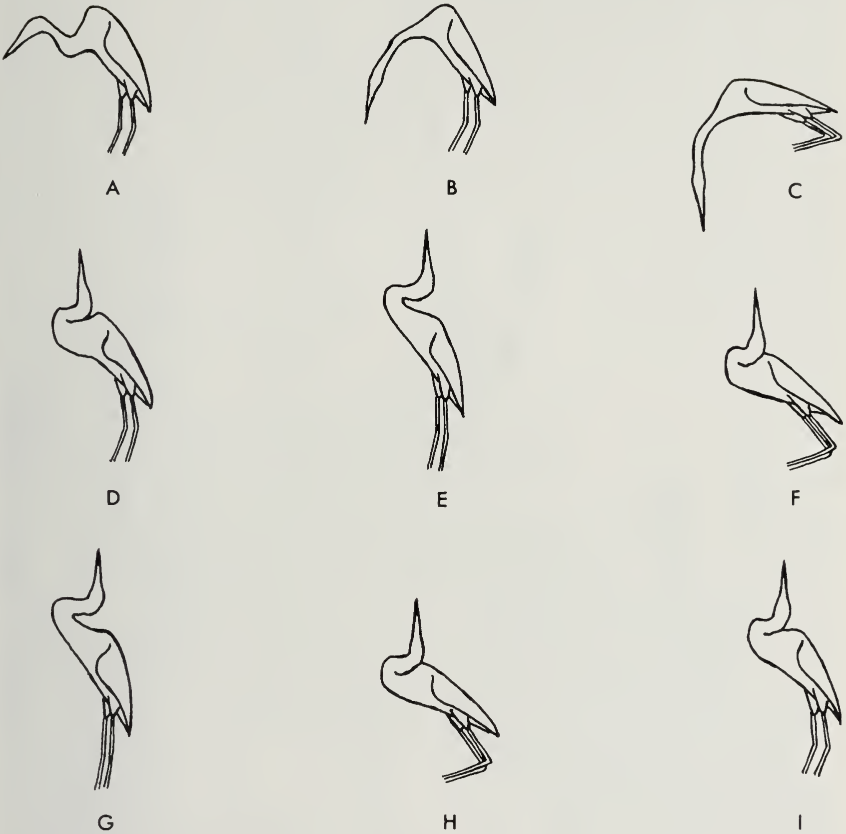

FIG. 1. Snap-Stretch display sequence. A–C, components of the Snap; D–I, components of the Stretch. See text for a discussion of the movements.

(3) In one smooth motion, the head is raised and laid on the mantle region, with the bill pointed toward the zenith. At this point the body axis is oriented about 60° above the horizontal, the wings are held tight against the body, and the legs are partially straightened (Figs. 1D, 2). Moderate feather erection is still present.

(4) The legs straighten lifting the body upward, and the wings begin to open and droop slightly as the heron approaches the maximum height. At the pinnacle of the upward motion, the neck is partially uncoiled and the head is lifted clear of the mantle region (Fig. 1E). Meanwhile, the eyes bulge and the mandibles begin opening.

FIG. 2. The Stretch display performed by a male Louisiana Heron from its nest.

(5) As the head lowers onto the back the legs bend, causing the body to descend toward the nest, and the wings are further opened and partially extended out to the sides (Fig. 1F). During this downward pumping motion, the mandibles are brought together to produce a mechanical "snap" sound.

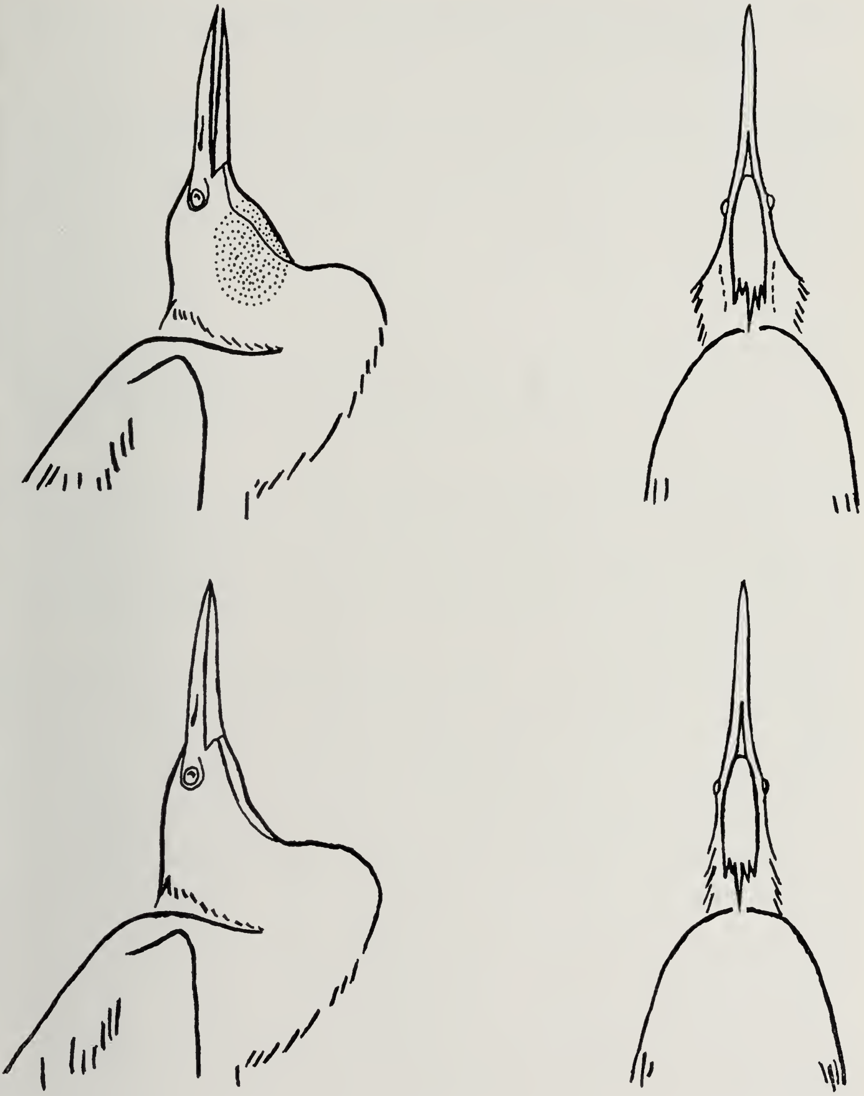

FIG. 3. Swelling of the throat region (indicated by stippling) in preparation for the "*unh*" call of the Stretch display (above) and deflation during the call (below).

(6) Steps 4 and 5 are usually repeated once or twice (Fig. 1G–H). After the last downward pump, the heron rises and assumes the posture described in step 3 and now usually gives one or more low-pitched, resonant "*unh*" calls. Each call is accompanied by swelling and de-

> flating of the throat and upper region of the neck as the bill is slightly opened then closed (Fig. 3). During this calling the head often relaxes slightly off the vertical.

Ending the display, the male lowers the head and turns it from side to side, looking around the heronry, possibly to locate females in the vicinity.

Excluding the calls, a normal Snap-Stretch requires 3 to 5 sec depending on the duration of the twig-grasping component. High wind velocities can either prolong individual performances or result in a decrease in frequency.

A great deal of variation occurs in the Snap-Stretch of the Louisiana Heron. The male may (88.4%, N = 96 displays) or may not grasp a twig in the downward stroke of the Snap. In 7 displays I observed, the male grasped and released one twig, then seized a second before performing the Stretch. Sometimes the shaking is so slow and deliberate that no movement of the mangrove tree results, but often such force is exerted that the nest or mangrove moves. The downward pumping in both the Snap and the Stretch varies from smooth, unhurried movements, to rapid and forceful ones. The presence of a female near the displaying male seems to increase the probability of forceful performances of both displays. In some Stretch displays, during the upward lift of the body and head, the bill may leave the vertical (sideways or backwards) by as much as 15 to 20°.

Though the Stretch is most often immediately preceded by the Snap, male Louisiana Herons sometimes perform the Stretch alone. These were most often associated with the sudden appearance of a female (14 of 17 observations) and may indicate a high degree of excitation on the part of the male.

The Snap too may occur by itself. Meyerriecks (1962) applies the term "low-intensity" to these isolated Snaps. However, I observed Louisiana Herons performing Snaps characterized by vigorous twig seizing and forceful downward pumping motions, without adding a Stretch. Isolated vigorous Snaps were observed at all stages of the courtship phase right up to copulation. The frequency of Snaps that occur outside the Snap-Stretch association varies among individuals at similar stages of reproductive activity and tends to increase in each individual as its courtship period advances. For example, male A1 in a period of 60 min performed 49 Snap-Stretch sequences and 15 isolated Snaps. Male B3 in a period of 38 min exhibited 44 Snap-Stretch sequences and 22 isolated Snaps. In these instances, any isolated Snap that appeared to be an interrupted Snap-Stretch sequence was discounted, and A1 and B3 both had been displaying continuously since the early morning about 6 hours earlier.

Since all other ardeids thus far investigated perform the Snap and Stretch separately, the linkage of the Snap and Stretch in the Louisiana Heron appears to represent a derived condition. I suspect that the Louisiana Heron is

TABLE 1
VARIATION IN NUMBER OF PUMPS AND CALLS PER STRETCH DISPLAY

	Character	Range	Mode	Mean[1]
male A1[2]	pumps	1–4	2	2.0
(N = 136)	calls	1–6	4	2.4
male B3[2]	pumps	1–3	2	1.8
(N = 117)	calls	1–10	5	3.1
total displays[3]	pumps	1–4	2	1.9
(N = 438)	calls	1–10	4	2.6

[1] Mean values include displays that possessed no calls.
[2] Data for males A1 and B3 were collected during the 1973 breeding season.
[3] Data for total displays are for the 1972 and 1973 breeding seasons.

still in the process of evolving the Snap-Stretch association, since the Snap and Stretch are at present also performed separately.

The number of upward and downward pumping motions (1 to 4 per display) and the number of calls (0 to 10 per display) vary among males and among performances by a single male. In Table 1, the 2 males showed individual variations in the number of components of the Stretch, but differed greatly only in the number of calls per display. Twenty-one % of 438 Stretch displays included no call. Blaker (1969) reported that 37% of 27 Stretch displays performed by unmated male Cattle Egrets possessed no call. Meyerriecks (1962) stated the number of pumps performed by Louisiana Herons at Lake Alice, Florida, varied from 1 to 4 with 3 being most typical.

A variation observed only 9 times was the alternation in the sequence in which pumps and calls were performed in the Stretch. Following a Snap, a male pumped twice, gave one call, then two more pumps and three calls without performing another Snap. Another male performed the Snap, did 2 pumps, gave 1 call, followed by another pump and 3 calls. A third male performed the Snap, did 1 pump, gave 1 call, followed by another 1 pump and 1 call.

Variations were also noticed in the "*unh*" calls between individuals. While no recordings were analyzed, I could distinguish differences between some displaying males. The "*unh*" vocalization varied from soft and low-pitched to harsh and loud.

The large variability in the performances of the Snap and Stretch requires some comment. Those courtship displays with a greater number of each component may make the displaying male more obvious and convey more information to a potential mate and possibly neighboring males. Morris (1957) has pointed out that display postures that exhibit differences from one performance to another indicate that only a "typical intensity" for the display has developed. With a high or low motivational state on the part of the performing animal, minute variation in the form of even the most "fixed" display can be detected. In the Louisiana Heron, the form and vigor of the Snap and Stretch varies with the amount of stimulus (e.g., the presence of a female and sexual state of the male). Finally, since both morphological and behavioral characters are in large measure genetically determined among birds, and since anatomical features are known to vary from individual to individual, variations on either side of the central tendency for the phenotypic expression of a fixed action pattern should not cause surprise.

Various anatomical features of the Louisiana Heron are accentuated by the Stretch. The magenta iris, black bill tip, turquoise-cobalt orbital skin, and white throat are made more conspicuous by the vertical motions of the displaying male. The white of the throat, belly and partially opened wings, are particularly obvious in a frontal view from a distance of more than 30 m away as the male moves up and down during the Stretch. These anatomical and behavioral features may be functioning as individual releasers or all acting together in heterogeneous summation (Seitz, *in* Tinbergen 1951) to render the Stretch more obvious.

Both the bill-snapping and the "*unh*" call of the Stretch also focus attention on the displaying male. With wind velocities of less than 10 km per hour away from the observer, both the call and the bill-snapping are audible from as far away as 10 m. These sounds alone may serve to notify females wandering through the heronry of the presence of the displaying male, even one that is displaying from a site in dense vegetation and not visible from more than 3 to 4 m away. Because greater wind velocities interfere with the perception of the sounds, the visual clues are probably the primary factors attracting females to the displaying male.

Discussion.—The erection of the crest, upper and lower neck, and scapular aigrettes during the Snap-Stretch may be indicative of agonistic components in the Louisiana Heron. There is an increase in the degree of feather erection by the male in the presence of a female. Still, the Snap-Stretch sequence is primarily sexual in function.

The Snap often possesses actual twig grasping in the Louisiana Heron, whereas the same display of the Green Heron and the Great Blue Heron rarely exhibit twig grasping (Meyerriecks 1960, 1962). In addition, the Snap of the Louisiana Heron is not of the bowing type as performed by the Reddish Egret (Meyerriecks 1960). The Snap of the Louisiana Heron appears to be unusual in 2 respects: it is often associated with the Stretch to form a single behavioral sequence, and the Snap possesses a downward pumping motion. Douglas Mock (pers. comm.) has informed me that the Great Egret (*Casmerodius albus*) also possesses a downward pump in its Snap.

The Stretch of the Louisiana Heron exhibits 3 basic movements: head laid on back with the bill oriented skyward, upward jump off, and downward pumping motion. Daanje (1950) has suggested that the second phase of the Stretch (the "jump off") in *A. cinerea* is derived from the intention movements of preparing to takeoff in flight. The Stretch of the Louisiana Heron exhibits numerous components similar to the movements of taking off in flight, and may resemble the more primitive condition by retaining an actual "jump off" motion. Tomlinson (1974) reports a downward pumping motion and bill-snap in the Stretch of the Purple Heron (*A. purpurea*).

Circle Flight Display

The Circle Flight of the Louisiana Heron is performed exclusively by the male, and consists of the following movements:

(1) The heron bends its legs slightly and leans forward, head and neck are tucked against the body, and the wings held to the body in preparation for taking off. No feather erection is visible.

(2) The legs straighten, providing the thrust for jumping off, as the head and neck are fully outstretched. The bill axis is oriented slightly upward from the plane of the body, tail is spread, and the wings beat in slow, very deep strokes creating a loud "whomp-whomp-whomp" sound. The legs temporarily dangle below the heron during the initial takeoff, then are brought up and held straight behind, where they move up and down with each wing beat.

(3) The heron continues to gain altitude and distance from the takeoff site, wings still beating in slow, deep arcs and head fully extended, for as far as 10 to 12 m.

(4) The midsection of the neck begins showing formation of a downward bend, and soon the head is tucked back onto the mantle region.

(5) As the deep wing flapping gives way to normal wing beating, the heron assumes the normal flying posture. The heron turns from a straight flight line, flies in a roughly circular path going past the territorial bush, executes another sweeping turn, and approaches the territory in basically a straight flight path.

(6) When 10 to 25 m from the nest, the bird fully extends its head. The legs begin moving up and down again, then finally drop downward. The tail is spread fully, and the wings are alternately flapped rapidly and held motionless for gliding.

(7) The heron begins giving a long series of "*culh-culh*" vocalizations while moving the bill in up and down motions. The number of these

calls ranges from 5 to 12 per display. There usually is erection of the crest and upper and lower neck feathers, and aigrettes as the heron begins descending toward the nest. The vocalizations continue, with the gliding giving way to rapid wing-flapping, as the heron slows its flight.

(8) The legs are lowered as the heron lands on its territory, usually on or near the nest. Landing is usually followed by a continuation of head nodding motions with additional calls (Fig. 4). When these nodding motions cease, so do feather erection and vocalizations.

In general, the male Louisiana Heron takes off into the wind when performing the Circle Flight display. Initial Circle Flights at the beginning of the courtship period may cover a path as large as 50 to 75 m in diameter. This circuit begins shrinking as the courtship period continues, and dwindles to its shortest dimensions just before pair formation, as small as 20 to 25 m in diameter. On windy days, the takeoff distance is greatly reduced, and the head is tucked in sooner. Under these circumstances, the male usually flies a greater distance past the nest bush and an exceptionally long approach distance results.

The Circle Flight is performed less frequently than the Snap-Stretch or even the isolated Snap. The length of a performance of the Circle Flight ranges from 15 to 20 sec, depending on the size of the arc the male flies. Its rate of occurrence increases when a female Louisiana Heron is nearby, but her presence is not essential. It also becomes more frequent with the passage of time after the male first establishes a territory.

Most variations in the performance of the Circle Flight are probably due to external conditions. The effect of high wind velocities has been discussed. If a male has a nest deep in dense bushes that prevents an immediate takeoff, he must climb to an open site for takeoff. During this climb the wings are drooped and partially extended out to the sides for balance. Often the male does not return to the takeoff site, but lands on another part of his territory. Sometimes he even drops onto the territory of a neighboring male and is driven off. Occasionally a returning male diverges from the straight-line return to attack another Louisiana Heron in the vicinity of his territory, or one that has flown onto his territory during the Circle Flight.

While females apparently do not perform this display, frequently as many as 3 female Louisiana Herons were observed following a single male during a Circle Flight. The flight of the females on these occasions resembled normal flight with the following exceptions: shortly before landing, the females extended their heads forward and often gave several "*culh-culh*" calls; after landing they often engaged in head nodding and calling. On such occasions

Fig. 4. Male engaged in the "Greeting display" phase of the Circle Flight after landing on the nest bush. Compare this posture with that in Fig. 5.

the females made fewer calls than the male. Meyerriecks (1960) reported mutual performance of the Circle Flight by male and female Green Herons, Reddish Egrets, and Snowy Egrets.

The posture assumed by the male and vocalizations he gives in his approach to the nest are the same as in the Greeting display, engaged in by both the male and female Louisiana Heron after pairing. In many instances, the female was observed to jump onto the nest bush as the male returned and to join him in head nodding and calling. However, the male usually chased the female away. As is the case with the Snap and Stretch displays, the Circle Flight is no longer performed after pair formation.

Discussion.—I agree with Meyerriecks (1960) that the Circle Flight is more indicative of sexual than hostile behavior. The Circle Flight display probably functions to attract potential mates.

The Circle Flights of the Louisiana Heron and Reddish Egret are similar. The Reddish Egret performs head-tossing movements and "*crog-crog*" vocalizations during the return approach to the nest (Allen 1954, 1955). Meyerriecks (1960) calls the aerial displaying the "Aerial Stretch display" and the component performed after landing the "Stationary Stretch display." Further discussion of the return flight of the Circle Flight is found in the section describing the Greeting display.

Bill-nibbling

Bill-nibbling is performed by both male and female Louisiana Herons. It is common during precopulatory and postcopulatory behavior and as a part of the greeting ceremony after pair formation. A series of sounds resembling gentle "rattling" is made by rapidly opening and closing the mandibles. The bill is usually oriented downward towards the nest, but either sex often extends the nibbling mandibles over and around to the sides of its mate. Louisiana Herons were also observed to move the nibbling mandibles in side-to-side shaking motions in front of the mate. The mandibles are sometimes laid on or into the feathers of its mate, but I have not observed feather grasping such as reported for the species by Huxley (in Bent 1926) and Meyerriecks (1962). No feather erection was noted during Bill-nibbling.

Bill-nibbling functions in appeasement and reducing hostile tendencies between 2 herons. During precopulatory encounters, the female performs Bill-nibbling in association with the Withdrawn Crouch and seems to reduce the male's aggressiveness towards her. In this instance, the bill is oriented downward or away from the male and is not waved over and around him.

Discussion.—Laying the nibbling mandibles on the feathers and waving them over and around the mate probably represents ritualized allopreening (Hudson 1965). Hudson (1965) and Blaker (1969) summarize the presence of Bill-nibbling in the Ciconiiformes.

Greeting Ceremony

This is not a display, but rather a relatively rigid display sequence. The greeting ceremony is composed of the Greeting display, Bill-nibbling, and often twig passing. The male Louisiana Heron constructs the foundation of the nest by himself during the courtship period, but after pair formation the labor is divided. Both engage in a greeting ceremony which is characterized by the male bringing nest twigs and passing them to the female who works them into the nest and finishes the structure. This results not only in the nest being completed, but also in reinforcing the new pair bond.

FIG. 5. Greeting display performed by a new pair of Louisiana Herons. The male (left) holds the twig skyward in his bill as he passes it to the female. Note the amount of feather erection by both herons.

A male performing the Greeting display returns to the nest with a twig in his mandibles and extends the head fully upward and exhibits extreme feather erection of the crest, upper neck, to a lesser extent the lower neck, and the aigrettes. Simultaneously, the wings are held out to the sides, and the bill, with the twig in the tip, is pointed repeatedly toward the zenith, then downward toward the nest, while the male gives several "*culh-culh*" calls (Fig. 5). The female on the nest engages in the same behavior as she reaches out and takes the twig in her mandibles from the male. Both herons head-nod several more times, giving additional calls, and the pair usually engages in Bill-nibbling. Feather erection ceases soon after the female places the twig into the nest as the male looks on intently. The male then leaves, and the procedure is repeated again until the nest is completed. If the nest is erected deep inside a dense mangrove bush, the male extends his head down into the bush and the female reaches up from within the foliage to take the twig.

As the ceremony is repeated again and again, there is a noticeable decrease in the degree of feather erection, amount of head nodding, and number of calls. The crest, feathers of the upper neck, and aigrettes are not erected as much as during the period immediately after pair formation, when twig passing behavior began. Erection also lasts a shorter time in the later stages. The male may nod his head only once or twice and give just a few calls, and the female in response may simply reach out and take the twig from the male after only a single head nod toward the zenith. In some instances, the female engages in the ceremony and works the twig into the nest without rising from the prone position. This variation is especially frequent during the incubating and brooding phases.

After nest construction is completed and the eggs are laid, one heron remains away from the nest for long periods of time while its mate assumes incubating or brooding duties. Upon return of the mate, both herons engage in the ceremony during nest relief. As the returning mate begins an approach glide of 15 to 20 m toward the nest it extends its head fully outward, much as in the approach phase of the Circle Flight. Feather erection, head nodding, and vocalizations are identical to those of the Greeting display. The returning bird never lands directly on the nest, but on top of the nest bush or one nearby, maintaining the fully extended head. The wings are held away from the sides, and head nodding and calling continue. The heron then begins moving toward the nest while continuing this posturing and calling. Its mate then begins reciprocating, and the pair engages in the Greeting display while face to face or standing side by side. Bill-nibbling usually is performed by both herons during this time. The relieved heron then flies away, leaving the nest duties to the returned male. If the incubating or brooding heron fails to rise from the nest when its mate returns, the newly arrived heron continues performing the greeting ceremony, with intense Bill-nibbling until its mate rises off the nest.

Often the mate that has been relieved flies off a short distance, finds a twig, then returns and presents the twig to its mate while performing the Greeting display. This is done repeatedly with as many as 9 twigs presented in a period of 5 min, though 2 to 3 twigs in 2 min is more common. After the twig is passed, it is then added to the nest. Twig passing is common during the incubating and early brooding phases, especially if the relieved bird has been on the nest for a long period, and may persist until late in the breeding cycle when the nestlings are up to 2 weeks old. The nest at this time is still in good condition and probably does not require additional twigs for repair. I believe the twig passing behavior and greeting ceremony under these circumstances serves primarily to reinforce the pair bond during a period when the partners are separated for great lengths of time. The role of the greeting ceremony in pair bond maintenance for several North American ardeids is discussed by Meyerriecks (1962). Although sex identification after pair formation is often impossible because of fading soft part colors, I believe both male and female Louisiana Herons engage in this behavior to about the same degree. This conclusion is supported by observations on many pairs that performed several nest reliefs during the day, in which, each member of the pair returned with twigs after being first relieved by its mate.

The number of calls uttered by a heron varies from 2 to 17 during the Greeting display. It is my impression that more calls are given when the pair has been separated for a period of time.

Performances of elements of the Greeting display were observed under different circumstances from those noted above. Between long sessions of incubating or brooding, a lone parent often leaves the nest and moves a short distance away to preen or sunbathe. Upon returning to the nest, it often performs the Greeting display alone before resettling on the eggs or nestlings. This shows how spontaneous the performance of the display is when an adult Louisiana Heron returns to the nest. Under similar circumstances, but with older nestlings (1 to 2 weeks old), the parent is often met upon its return by aggressive, lunging snaps from its young. The adult may then perform the Greeting display which usually ends the aggressive behavior of the nestlings. When a territorial male moves towards an intruding female to attack and drive her away, the female Louisiana Heron occasionally performs the greeting ceremony (Greeting display with Bill-nibbling). The male sometimes returns the display but usually drives the female off during the early part of courtship. In late courtship, the greeting ceremony probably functions to reduce the male's aggressiveness towards the female until he allows her to stay on the territory. Fledged Louisiana Herons perform a similar greeting ceremony to one another. The display is enacted when 2 siblings approach one another after a time of separation.

By beginning the displays at a distance from the nest the incoming heron apparently gives its mate time to recognize the returning partner by sight or sound. This may safeguard against aggressive incidents that might occur between the pair members if the returning heron were to land suddenly. Fighting on the nest would be selected against if it upsets the nest itself or endangers the eggs or nestlings in it. The display occurs in several different contexts and seems to function in mate recognition, reduction of aggressive tendencies between mates, appeasement, and reinforcement of the pair bond in the Louisiana Heron. The last phase of the Circle Flight and the Greeting display are very similar, but in the return flight of the Circle Flight, no twig is grasped and waved up and down in the mandibles.

SUMMARY

The Upright display involves slight feather erection of the crest, upper neck, while the heron raises the head upward. In the Forward, the heron exhibits extreme erection of the crest, upper and lower neck feathers, and aigrettes while the head is extended upward. Both aggressive displays are typically accompanied by the "*aaah*" call. While Twig Shaking, the heron moderately erects the crest, upper and lower neck feathers, and aigrettes as it extends the head out to grasp and shake a branch.

The Louisiana Heron appears to be unusual in that it tends to combine the Snap and Stretch displays into 1 sequence, though each is observed being performed separately. As the male moderately erects the crest, upper and lower neck feathers, and aigrettes, he extends the head out and down with the bill oriented downward. Bending of the legs results in a lowering of the head and body. At the farthest downward extension, a branch is usually grasped. Thereupon, the Snap ends. Next, the heron rises, lays the head on the mantle, and orients the bill toward the zenith. In an upward movement, the head is partially lifted off the mantle, the wings begin to open and droop, and the bill is slightly opened. As the heron drops by bending the legs, the opened mandibles are snapped closed, and the wings are partially fanned out to the sides. The up and down motions are often repeated one or more times before the male returns to the head-on-mantle posture and gives the "*unh*" call. The intensity and number of each component in the Snap and Stretch vary greatly.

In the Circle Flight, the male jumps into the air, the head is extended fully outward and held there for an exaggerated amount of time as the wings beat in deep arcs. The head is then tucked back as normal flight is assumed in a circular path. As the male returns to the nest, the legs drop, the crest, feathers of the upper and lower neck, and aigrettes are erected, and the head is fully extended. Several "*culh-culh*" calls are given during this time.

Both male and female Louisiana Herons engage in Bill-nibbling, in which they open and gently close the mandibles and thereby create a "rattling" sound. This behavior is thought to function in appeasement and in reducing the agonistic behavior between herons.

In the Greeting display, the crest, feathers of the upper and lower neck, and aigrettes are erected, the head is extended up, and the bill usually holding a twig is repeatedly oriented to the zenith and then waved downward, as the heron gives several "*culh-culh*" calls. Bill-nibbling usually accompanies the Greeting display. This behavior is performed by both members of the pair during twig passing associated with nest building and the nest relief of an incubating or brooding mate. The greeting ceremony probably functions in appeasement, reducing agonistic behavior, and mate recognition.

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BREEDING BIOLOGY OF CLIFF SWALLOWS IN VIRGINIA

Gilbert S. Grant and Thomas L. Quay

The Cliff Swallow (*Petrochelidon pyrrhonota*) has recently extended its breeding range southeastward into the Piedmont regions of Virginia, North Carolina, South Carolina, Georgia (Tedards 1965, 1966, Scott 1966, Dopson and Peake 1967, Parnell 1967, Cohrs and Cohrs 1972), and Florida (Sykes 1976). This paper summarizes our studies of the breeding biology of one of these new populations of Cliff Swallows near the John H. Kerr Reservoir on the Roanoke River in the Piedmont of Virginia and North Carolina.

MATERIALS AND METHODS

Systematic examination of Cliff Swallow nests began on 12 June and ended on 21 August 1969. We gained access to nests by using a boat and a ladder. The nest contents were examined with a flashlight and a dental mirror.

Of the 36 bridges within the perimeter of the reservoir, only 7 had significant numbers of nesting swallows. We found 354 nests under these 7 bridges, but 84 nests were inaccessible, 90 were either always empty or partially destroyed old nests, and 39 were occupied by House Sparrows (*Passer domesticus*). Nest success data from 72 of the remaining 141 nests were used. The 69 nests excluded were either examined too infrequently or young were found on first examination of nest contents and clutch size could not be determined. The nests at 2 colonies, Goodall's Landing and Occoneechee, were examined at weekly intervals and the largest colony, Bluestone Landing, was visited twice a week. All of the 72 nests were in Virginia, on the upper reaches of the reservoir near Clarksville.

RESULTS AND DISCUSSION

Nest lining.—The lining of 119 active Cliff Swallow nests was recorded. Of these, 102 were lined solely with straw, 4 with straw and chicken feathers, 5 with straw and Cliff Swallow feathers, 4 with straw and unidentified feathers, 1 with straw and a material resembling cigarette filters, 1 with hair, and 2 had no lining at all. Nests have been found lined with straw, wool, and feathers (Davie 1898); grass and feathers (Forbush and May 1939); grass stems, feathers, and other materials (Bent 1942); straw or hay (Samuel 1971); and fine grasses with occasionally a few sticks, hairs, and feathers, but with many nests nearly devoid of any material (Emlen 1954).

Clutch size.—The mean clutch size of 60 nests that had only one brood for the nesting season was 3.32 ± 0.72 (Table 1) (range 2 to 5 eggs). Twelve nests had 2 complete broods. We were unable to determine the clutch size of the first brood in these, but the mean clutch size of the second brood was 3.00 ± 0.85 (Table 1), also with a range of 2 to 5 eggs. Mayhew (1958) felt that 3 to 4 eggs per clutch was the normal condition in California and Erskine

Table 1

Nesting Success of Cliff Swallows at Kerr Reservoir, Virginia

		Eggs			Young		% Total Nesting Success
Clutch Size	No. Of Clutches	No. Laid	No. Hatched	% Hatched	No. Fledged	% Fledged	
First Clutches							
2	6	12	11	91.7	11	100.0	91.7
3	32	96	79	82.3	74	93.7	77.1
4	19	76	61	80.3	51	83.6	67.1
5	3	15	11	73.3	9	81.8	60.0
Total	60	199	162		145		
Mean		3.32	2.70	81.4	2.42	89.5	72.9
S.D.		0.72	0.99		1.04		
Second Clutches							
2	3	6	4	66.7	4	100.0	66.7
3	7	21	15	71.4	15	100.0	71.4
4	1	4	3	75.0	3	100.0	75.0
5	1	5	5	100.0	4	80.0	80.0
Total	12	36	27		26		
Mean		3.00	2.25	75.0	2.17	96.3	72.2
S.D.		0.85	1.20		1.04		

and Teeple (1970) reported a mean clutch size of 3.74 in New Brunswick. Myres (1957) found the mean clutch size to range from 3.6 to 3.9 eggs (54 nests) in a British Columbia colony and Samuel (1971) found an average first clutch of 3.31 eggs (35 nests) and an average second clutch of 2.89 eggs (9 nests) in West Virginia.

Incubation period.—The length of time from the laying of the last egg to the hatching of the last young averaged 13.5 days (20 nests) in this study, ranging from 11 days (1 nest) to 16 days (2 nests). Using this same measure, Mayhew (1958) found the incubation period to be 16 days (2 nests) in California and Samuel (1971) found 15 days (7 nests) to be the mean in West Virginia. Myres (1957) took the incubation period to be 14 days, but stated 13 days may be more accurate and Burns (1915) gives 12–14 days. Cliff Swallows begin incubation the day before the last egg is laid (Mayhew 1958, Samuel 1971).

Brood size and egg mortality.—The mean brood size (number of eggs hatched per nest) was 2.70 ± 0.99 (Table 1) in the 60 first broods. Thirty-seven of 199 (18.6%) first-clutch eggs failed and there were 2 nest failures (no eggs hatched) in this sample. In the 12 nests with second broods, the mean brood size was 2.25 ± 1.20 (Table 1). Nine of 36 (25.0%) second-clutch eggs failed to hatch and there was only one nest failure in this group. Hatching failure may be due to infertility. Samuel (1971) found that 35.2% of all Cliff Swallow eggs laid (first and second broods) did not hatch.

Nestling period.—Samuel (1971) found that the period of time between hatching and leaving the nest averaged 23.6 days in 6 broods. Mayhew (1958) found first-flying young 23 days after hatching and Burns (1921) found young left the nest 16 to 24 days after hatching. One young made its first flight at 22 days at Kerr Reservoir. Cliff Swallows often remained in the nest several days after they were able to fly, making an exact determination of the duration of the nestling period difficult to compute.

Nestling mortality and total mortality.—The mean number of young fledged per nest was 2.42 ± 1.04 (Table 1) with a nestling mortality of 10.5% in the first broods. The total first-brood nesting mortality was 27.1%. Second clutches fledged 2.17 ± 1.04 young (Table 1) for a 3.7% nestling loss and a total nesting mortality of 27.8%.

More eggs hatched, more young fledged, and there was an overall higher nesting success in first-brood nests with smaller clutches (Table 1). Although the sample size was small, nesting success in second broods tended to increase with larger clutches. However, by multiplying percent total nesting success against clutch size it can be seen that the larger clutches produced more young despite a lower percent of fledging and hatching success in first broods. Greater success with larger clutches in second broods versus those of first broods was possibly correlated with insect abundance, but quantitative measurements were not made. Both weather and the experience or skill of the adults might have been better during second broods.

Samuel (1971) found a total nesting mortality (both clutches combined) of 41.5% in West Virginia, while the nesting mortality for all clutches at Kerr Reservoir was 27.2%. In Samuel's (1969) study, the high mortality was attributed to nest abandonment caused by barn alterations, House Sparrow interactions, fallen nests, and unknown reasons. We noted little influence of House Sparrows on the reproductive success of Cliff Swallows except under bridges with small numbers of swallows. No nests fell down during our study at Kerr Reservoir. Swallows nesting under bridges were obviously not subjected to the same set of losses incurred by those nesting inside of barns. Samuel (1969, 1971) believed that the unknown-reasons group may have included abandonment by birds joining migrating flocks. Foster (1968) also reported instances of Cliff Swallows departing as a colony and leaving eggs and nestlings behind in the nests. Five nests (3 with eggs and 2 with young) were abandoned for unknown reasons at Kerr Reservoir. The different colony sites involved and the asynchronous timing precluded the departing-as-a-colony phenomenon reported by Foster (1968) and Samuel (1969, 1971). Stewart (1972) reported heavy nestling losses in Cliff and Tree swallows (*Iridoprocne bicolor*) when adults abandoned young as a result of 24 hours or more of continuous rain. Although most birds had departed by 31 July, adults with young generally remained at these Virginia colonies until the last young left the nest (21 August).

Second broods.—Cliff Swallows typically raise one brood, although 2 broods have been suggested by Bent (1942) and McCann (1936). Samuel (1971) studied 9 pairs that raised 2 broods in West Virginia. The 12 second broods at Kerr Reservoir were all found in nests that had contained first broods earlier in the nesting season. It seems that 2 broods could occur commonly under optimum conditions at Kerr Reservoir. Grinnell (1937) found that 48 days elapsed between the day of first arrival and first-flying young and Samuel (1971) found this period to range from 38 to 48 days. Swallows were first noted on 12 April 1969 (our first visit; they probably arrived a few days earlier) and the last young left the nest on 21 August 1969. Thus, 132 days is more than ample time to accommodate 2 broods, but only 16.7% of the swallows completed 2 broods in 1969. Cliff Swallows arrive at nesting sites in successive waves of migrants (Mayhew 1958) and it seems probable that favorable spring weather could initiate early synchronous first clutches and thereby facilitate the completion of second broods.

SUMMARY

We studied the breeding biology of the Cliff Swallow in Virginia where it has recently become established as a new breeding bird. Data are presented on nest lining, clutch size, incubation period, hatching success, brood size, egg mortality, nestling period and mortality, and second broods. Little difference in breeding biology was found between the Virginia colonies and those in the remainder of their range.

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WEATHER INFLUENCES ON NOCTURNAL BIRD MORTALITY AT A NORTH DAKOTA TOWER

Michael Avery, Paul F. Springer, and J. Frank Cassel

Most studies of bird losses at towers have dealt with weather conditions in a general manner (e.g. Tordoff and Mengel 1956, Kemper 1959, Taylor and Anderson 1973) because losses usually were not monitored on a daily basis throughout the entire migration season. Thus, weather conditions prevailing on nights of large, spectacular kills have received the most attention. Such nights are usually characterized by overcast skies, often with precipitation, winds favorable for migration, and in the fall the passage of cold fronts (e.g. Brewer and Ellis 1958).

In the course of a study of bird migration and mortality at the U.S. Coast Guard's Omega Navigation Station, located approximately 3 km west of LaMoure, North Dakota in the James River Valley (Avery et al. 1975), it was apparent that while occasional large kills occurred on overcast nights, considerable losses took place throughout the migration seasons under non-overcast skies, particularly in the spring. Since mortality was monitored daily and accurate weather data were available from nearby, it was possible to analyze the losses with respect to cloud cover and wind conditions during 4 entire migration seasons.

METHODS

The 366-m Omega tower is supported by 3 sets of 5 guy wires (34.9–60.3 mm diameter) spaced 120° apart. The guy wires are attached at heights of 53, 109, 167, 228, and 293 m. The lower 2 guys are anchored 122 m from the tower, the next 2 at a distance of 213 m, and the last at 297 m. In addition, 16 evenly spaced transmitting cables (50.8 mm diam.) extend from the top of the tower to a circular perimeter road 732 m away.

Searches for tower casualties were made every morning at daybreak (except for 7 days) during the study periods: 30 March–4 June and 8 August–15 November 1972 and 2 April–2 June and 12 August–3 November 1973. Because the size of the tower site and the dense vegetation on it made it difficult to find all bird casualties, the area under the guy wires (approximately 168 ha) was divided into 4 concentric strata (Avery et al. 1975): A, 0–46 m (0.66 ha) from the tower; B, 47–92 m (1.97 ha); C, 93–183 m (7.88 ha); and D, 184–732 m (157.61 ha). During the daily searches, stratum A was checked completely. The approximate areas searched in the other strata were: B—0.37 ha (18.8%), C—0.50 ha (6.3%), and D—1.51 ha (1.0%). The location and condition of each bird were recorded as it was collected, and only specimens judged to have died during the previous night were included in the analyses presented here, unless stated otherwise.

Because official weather data are not available from LaMoure, hourly weather reports were obtained from the Federal Aviation Administration Flight Service Station at Jamestown, 72 km north-northwest of LaMoure. A few of the records were discarded inadvertently by the station prior to analysis; thus, cloud cover and wind data are not available for these nights. Each of the 225 nights for which we have records of cloud cover was characterized as overcast or non-overcast. Four classes of cloud cover are recognized in the official weather reports—< 0.1 sky cover, 0.1 to < 0.6, 0.6 to 0.9, and > 0.9. These were assigned the numbers 0, 1, 2, and 3, respectively, and the 13 hourly figures from 1800–0600 CST were summed. The mean was calculated and a night was designated overcast if the mean was ≥ 2.5. All other nights were called non-overcast. This distinction is somewhat arbitrary and, conceivably, if different criteria were used, slightly different interpretations of the data would result. Wind direction and estimates of cloud cover made at the Omega tower corresponded well with the official weather reports from Jamestown.

The mean, nightly, surface wind direction was calculated from the hourly records; and the mean directions were grouped into four 90° sectors. Nocturnal bird migration in this region is primarily along a northwest-southeast axis (Richardson and Gunn 1971, Avery et al. 1976), and in this paper winds are referred to as favorable if from the 106°–195° quadrant on spring nights and 286°–015° on fall nights.

Losses in the 3 most frequently killed families, Rallidae, Parulidae, and Fringillidae, were examined during their respective periods of peak migration as indicated by field surveys conducted several times weekly near the tower site. Only the losses on nights within each of these peak migration periods were used in these analyses. Chi-square goodness-of-fit tests were used to determine if, within each family, the losses occurring during the entire peak periods in each cloud-wind category were in the same proportions as the number of nights in those categories. The G-test (Sokal and Rohlf 1969) was used to ascertain independence between cloud cover and distance of kill from the tower (Table 4) and between cloud cover and season (Table 5). Prior to analysis, the data used in Tables 4 and 5 were corrected for differences in the area searched in each stratum. In all tests $p \leq 0.05$ was accepted as statistically significant.

RESULTS AND DISCUSSION

The 5, largest, single-night kills and the accompanying weather conditions are listed in Table 1. All occurred under an overcast sky with the exception of the night of 14–15 May 1972 which was moonless and clear. Weather data revealed no conditions of overcast or poor visibility anywhere in the region that night. The behavior of birds at the tower during the kills on overcast nights was generally similar to that described by previous authors (e.g. Cochran and Graber 1958) and is treated in more detail in another paper (Avery et al. 1976).

Although the largest collections of dead and injured birds were made following overcast nights, mortality occurred consistently on clear nights as well. Table 2 shows that during spring migration the percent of losses of rails and fringillids occurring on overcast nights was about the same as the rate of occurrence of those nights; however, spring mortality in warblers and fall mortality among all 3 families occurred on overcast nights in greater-than-expected percentages ($p \leq 0.05$).

During their peak periods of spring migration, rails and fringillids were

TABLE 1

THE 5 LARGEST SINGLE-NIGHT LOSSES AT THE OMEGA TOWER IN 1972 AND 1973

Night of kill	Birds found	Weather conditions during night
25–26 Sept. 1973	69	overcast, light rain, light ENE wind
4– 5 Oct. 1972	48	overcast, NE wind 5–15 k
14–15 May 1972	27	clear, light S wind
10–11 May 1972	25	overcast, drizzle, light S wind
21–22 Aug. 1972	23	overcast, NW wind 10–15 k

killed in significantly greater numbers on non-overcast nights with southeasterly winds than on nights with other conditions (Table 3). Conversely, warblers were killed in significantly greater numbers on overcast nights. In the fall, losses at night during peak migration periods under the various conditions of cloud cover and wind direction were distributed in about the same frequency as the occurrence of nights with these conditions except for warblers and fringillids which were killed in significantly greater numbers on overcast nights with northeasterly winds.

The high proportion of fall losses on overcast nights within 12 h after the passage of a cold front is consistent with other published reports (Brewer and Ellis 1958, Tordoff and Mengel 1956, Laskey 1960, Taylor and Anderson 1973). The fall losses presented in Tables 2 and 3 were due primarily to the few, large, single-night kills (Table 1), each of which was preceded by a cold front through the LaMoure area.

TABLE 2

PERCENT OF LOSSES OCCURRING ON OVERCAST NIGHTS AT THE OMEGA TOWER IN 1972 AND 1973

Family or group	Spring[1] (%)	Number of birds	Fall (%)	Number of birds
Rallidae	35	34	41*	22
Other non-passerines	36	11	50	10
Parulidae	64*	44	81*	135
Fringillidae	32	104	64*	100
Other passerines	48	57	70	46
Total	42	250	70	313
Percent of overcast nights	32		22	

[1] * Indicates statistical significance between % of loss and % of overcast nights.

TABLE 3

PERCENT LOSSES IN RELATION TO CLOUD COVER AND WIND DIRECTION AT THE OMEGA TOWER IN THE PEAK MIGRATION PERIODS IN 1972 AND 1973

Family	Cloud cover[1]	Surface wind quadrant[2]				No. of birds and (nights)
		NW 286–015°	NE 016–105°	SE 106–195°	SW 196–285°	
Spring						
Rallidae	o	20(27)[3]	40(39)	40(23)	0(12)	5(26)
	n	29(42)	12(16)	53(24) *	6(18)	17(55)
Parulidae	o	32(15)	0(23)	59(54) *	9(8)	22(13)
	n	20(47)	0(14)	50(25)	30(14)	10(36)
Fringillidae	o	21(15)	21(35)	57(40)	0(10)	28(20)
	n	3(43)	16(18)	68(27) *	13(12)	62(49)
Fall						
Rallidae	o	33(38)	67(31)	0(13)	0(19)	3(16)
	n	11(24)	11(20)	33(26)	44(30)	9(66)
Parulidae	o	23(13)	70(50) *	3(13)	4(25)	69(8)
	n	37(23)	21(27)	16(17)	26(33)	19(30)
Fringillidae	o	2(24)	91(24) *	2(29)	6(24)	54(17)
	n	20(24)	5(10)	10(27)	65(39)	20(41)

[1] o = overcast, n = non-overcast.

[2] * Indicates statistical significance between % of loss and % of nights with indicated weather conditions.

[3] % of nights in each wind category are in parentheses.

Spring losses were not characterized by large kills but were smaller and more evenly distributed throughout the season. There was no direct association of spring losses with frontal movements: the bulk of the losses occurred on nights with favorable (i.e. southeasterly) winds. Ceilometer observations made at the tower revealed that the bulk of spring migration took place on nights with southeasterly winds.

The percent of losses of birds recovered within various distances of the tower varied with cloud cover (Table 4). In each family or group the percent killed in stratum A on overcast nights was similar to that on non-overcast nights. Among rails and other non-passerines, the losses on non-overcast nights were distributed approximately evenly among the 4 strata. Losses to passerines on non-overcast nights consistently exceeded those on overcast nights in strata C and D. In each family or group, losses on non-overcast nights in stratum D were 3 or 4 times those on overcast nights. Non-passerines suffered substantially greater losses in the outermost stratum than did passerines, particularly on non-overcast nights. Overall, losses on overcast nights were concentrated near the tower in strata A and B, whereas losses on non-overcast nights were more evenly distributed, 9% occurring at least 184 m

TABLE 4

PERCENT OF LOSSES BY STRATUM AT THE OMEGA TOWER ON OVERCAST AND NON-OVERCAST NIGHTS IN THE 1972 AND 1973 MIGRATION SEASONS

Family or group[1]	Cloud cover[2]	Percent by stratum A	B	C	D	Number of birds
Rallidae	o	23	36	36	5	21
	n	22	28	28	22	35
Other non-passerines	o	43	21	29	7	9
	n	31	19	25	25	12
Parulidae*	o	44	43	13	1	137
	n	50	20	26	4	42
Fringillidae*	o	29	46	23	2	97
	n	30	35	28	8	107
Other passerines	o	34	38	27	2	59
	n	25	41	28	6	44
All birds*	o	36	42	20	2	323
	n	31	32	27	9	240

[1] * Indicates statistical significance between overcast and non-overcast nights.
[2] o = overcast, n = non-overcast.

from the tower. Within warblers, finches, and total birds, the distribution of kill by strata on overcast nights differed significantly from that on non-overcast nights.

Table 5 shows how the distance of kills from the tower varied with cloud cover and season. In both spring and fall, greater percentages of the seasonal losses were generally found in the 2 innermost strata under overcast conditions than under non-overcast. Conversely, in strata C and D, relatively more birds were found dead following non-overcast nights in both spring and fall than following overcast nights. When mortality between seasons is compared, spring losses were generally less than fall losses in strata A and B but exceeded the fall losses in strata C and D on both overcast and non-overcast nights. In both spring and fall, the differences in mortality between overcast and non-overcast nights within the strata were statistically significant and indicate that the distance of losses from the tower was influenced by cloud cover.

The differences in location of tower casualties in spring and fall is depicted in Fig. 1. This graph includes all of the tower casualties found in 1972 and 1973 and consists of raw data uncorrected for differences in areas searched. It shows that in each year the percent of fall losses exceeded those of spring within 92 m of the tower. Beyond 92 m the situation was reversed,

TABLE 5

PERCENT OF LOSSES BY STRATUM AT THE OMEGA TOWER ON OVERCAST AND NON-OVERCAST NIGHTS IN 1972 AND 1973

Season[1]	Cloud cover[2]	Percent by stratum				Number of birds
		A	B	C	D	
Spring*	o	34	34	28	4	104
	n	26	32	30	12	146
Fall*	o	37	45	17	1	219
	n	40	31	23	6	94

[1] * Indicates statistical significance in % of losses by strata between overcast and non-overcast nights.
[2] o = overcast, n = non-overcast.

except for the 184–229 m interval in 1972. These results, although not statistically significant in 1973, show that, except for this one exception, larger spring losses consistently occurred at greater distances from the tower than did fall losses.

Cloud conditions seem to have a considerable effect on the manner in which bird mortality actually occurs at the Omega tower. From the results obtained it appears that most fall mortality takes place when large numbers of birds are aloft on overcast nights. Such nights are usually closely associated with the passage of a cold front. On overcast nights, migrants congregate around the tower (Avery et al. 1976) and are killed near the structure by colliding with it, the guy wires and transmitting cables, or other birds. On the other hand, spring migrants are apparently aloft when winds are favorable, regardless of cloud cover (Table 3), and thus much mortality occurs on non-overcast nights when migrants are not congregated at the tower. On such nights, migrants actually seem to avoid the structure (Avery et al. 1976). Consequently, in the spring, sizable losses occur on non-overcast nights far from the central structure through collisions with outlying guy wires and the transmitting cables.

The regular occurrence of substantial bird losses on non-overcast nights is perhaps peculiar to the Omega tower with its widespread system of cables. Losses do occur on non-overcast nights at other towers with less extensive cable arrays (e.g. Stoddard and Norris 1967), but apparently they are not as great as at the Omega tower. Birds deviating from their flight path to avoid most towers may remove themselves from the danger of the supporting guy wires. The 16 transmitting cables extending from the top of the Omega tower, however, pose additional problems; and birds avoiding the tower, and hence the innermost supporting guy wires, are still liable to collide with the outer transmitting cables.

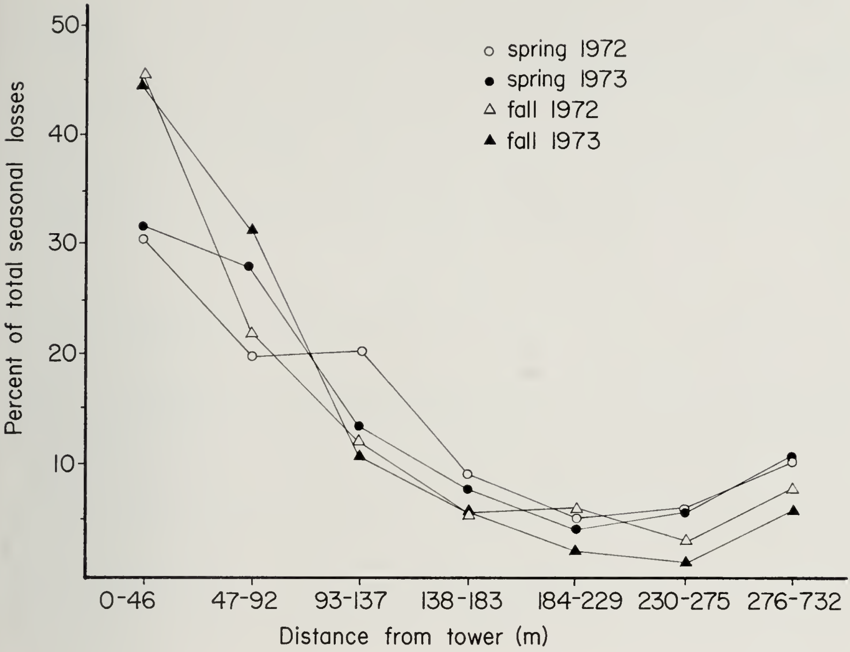

FIG. 1. The % of total seasonal losses collected at 46-m intervals from the Omega tower in 1972 and 1973.

Some of the differences in mortality among groups of migrants may be due to interspecific (or interfamilial) behavioral differences. For instance, at the Omega tower, warblers were prone to be killed close to the central structure (Table 4). Possibly warblers are influenced by red tower lights more so than are other groups, or perhaps warblers are less able to change direction to avoid inner guy wires than are other migrants. The sizable proportions of some kinds of non-passerines killed away from the tower, especially on non-overcast nights (Table 4), suggests behavioral differences that may be even more basic than family or group-level differences.

Overing (1936, 1937) also noted differences in the responses of various passerines to tall, lighted structures. On 20 October 1935, hundreds of Field Sparrows, *Spizella pusilla*, perched on benches at the base of the lighted Washington Monument; "None of these sparrows struck the monument that night, nor did they seem confused by the lights nor fly against the shaft, as the vireos and warblers were doing." The following fall, there was a similar occurrence. Of the 523 birds collected by Overing in the falls of 1935 and 1936, only 7 were fringillids. Further differences are suggested by Stoddard and Norris (1967) who noticed that during nights of heavy rainfall, fringillids tended to persist in their migratory flight while warblers, vireos, and thrushes sought ground cover.

No experimental evidence exists detailing differences among various taxa of nocturnal migrants in their response to tall, lighted structures. This area warrants more attention because conceivably such an investigation could lead to methods whereby losses of some species at towers can be reduced.

SUMMARY

An examination of the cloud cover and wind conditions that accompanied bird losses at a 366-m tower in southeastern North Dakota revealed that most fall losses occurred under overcast skies associated with the passage of cold fronts. In the spring, 58% of the mortality took place on non-overcast nights, generally with southeasterly winds. Rails were killed in relatively equal proportions on overcast and non-overcast nights in both spring and fall. Warblers were killed in significantly greater numbers on overcast nights in both seasons, as were fringillids in the fall. Losses on non-overcast nights tended to be distributed farther from the tower than were those on overcast nights. Fall losses were concentrated closer to the tower than were spring losses because fall losses occurred mostly under overcast skies as migrants milled about the tower. Spring losses seemed to occur primarily on non-overcast nights through collisions with outlying guy wires and the transmitting cables. Behavioral differences among species or families of migrants may be involved in migrant mortality at towers.

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BREEDING BIOLOGY OF HOUSE SPARROWS IN NORTH MISSISSIPPI

James N. Sappington

Detailed studies on various aspects of breeding biology of the House Sparrow (*Passer domesticus*) have been made in Europe (e.g., Summers-Smith 1963; Seel 1968, 1970; Mackowicz et al. 1970) and in the United States (e.g., Weaver 1943, Mitchell et al. 1973, North 1973, Will 1973). This study was conducted in Oktibbeha County, Mississippi, during the breeding seasons of 1972–1974 (Sappington 1975) and is the first to be made below 34° latitude. It includes data on the activity of breeding birds and helpers at the nest with corresponding analyses of nest-building, egg-laying, incubation, hatching success, nestling feeding rate, nesting efforts, fledging age, and fledging success.

MATERIALS AND METHODS

This study was conducted on the main campus and adjoining areas of Mississippi State University, Oktibbeha Co., Mississippi, 33° 28′ north latitude and 88° 48′ west longitude. It continued for 3 years, 1972 through 1974, with emphasis on the breeding season which normally lasted from February to August. Four nesting areas were studied: (1) 4 trees (*Magnolia grandiflora*) espaliered on the walls of Lee Hall in the central part of the campus, designated as "Tree"; (2) a large barn where sheep and horses were fed and kept overnight, designated as "Horse Barn"; (3) an equipment shed and orchard, designated as "Shed"; and (4) a cluster of buildings associated with a pig feed lot, designated as "Pig Farm." Only Tree colony was studied in 1972. All colonies were studied during 1973, but only Pig Farm and Shed colonies were studied in 1974.

Individual House Sparrows from each area were captured by (1) baited traps, (2) mist nets at roost sites (Sappington and Jackson 1973), (3) hand nets at nests, and (4) hand-lifting young from nest before fledging. Each captured bird was banded with a U.S. Fish and Wildlife Service metal leg band and/or color-marked with a coded combination of colored plastic leg bands and released or put back into the nest.

Only records of marked birds that were readily identifiable were used for analysis. The mated pair at each of 280 nests was identified by the arrangement of the metal and colored leg bands. Nest-building activities and feeding of nestlings were observed through 7 × 35 binoculars. The birds at Tree, Pig Farm, and Horse Barn colonies were accustomed to people passing near their nests at all hours of the day. No observation blinds were necessary in observing breeding activities at these locations. At Shed colony which occupied a single, remotely-located building, the birds were wary of observers. However, with an automobile as a blind, I was able to make observations within 6 m of the nest without disturbing the birds.

Construction of 221 nests at 100 sites was observed. I plotted the location of each nest on a sketch map and recorded the identifying markings of the mated pair and presence of any helper. Individual nests or blocks of nests located in the same area were observed for ½ or full-day periods beginning at 07:00 and lasting through 18:00 CST.

A total of 285 nest-days was spent in observing nest-building. A nest-day is defined as a day spent by one person observing a single nest.

At 229 nests I was able to establish the date of the appearance of the first egg. These nests were checked daily between 07:00 and 08:00 until the last egg was laid. The date of the laying of the first egg and appearance of the last egg in each clutch were recorded. For those nests in which incubation occurred, clutch size was determined to be the number of eggs at the beginning of incubation. The incubation period was taken as the time between the laying of the last egg and date of hatching of the last young when all eggs hatched.

One week after each clutch was completed, each nest was checked for hatching 3 times daily—between 07:00 and 08:00, 12:00 and 13:00, and 18:00 and 19:00. The dates of the hatching of the first young and the hatching of the last young were recorded. Hatching success (%) was calculated from the total number of eggs laid.

Feeding of nestlings, ranging in age from 1 to 20 days, was observed at 254 nests between 05:00 and 19:00 for 177 days. My observations include 145 days on which I made continuous observations from 05:00 to 19:00 and 32 days on which I observed nests for shorter intervals. Because of the placement of nests I was generally able to observe from 1 to 7 nests at one time, giving a total of 673 nest-days of observation.

The number of visits to the nest with food was used as a measure of feeding activity. Royama (1966) stated that feeding frequencies for another hole-nesting species (*Parus major*) are far too variable to be used as a true index of food consumption per nestling, but according to Pettingill (1970), no matter how food is supplied, the individual nestlings receive an equal amount during the course of the day due to automatic apportionment.

Records were kept of the number of visits to the nest by each parent and helper (a bird other than the parents). Observations were made during all weather conditions except heavy rain. According to Kendeigh (1952), cloudiness, fog, or wind do not affect feeding rates; only heavy rain affects them and then only temporarily. For calculations of total daily visits to the nest and visits per nestling, only those observation periods which lasted the entire day were used.

A nesting effort was arbitrarily considered to be an incubated clutch. Fledging was considered to be the time when a young bird took flight from the nest the first time. Age at fledging, or nestling period, was calculated from the day of hatching until the day of fledging. Fledging success (%) was calculated from the total number of eggs laid and number of eggs hatched.

Statistical analyses were performed using the UNIVAC 1106 computer at Mississippi State University. The analysis of variance, as well as basic statistics, including means, standard deviation, and standard error were obtained from these data by the first option of UNIVAR (1973 version), a basic statistics program written by D. M. Power. Basic statistics for samples of more than 2000 cases were obtained by using the program, BMD 01V, ANOVA for One-Way Design of the Biomedical Computer Programs (Dixon 1974).

When only 2 numbers were compared for significant difference, the Chi-square test was used. Yates' correction (Chase 1967) was applied when the expected frequency was fewer than 5 cases. When 2 percentages were tested for significant differences, as in percent success, a computer program written by Jerome A. Jackson of Mississippi State University was used. The program calculates a t-value which may be compared with a tabular t. The method of this test is based on the arcsine transformation as suggested by Sokal and Rohlf (1969).

I used a probability level of 0.05 as the criterion for significance in all statistical analyses.

RESULTS AND DISCUSSION

During the 3 breeding seasons of 1972–1974, 987 House Sparrows were color-banded at the 4 locations; 311 were adults, and 676 were juveniles. The male-female ratio of total marked adult birds was 1:1.03 (153 males and 158 females). Other studies have shown that the sex ratios for House Sparrows have not differed greatly from 1:1 (Summers-Smith 1963, Will 1973, North 1973). I also used observational data from roosting and feeding studies to get an indication of the male-female ratio for the study areas. Among roosting birds, males constituted 52.1% of the total, and among feeding birds, they constituted 50.1% of the total. These figures do not differ significantly from my findings of 49.2% males in the breeding situation. Of the marked adults, 82.6% were breeders (78.4% males; 86.7% females).

Summers-Smith (1958) stated that the mated male and female House Sparrow remain faithful to each other and to their nest site for life. He does, however, cite exceptions involving bigamy, desertions, and the holding of more than one nest site by a single male. In my study of 100 nest sites, the mated pair remained faithful to each other for only 60.5% of the cases during a particular breeding season. However, the number of males having only 1 mate (69) was significantly higher than those having more than 1 mate (45) during a breeding season. There was no evidence that pairs remained together for 2 consecutive breeding seasons. Although 39.5% of the males had more than one mate during a single season, no cases of simultaneous polygamy were observed.

Of 156 breeders of known origin, 125 (80.1%) nested at the location where they were banded. The difference between numbers of sedentary breeders and transient breeders was highly significant. Generally, breeding House Sparrows returned to the area where they were banded but not necessarily to the same nest site of previous years. Attachment to the nest site appeared to be strongest in the male. Of the total nest sites, 86.0% were retained by the male for the entire breeding season as opposed to 45.0% by the female. There was a highly significant difference between number of sites occupied by a single male (86) and number occupied by more than one male (14) during the breeding season but no significant difference between number of sites occupied by a single female (45) and number occupied by more than one female (55). Individual males showed very little attachment to their nest site after the breeding duties were over. In subsequent breeding seasons only 10% (6 of 60 cases) of the sedentary breeding males returned to their previous nest site. After the breeding season all birds used communal roosts instead of their nest sites for the fall and winter months. The old nests were torn out by people, or weathering deteriorated them. These factors may have been reasons why so few sparrows returned to their old nest sites in subsequent years.

During the 3 seasons of 1972–1974, 584 nests were built at 296 sites at the 4 locations. This activity embraced a time span of approximately 5 months each year. Typically, it began in early February and lasted until near the end of July. During the 3-year period the earliest nest was started 10 February, and the latest was started 21 July. Bent (1958) stated that nestbuilding occurs in various places of the United States during every month of the year.

Nest-building was observed at 221 nests of which 5 (2.26%) had helpers. Although cooperative nest-building is common among some weaver finches (Crook 1960, MacLean 1973), I have seen no previous reference to this practice by House Sparrows. A rhythmic pattern was manifested in both nest-building and egg-laying. Peak periods of nest-building were generally followed within a week by intensive egg-laying. Others have reported similar patterns (Mitchell et al. 1973, Summers-Smith 1963, Weaver 1939).

Of 584 nests built, 532 contained eggs. Egg-laying during each of the 3 years embraced a span of approximately 5 months beginning in late February and continuing through July. The first egg was laid 24 February, and the last egg was laid July 28 for the 3-year period.

I did not quantify the amount of time spent incubating by each sex of the mated pair. Weaver (1943) stated that only the female incubates since the male was never observed to sit on the eggs. On the other hand, Daanje (1941) stated that both sexes incubate the eggs. Summers-Smith (1963) found that both sexes spent spells of time on the eggs during incubation, but since the male does not develop a brood patch, it cannot be truly said that he incubates. I observed that the male relieved the female at the nest 5 or 6 times per day for periods up to 20 min in length. Presumably the female was feeding at this time. At night only the female sat on the eggs. Although communal behavior in egg-laying and incubation has been exhibited by other social species, Mexican Jay (*Aphelocoma ultramarina*) (Brown 1970) and Smooth-billed Ani (*Crotophaga ani*) (Davis 1940), there was no evidence of such behavior in the House Sparrow.

For 229 nests the mean incubation period was 12.2 days (S.E. = 0.12) (Range = 10 to 17 days). The 17-day period occurred in the Horse Barn colony in 1973 and may be attributed to the sudden occupancy of the area by a Barn Owl (*Tyto alba*) which caused such stress that both incubation and feeding were often halted for several hours at a time. My data do not differ significantly from that found by others (12 days, Weaver 1943; 11.2 days, Seel 1968; 11.3 days, Mitchell and Hayes 1973). Weaver (1943) and Summers-Smith (1963) stated that the hatching period may be spread over 2 or 3 days. I found a much shorter time span for hatching completion. Hatching began in the early morning and did not last beyond 18:00 of the same day. There was only 1 exception in which 1 nest in 1973 required 2 days for

Table 1

Comparison of Mean Daily Visits to Nests With Helpers (W) and Nests Without Helpers (WO)

Parameter[1]	Mean	Standard Error
Visits by parents		
W	222.7**	± 2.0
WO	206.6	± 2.9
Visits by helpers	31.4	± 0.5
Total visits		
W	254.1**	± 2.8
WO	206.6	± 2.9
Visits per nestling		
W	71.5**	± 0.4
WO	58.1	± 0.7
Number of nestlings		
W	3.6	± 0.04
WO	3.6	± 0.04

[1] Based on 321 nest-days of observation at nests with helpers and 352 nest-days of observation at nests without helpers.
** ($p \leq .01$).

hatching completion. For the entire study period the earliest hatching date was 11 March and the latest was 16 August.

Feeding of nestlings was observed at 254 nests, of which 161 (63.4%) had multiple-feeders (helpers). A chi-square test indicated there were significantly more nests with helpers than without helpers. In nests with helpers mean daily total visits amounted to 254.1 of which 31.4 (12.4%) were from helpers (Table 1). Nests without helpers received a mean of 206.6 daily visits, significantly fewer ($p < 0.01$) than at nests with helpers. For all nests observed the mean daily feeding frequency was 229.3 with 64.5 per nestling. The mean hourly feeding rate was 16.5 (S.E. = 0.09) with a mean of 3.6 nestlings per nest. Kendeigh (1952) reported a feeding rate of 20 times per hour for nestling House Sparrows with 4 young per nest. Comparison of our data sets using chi-square indicates that they do not differ significantly. Temporal patterns were present in the hourly feeding rate (Sappington 1975). Three peak periods occurred daily, late morning, mid afternoon, and late afternoon. Feeding was minimal between 05:00 and 06:00 and between 18:00 and 19:00.

A great deal of variation occurred in both total visits to the nest and visits per nestling depending on ages and number of young per nest. However, these parameters varied very little (no significant difference) after the 8th day of age in nests with both 3 and 4 nestlings (Sappington 1975). It appeared that the feeding rate changed very little after the first half of nestling life. Summers-Smith (1963) found that the frequency of feeding nestling House Sparrows increased until the 14th day, after which there was a decrease. My results were similar to those of Seel (1969) who discovered a common pattern of feeding in broods of nestling House Sparrows of all sizes which was a rising phase up to nestling day 8½ to 11½, followed by a levelling off phase. Increased feeding in my study was halted at the approximate time that homeothermy is supposedly accomplished in the nestling House Sparrow (Pettingill 1970).

One might surmise that the larger the brood the more visits to the nest. I found a direct relationship between brood size and daily visits to the nest, but there was an inverse relationship between brood size and visits per nestling (Sappington 1975). Seel (1969) found the same relationship for broods of 1 to 3 nestling House Sparrows, and Moreau and Moreau (1940) found that the smaller the brood the greater the number of feedings that each received. These findings agree with the results of von Haartman (1953). He found that it is not the number of nestlings but their reactions that stimulated parents to bring food.

Kendeigh (1952) found that nests with fewer birds fledged earlier. My study generally showed this trend but the differences are very slight and are non-significant for nests which fledged 2, 3, 4, or 5 birds with or without helpers. Moreau and Moreau (1940) also found that the smaller brood does not fledge earlier.

I observed that a marked change in the behavior of both the nestlings and helpers occurred 2 or 3 days prior to fledging. Nestlings become exceedingly quiet, lying crouched in the nest. Helpers no longer fed them. On the day of fledging parents rarely fed the young until they left the nest. Fledging generally occurred in the early morning and seldom did all young leave the nest at once.

Summers-Smith (1963) and Weaver (1943) found that the fledging period of a single nest may be spread over 2 or 3 days. From 180 nests in my study all young fledged by 12:00 on the same day. Never were there more than 4 h between the fledging of the first and last nestling from the same brood. This synchronized pattern of fledging should not be considered unusual, but could be expected because of the small age differential in nestlings within the same brood as experienced in this study.

My study of 180 nests showed that time spent in the nest varied from 14 to 23 days with an overall mean of 17.1 days (S.E. = 0.15). The 23-day period which occurred in Horse Barn colony may be attributed to the presence of the Barn Owl. Summers-Smith (1963) gave a nestling period of 11 to 19 days (mode of 18) for Great Britain. Kendeigh (1952) cited the nestling period to be 14 to 16 days for Illinois. Weaver (1942) found that the time spent in the nest varied from 12 to 16 days with a mean of 14.4 days for New York. Although my study showed a higher nestling period than did the Illinois or New York study, there was no significant difference. Also, there was no significant difference in mean number fledged from nests with helpers (2.8) and nests without helpers (2.9).

Each nest site was used an average of 2.84 times (S.E. = 0.10) during a single breeding season. This figure is somewhat higher than those of 2.1 (Summers-Smith 1963), 2.0 (Will 1973), or 1.68 (Weaver 1943) but approaches 3.0 found at a site studied by Mitchell et al. (1973). Use was highest in 1974 when each nest site was occupied an average of 3.2 times. In 1974 there was a scarcity of sites as compared to the 2 previous years. Nest sites were limited to only the Pig Farm and Shed locations during 1974, and at the Pig Farm 5 of the 7 buildings normally used were torn down, thus limiting the number of available sites.

The number of incubated clutches per pair (N = 142) ranged from 1 to 4 with a mean of 1.84 (S.E. = 0.07) which compares favorably with 2.1 of Craggs (1967) and Summers-Smith (1963). Percent of pairs having 1, 2, 3, or 4 nesting efforts were 39.4, 40.9, 15.5, and 4.2 respectively. The number of eggs laid per female per season (N = 596) ranged from 3 to 16 with a mean of 7.46 (S.E. = 0.29). This figure is not significantly different from the 7.95, 8.94, or 8.61 eggs per female per season reported by Weaver (1943), Will (1973), and Summers-Smith (1963) respectively. The number of eggs hatched per pair (N = 495) ranged from 2 to 16 with a mean of 6.37 (S.E. = 0.26) as compared with 5.88 (Will 1973) and 6.11 (calculated from data from Summers-Smith 1963).

Breeding success was based on results from 224 nests. Clutch size ranged from 2 to 6 eggs with a mean of 4.2 (S.E. = 0.06). Nests containing 4 eggs each accounted for 60.3% of the clutches. McAtee (1940) found that clutch size in Maryland ranged from 2 to 6 with a mode of 5. Bent (1958) gave a range of 3 to 7 with a mode of 5 throughout the United States. My average is well within these ranges. Others report similar means from Great Britain—3.9 Seel (1968) and Craggs (1967), 4.1 Summers-Smith (1963)—and from the United States—4.3 Mitchell et al. (1973), 4.4 Will (1973), 4.7 Weaver (1943). My average is not significantly different from these previous studies. The number hatching per nest was 3.4 (S.E. = 0.08) in nests in which at least 1 hatched. The number fledging per nest was 2.8 (S.E. = 0.09) in nests in which at least 1 fledged.

Hatching success, based on all eggs laid (Table 2), was 83.2% which is

TABLE 2

OVERALL BREEDING SUCCESS OF HOUSE SPARROWS AT MISSISSIPPI STATE, MISSISSIPPI

Category	Value
Total clutches	224
Clutches lost	19
Eggs lost	72
% of eggs surviving	92.1%
Number of eggs hatched	758
% of total eggs hatched	83.2%
% of surviving eggs hatched	90.4%
Number of young fledged	584
% of total eggs	64.1%
% of incubated eggs	69.6%
% of eggs hatched	77.0%

significantly higher ($p < .01$) than 71.0% (Summers-Smith 1963), 61.0% (Mitchell et al. 1973), or 65.8% (Will 1973). It is also somewhat higher than the average of 77.0% which Nice (1957) attributed to altricial hole-nesting species, but is not significantly different from 85.4% calculated for House Sparrows from data reported by Seel (1968). Fledging success, based on total eggs laid, was 64.1% for the entire period (Table 2). This figure compares with 66.0% given by Nice (1957) for hole-nesting altricial birds, but is significantly higher ($p < .01$) than 50.0% (Summers-Smith 1963), 41.0% (Mitchell et al. 1973), or 35.1% (Will 1973) reported for House Sparrows in other studies. Although some previous studies were quite detailed, specific mention of cooperative breeding activities is almost lacking and at best fragmentary. One might assume that my high breeding success could be attributed to the activity of helpers. However, there was no significant difference in fledging success from nests with helpers (68.5%) and nests without helpers (72.2%). The higher breeding success in my study does not appear to be the result of assistance by helpers, but may be attributed to the small percentage of eggs lost to breakage and predation (7.9%), high hatching success of surviving eggs (90.4%), and rather small percentage of nestlings (23.0%) which died or fell to predators.

SUMMARY

Breeding biology of the House Sparrow (*Passer domesticus*) was studied in 4 colonies of marked birds during the breeding seasons of 1972–1974 in Oktibbeha Co., Mississippi.

The male-female ratio of breeding birds was 1:1. The male generally remained faithful to his nest site (86.0%) but not so faithful to his mate (60.5%) for the entire breeding season.

Each nest site was used an average of 2.84 times per season, but the number of incubated clutches per pair was 1.84. There was a trace of cooperative nest-building, but there was no evidence of communal egg-laying or incubation. Rhythmic patterns were manifested in both nest-building and egg-laying with peak periods of nest-building followed within a week by intensive egg-laying.

Mean clutch size was 4.2 eggs. The mean incubation period was 12.2 days. A mean of 3.4 eggs hatched, and 2.8 young fledged per nest. Young fledged at 17.1 days of age.

Nestlings were fed at a mean rate of 16.5 times per hour. Feeding of nestlings by sparrows other than the parents was observed in 161 of 254 nests in which feeding was significantly higher than in those nests without helpers. Helpers accounted for 12.4% of the feeding in those nests which they visited.

Hatching success (83.2%) and fledging success (64.1%) were significantly higher than those reported by other researchers but do not appear to be the result of assistance by helpers; they may be attributed to the small percentage of eggs lost to predation and breakage, high hatching success of surviving eggs, and low mortality of nestlings.

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NESTING BEHAVIOR OF YELLOW-BELLIED SAPSUCKERS

Lawrence Kilham

This communication presents aspects of the nesting of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) either not mentioned in previous accounts (Bent 1939; Johnson 1947; Howell 1952; Kilham 1962a, b; Lawrence 1967) or, if mentioned, open to amplification and new or other interpretation. Activities covered extend from the start of excavating through egg-laying and incubation to fledging. They do not include agonistic and courtship behavior which are being described separately.

METHODS

With 5 pairs studied in special detail and 4 others for a more limited time, I made observations from ½ to 2 hours a day every day, with a few missed from late April or early May through fledging in July, either between 08:00–10:00 or 15:00–17:00, these times having been found to be equivalent in terms of heights of activity. Percentages of time that the male or the female of a breeding pair spent in such activities as incubation or brooding refer, as shown in Tables 1 to 4, to total observation times, a method also used by Lawrence (1967). They are given for convenience of description and are not intended to imply total coverage that would have demanded dawn to dusk observations 7 days a week throughout the nesting period. In addition to counted hours (281) I spent many uncounted ones in partial observations on 12 other nesting pairs in Lyme, New Hampshire.

In regard to attentiveness I have not used methods employed, among others, by Stickel (1965), Lawrence (1967), and Skutch (1969). Stickel, who gives the most detail, designates "attentiveness as the time adults spent excavating a cavity, sitting beside it, guarding and incubating eggs, and once the birds had hatched, as that time the parents remained at the nest cavity." What Stickel refers to as sitting by a nest, guarding it, etc., I have considered under the general term of "loitering." Only those times, therefore, that the sapsuckers actually spent in the work of excavating, sitting on eggs, or brooding young within the nest, have been considered in making calculations. A session at the nest, in contrast, has been regarded as the total time that one of a pair spends in or by the nest until relieved by its partner.

Descriptions of the vocalizations, drummings, tappings, and displays of *S. varius* mentioned in this report are given elsewhere (Kilham 1962a).

EXCAVATION

Share done by males and females.—The amount of work done by either sex depends on circumstances. At 5 nests that were first excavations of the breeding season, I found that the males did nearly all of the work. When they excavated, they worked continuously from 15 to 30 min at a stretch. When females changed places with them they spent much of their time in preening and resting as Lawrence (1967) has described. Their excavating was often token in character, with little sawdust removed, particularly after completion of the entrance corridor. But females can work under special circumstances. When Pair A abandoned a first excavation in 1974 and began a second one, Female A (FA) did 68% of the excavating observed in the first 4 days. This was excavating of the hardest type, for FA dug through 6.5 cm of the living, outer shell of an aspen (*Populus tremuloides*). The aspen had heart rot due to infection with *Fomes igniarius* (Kilham 1971). When the easier digging at the center was reached, the male took over and did 79% of the excavating. The cavity was completed in the next 5 days.

FA worked so continuously in her first stretch that she took no time for resting and preening during periods of observation and on a number of occasions refused to leave when her mate came to change places. Why should she have worked in this manner? A possibility is that females are a reserve in regard to excavating. By not working under usual circumstances they conserve energy for forming and laying eggs. When a first excavation fails, a female that had been becoming ready physiologically for egg-laying, suddenly finds herself with no place to do so. As a result her drive to excavate may become even greater than that of her mate.

Tight fit of nest entrances.—A feature of holes in *Fomes*-aspens is that entrance corridors carved by males, when they do most of the excavating, are a snug fit for their bodies. Females do not usually enter nest cavities until the time of egg-laying when, if their body size is larger than that of their mates, they may have a hard time getting in. The first time I saw female C (FC) enter her nest cavity was on 20 May. She had to wriggle to force her way. After remaining inside for 5 min she had difficulties getting out. She pushed her head outside 5 times, moving it violently up and down as she struggled, without success until the 5th time, to force herself through. Even later on, when feeding young, she pumped her head up and down in struggles to emerge. I have observed the same phenomenon for a female Downy Woodpecker (*Picoides pubescens*) that had an even more difficult time emerging at the start of egg-laying. Female A, who had carved her own corridor, had no such difficulties.

Attempt to reuse nest hole of a preceding year.—Sapsuckers carve fresh nest holes each year. On 15 April 1975 Male D made the start of an excavation in a *Fomes*-aspen 8 days before I saw the female. The excavation was completed in May and used successfully. A pair of sapsuckers (Pair H) returned to the same aspen in 1976 but instead of starting a new excavation, for which there appeared to be no suitable sites, they attempted to reuse the old hole of the year before. This was evidenced by tapping, by the male entering and giving breeding calls from the entrance, and by courtship flights. On 29 April Male H entered twice, coming out with black fecal matter that appeared to be distasteful, for he wiped his bill many times on a pine limb.

Pair H abandoned the hole in early May and excavated a fresh one in a new *Fomes* aspen. It seemed from this experience that accumulation of fecal matter, which I had measured as being 6 cm deep at the end of the 1975 nesting season, had possibly acted as a deterrent to reuse of the old hole.

EGG-LAYING

FA was in Nest A from 05:35 until 06:35 on 2 June. This was longer than any single stretch that she spent during the incubation period. When MA came to the entrance at 05:57 as if to change places, she remained out of sight and when he returned at 06:21 she struck out sharply, driving him away. Similar behavior was observed in Female G on 24 May when she had 4 eggs in the nest. This dominance of the female at time of egg-laying may be a general phenomenon, for I have also noted it in the Common Flicker (*Colaptes auratus*; Kilham 1959).

In 1976 Pairs H and I finished their excavations by the middle of May. Egg-laying and the start of incubation that should have followed appeared to be delayed by 9 days of cold, wet weather. Although I did not find when first eggs were laid in either nest, Nest H contained 1 egg on 23 and 4 on 28 May, the first day of incubation. Of these eggs, only 2 hatched. The history of Nest I was more complicated. There were 3 eggs on 23 and 4 on 24 May. Neither the male nor the female appeared much disturbed when I put a ladder up to their nest. I was thus unable to account for destruction of 3 eggs that I watched Male I carry from the nest on 25 May. On 29 and 30 May a single egg remained. Four more were laid between 1 and 4 June. Of this total of 5 eggs, 3 hatched. There were thus high rates of failure (50% in H and 40% in I) in both nests. These failures to hatch may have related to exposure during the prolonged spell of cold weather. The percentages of egg failure appear high. Ricklefs (1969) found that only 8.1% of 3226 eggs of 6 passerine species failed to hatch. All 5 of the unhatched sapsucker eggs were removed by the parent sapsuckers within a day.

INCUBATION

Although most pairs settled down to incubating promptly, the females of Pairs C and D frequently loitered outside of their nests following changeovers with their mates during the first 5 days of incubation. In the last 6 or 7 days of incubation, they became more attentive than the males, FC doing 60% and FD 86% of the total incubating.

Experience of a following year with Pairs H and I is shown in Table 1. Here the 2 females incubated from the beginning of the period and were as attentive or nearly so as the males in their sessions at the nest. As their ses-

TABLE 1

ATTENTIVENESS OF MALES (M) AND FEMALES (F) OF 2 PAIRS OF SAPSUCKERS DURING INCUBATION AND BROODING; BOTH FEMALES WERE BLACK POLYMORPHS

Activity	Pair and Sex	Total time of sessions (min)	Attentiveness
Incubation	HM	610	94%
	HF	293	94%
	IM	239	97%
	IF	189	93%
Brooding	HM	375	80%
	HF	236	83%
	IM	107*	85%
	IF	184*	58%

* Regular brooding only lasted 4 days in contrast to 9 days for Pair H.

sions were fewer than those of the males, the latter did the greater part of the incubating in both pairs.

I have found sapsuckers very restless during incubation periods, often looking or coming out of their nest holes, regardless of how near or far away I sat watching. These periods of abandoning the eggs added up to considerable amounts of time, especially in the case of the females. Thus in nearly 31 hours of watching at Nests A, C, and D (Table 2) I found that eggs were left uncovered for a total of 5 hours or close to 16% of the time.

Can weather affect incubating? This appeared to be the case on only one day for the 3 pairs of sapsuckers shown in Table 2. The hottest day of the spring of 1974 was on 10 June which was the 8th day of incubation for Pair A. The temperature was 36°C in the shade and presumably hotter in the nest hole that was exposed to the mid-afternoon sun. Although the members of this pair had been incubating close to 100% of their time for the previous 3 days, they became very restless on 10 June leaving their eggs unguarded for 34 out of the 60 min that I watched them.

PERIOD OF FEEDING YOUNG

Brooding.—I have considered brooding as the days when each member of the pair remained on the nest for a high percentage of its time until relieved by its mate. Tables 1 and 3 give ranges of these percentages that, as shown in Table 1, were lower than those noted during the period of incubation. As nest J were brooded 82% of the time I watched, the 3 young of nest I were

TABLE 2

AMOUNTS OF TIME EGGS WERE LEFT UNCOVERED DURING PERIODS OF OBSERVATION IN INCUBATION PERIODS OF 3 PAIRS OF SAPSUCKERS

	Pair A	Pair C	Pair D
Duration of observations (min)	520	782	550
% of observation times eggs left uncovered	6%	18%	23%

shown in Table 3 brooding was of 8 to 10 days duration. I did not consider as brooding the periods of 2–4 min that sapsuckers spent in nests on subsequent days. On some of these I could hear excavating. This suggested that the males (and less often the females) were producing sawdust used in relation to removal of fecal matter from the nest (Kilham 1962b).

There were 2 exceptions to stoppage of brooding on a definite day. One was with Pair A that, after ceasing to brood on 24 June, brooded for 42 of 60 min on 26 June which was rainy and exceptionally cold. The other was with Pair I (Table 1) where the brooding was regular only through day 4, then irregular and infrequent until day 7 when it ended.

As shown in Table 4 and described in the following section, I had nests with 1, 2, 3, and 4 young. A point of interest was that whereas the 2 young of Nest J were brooded 82% of the time I watched, the 3 young of Nest I were brooded 67 and the 4 young of Nest A 73%. While the differences were not great, the nest with the fewest young received the most brooding. Royama

TABLE 3

RESULTS OF OBSERVATIONS ON THE NUMBER OF DAYS 3 PAIRS OF SAPSUCKERS BROODED THEIR NEWLY HATCHED YOUNG AND THE WAYS DUTIES WERE SHARED BETWEEN MALES (M) AND FEMALES (F)

	Pair A		Pair C		Pair D	
Parameters	M	F	M	F	M	F
Amounts of time sexes brooded (min)	251	220	163	164	94	120
Percentages of total time	53%	47%	50%	50%	44%	56%
Average duration of periods M and F brooded (min)	19		16		13	
Duration of brooding (days)	9		10		8	
Observation time (min)	644		360		321	
Percent of observation time that sapsuckers brooded	73%		91%		67%	

TABLE 4

EFFECTS OF NUMBER OF YOUNG IN THE NEST (1, 2, 3, OR 4) ON FEEDING RATES OF PAIRS OF SAPSUCKERS AND ONE LONE MALE*

	Pairs of Sapsuckers							
	J = Lone Male		H		I		A	
Period	No. of young	Rate/h	No. of young	Rate/h	No. of young	Rate/h	No. of young	Rate/h
Brooding			2	7.3	3	9.3	4	10.6
End of brooding thru day 15 after hatching	(Nest not under observation)		2	13.4	3	15.4	4	17.1
Last 9 days before nest leaving	1	6.2	1**	10.1	(End of nest; predation by weasel?)		4	20.8
Day of nest leaving	————		26		————		28	

* Observation time, 89.4 h.

** 1 died; cause unknown.

(1966) writing of the Great Tit (*Parus major*) emphasizes that there was greater heat loss in small broods, where young were less efficient at keeping each other warm. They would, therefore, need more brooding and/or more feeding.

Feeding young.—A feature of feeding young noted at all nests was that the sexes shared the tasks almost equally, with the males making 6 to 10% more visits than their partners (Fig. 1). Figure 2 gives the combined male plus female feeding rates of Pair A. I found by inspection that Nest A contained 4 young and I visited it for an hour or more every day from hatching on 15 June to fledging 28 days later. After a low average of 10.5 when parents were spending much of their time brooding, the rate jumped to 24 visits per hour with its cessation. This high average continued to within 4 days of fledging when it fell to 16. Findings with Pair D, recorded in a similar manner, followed an almost identical curve. A feature of Lawrence's paper is the all-day feeding rate. My nests were visited either in the mid-morning or mid-afternoon, at which times I found no differences in rates as would seem to be the experience of Lawrence (1967:116) as well.

As stated by Lawrence (1967:113) "it is difficult to arrive at a valid analysis of the feeding rate without knowledge of the exact number of young." I was fortunate in 1976 to have 3 nests that, being within 3 to 5 m of the ground were easily accessible by ladder. These nests contained 1, 2, and 3

FIG. 1. Observations on 3 pairs of nesting sapsuckers showing that while the task of feeding the young was shared by both sexes to a nearly equal extent in all pairs, that of nest sanitation varied considerably. Observation times, here combined, were between 08:00–10:00 and 15:00–17:00.

young, while Nest A in 1974 contained 4. As shown in Table 4 the feeding rates declined in stepwise fashion from Nest A with 4 young to Nest H with only 2. But the decline was not proportionate to the number of young, for the fewer the nestlings, the more each one received from its parents. These extra feedings may have hastened the time of nest leaving; the single nestling in Nest H, for example, having left on day 26 as contrasted with the 4 nestlings of Nest A that left on day 28.

Pair H provided an exception to the finding that males and females, in general, fed young almost equally. Although the members of the pair had shared the feedings almost equally when they had 2 young, the male did almost all of the feeding (75%) in the last 9 days when only a single nestling remained.

Vocalizations of nestlings.—The vocalizations of nestling sapsuckers are described by Lawrence (1967:125) as well as by Kilham (1962a). They carry for considerable distances and can be of aid in locating nest trees. They might, therefore, also serve to attract predators. If they are a hazard they must, it would seem, provide compensating advantages. It is conceivable that the harsh "check-check-checks" of the young stimulate parents to keep the feeding at a high rate and to thus raise more young. A line of evidence suggesting that the vocalizations do stimulate adult sapsuckers involves intrusions by lone adult male and female sapsuckers. In sapsucker nests that I followed every day through the nestling period I seldom saw these intruders until the last week or two of the nestling period when they began coming to nest trees, sometimes repeatedly, to look into the nest hole in spite of being driven away.

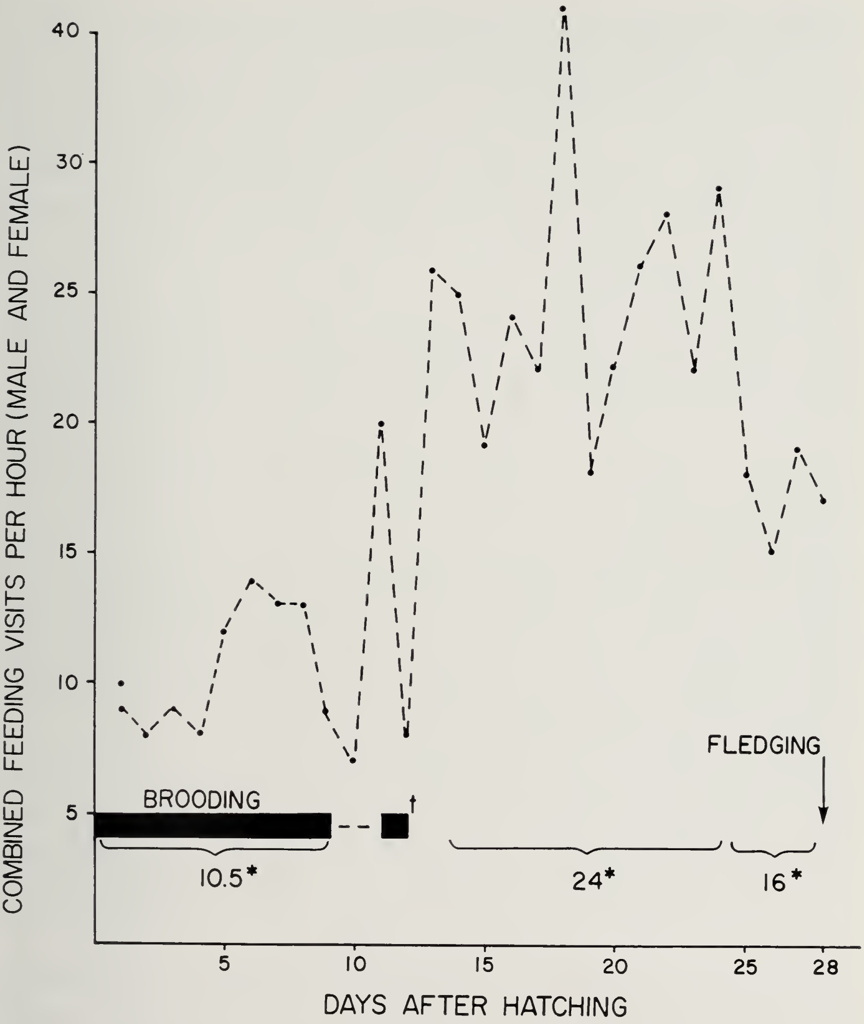

FIG. 2. Curve of combined male plus female feeding rates of a pair of nesting sapsuckers, showing sharp increase of rate at termination of brooding. Observation times, here combined, were between 08:00–10:00 and 15:00–17:00.

They thus behaved as if something, such as the vocalizations that carried for a distance, were attracting them.

A parent sapsucker, on the other hand, may return repeatedly to an empty and silent nest. The young of Pair A left early on the morning of 13 July. Male A came to the hole later, bowed in 3 times, then left to add sap to his bill-full of insects before returning. He made 5 such visits before flying off to feed the insects plus sap to a juvenile. The behavior of Male I was even more striking. After his young had been killed by a predator, he came to the hole 10 times in 17 min with a load of insects that became steadily larger as he continued to catch insects between visits. On his 10th visit, MI swallowed the insects and left. The return of MA and MI to their silent nests was possibly due to habituation over previous days. Skutch (1976) noted a Golden-naped Woodpecker (*Melanerpes chrysauchen*) that continued to bring food for 6 days after a nest was desolated.

The range of vocalizations of nestlings is considerable and probably conveys a variety of messages ranging from hunger to alarm. A peculiar episode took place at Nest D the day before nest-leaving when an intruder, a female, ascended the nest aspen cautiously, then poked in at the nestlings. They immediately set up a wailing noise that I had not heard previously and continued it for 30 sec after the intruder had left. The reaction suggested that the young sapsuckers were able to recognize the intruder as being a foreigner and not their own mother.

Nest sanitation.—Both Johnson (1947) and Lawrence (1967) noted that males do most of the nest cleaning, but I have found more variation in this task than in feeding the young (Fig. 1). Among 7 pairs of sapsuckers followed in the same manner, the amount of the work done by the females ranged from 0% in 3, to 2, 22, 30, and 56% respectively in 5 other nests. In one out of 7 therefore, the female did more than the male.

Another parameter showing variation is the day when parents cease to remove feces. In 3 nests, those of Pairs F, H, and A, this was 4, 5, and 8 days before the young left the nest. The amount of black, tarry fecal matter that accumulated in Nest H was 5 cm and in Nest A, 6 cm deep as measured afterward. Male G, in contrast to males of other pairs, removed 7 large bill-fulls of feces in 30 min on 22 July, the day before fledging, and Lawrence (1967:120) saw a male remove feces after 1 fledgling had left.

Emergence.—At 07:10 on 30 June, about 30 sec after it had been fed, a juvenile flew from its nest hole on a circular, downward flight that carried it 6 m to a stub, where it rested silently. The young one had been looking about with its head out of the hole for the previous hour. Neither at this nor any other nest have I seen parent sapsuckers make special efforts to induce young to leave.

OTHER ASPECTS

Lone parents.—I have encountered 5 nests where young were tended by widowed parents, of which 3 were females and 2 males. Behavior differed between the sexes. Whereas the females fed their young at exaggerated rates of up to 20 to 28 times per hour, bringing little prey with each visit, the males fed at a slow rate, closer to what they would have used had their partners remained alive. Thus lone Male J (Table 4) fed its single young at a rate of 6.2/h in the last 9 days of the nestling period. Male H, who also had a single young but had a mate, fed at a rate of 7.7/h.

Of the 5 nests with lone parents, 4 failed, 1 due to predation and the others, I believed, to starvation, for the vocalizations of the young became very feeble. Male J raised one young successfully and Lawrence (1967:117) describes a lone male that raised and fledged 2 young. It would seem from these experiences that males are more apt to succeed in raising young alone than are females. As described elsewhere (Kilham, in press) one of the lone females I watched succeeded in attracting a new male that, after 2 days, started to feed her young. The nest, however, was destroyed by predation on the following night.

Predation by weasel (?).—The aspen of Pair I was 1 m from a stone wall. I noticed a weasel (*Mustela* sp.) running along the wall on 11 June when Female I made "*quare*" notes in alarm. The weasel stood up to look at me at close range. On 30 June I found remnants of a nestling, with wing feathers still in sheaths, below the hole and similar remains at the bottom of the nest. The predator had seemingly been able to enter. There was no ring of tooth marks around the entrance, such as I have noticed when raccoons attack a sapsucker nest (Kilham 1971). On examining a rough place on the bark at the foot of the aspen, I collected over 30 whitish hairs a centimeter or slightly more in length; hairs that might have come from the belly of a weasel. Although a snake might have entered, there are no tree climbing snakes in woodlands of central New Hampshire, to my knowledge, and a snake would have swallowed its prey whole. A presumption, therefore, was that a weasel was the predator. Johnson (1947) described attacks of a weasel on a sapsucker nest.

Temperament.—How close should one sit when in the open and without a blind? When a sapsucker is disturbed by one's being too close, it makes repeated "*waan*" notes, raises its crest, alights on the opposite side of the nest tree from the observer, and may bow into the hole repeatedly before entering. These signs of shyness are generally present at the start of a breeding season, but largely disappear as nesting progresses. The members of a pair may then appear remarkably tame. When I set a step ladder by Nest H, the parents fed their nestlings without hesitation when I was less than 3 m away. An occasional individual is more shy. Female I was unusually nervous, but this was mainly on her first visit to the nest after I had arrived. By a second or third visit she entered the nest with little hesitation. I never felt that my sitting close (at 7–8 m) ever kept her from an intended visit to eggs or young. The curious thing was that at Nest H where the members of the pair were both tame, MH made 59% and his mate 41% of the feeding visits. At Nest I, at the same height (4 m) above the ground, MI made 105 and FI, the shy female, 104 of the feeding visits made as I watched close by; these figures supporting an impression that FI was not unduly disturbed. The reason for sitting close to the nests was that I wanted to see, as clearly as possible, the types of prey parents were feeding nestlings.

Insects fed to nestlings.—Sapsuckers are versatile insect catchers, moving rapidly up trunks and limbs to glean from bark; flying against clusters of leaves and, on warmer days, catching prey in midair. They occasionally go to the ground, possibly more on wet days. They thus appear to catch insects of a wide variety in New Hampshire and I have never noted that they pick up ants any more than casually. Only a very small fraction of their prey, furthermore, is caught near their sap holes (Kilham 1964).

The size of prey may vary considerably. On 7 June 1968 I watched a male fly to the ground to catch a luna-sized moth which it carried to an "anvil" of rough bark. He pulled off the wings, then fed the body to a nestling that was 4 days from fledging. The male stayed by to poke in at the nestling to assist it in managing its large meal. On 17 July of another year I watched a male struggle with a willow sawfly (*Cimbex*) 3.4 cm in length. After battling for some minutes, the sapsucker gave up and I recovered the crippled but unsubdued insect from the ground.

Although sapsuckers pick up very small prey such as ants, it has seemed, from observations made close to nests, that most insects fed to young are large and more soft-bodied. Thus, to cite Pair C as an example, I noted between days 5 and 18 after hatching, that the male in 32% of 59 visits and the female in 34% of 73 visits, had legs and gauzy wings of insects projecting a centimeter or more from their bills. On a number of occasions I have watched foraging sapsuckers pause to compact their load of insects, bringing into their bills all projecting appendages; then after more foraging, fly to feed their young with no sign of larger prey being visible. This has made it seem that what one actually sees in bills at times parents arrive at the nest may be only a crude index of how much larger prey they are actually catching. Beetles, furthermore, of a centimeter or more in size, are usually so beaten and dismembered as to be difficult to recognize.

In June in New Hampshire I have found large crane flies (*Tipula* sp.) to be common in woods where I have watched sapsuckers. These may have accounted for many of the legs and wings projecting from parents' bills. On one morning after a rain, FH flew to the ground and picked up a smooth larva, 2.5 cm long, possibly of a crane fly.

In two successive years the male at one nest aspen carried feces to a place

3 m above ground on a low tree, discarding his load against the bark. I cleared the ground below and was thus able to make daily collections. A sample of these, as kindly examined by Dr. G. Thomas Fisher, Dept. of Entomology, University of New Hampshire, contained for the most part remnants of major and minor workers of carpenter ants (*Camponotus pennsylvanicus*). These findings coupled with those of Beal (1911) have made me feel that the remains of ants pass through digestive tracts particularly well. As guides to what sapsuckers actually feed nestlings, however, they may be deceptive. Other views and experiences on the subject of sapsucker foraging are given by Lawrence (1967) and Tate (1973).

While sapsuckers bring sap as well as insects to nestlings, I have never seen them bringing fruit. This may be because trees fruiting in June and early July were scarce in woods where I did my watching. Sapsuckers are not unique in bringing sap to feed young, for Thönen (1966) has noted the same habit in the Three-toed Woodpecker (*Picoides tridactylus*) of Europe.

Black polymorph females.—In the course of studying sapsuckers over 25 years and finding 69 nests, I have encountered 12 females that were "black polymorphs" having black or nearly black crowns. Attempts to find consistent differences in their breeding behavior have been unsuccessful.

DISCUSSION

Males were the more domestic-minded of pairs of sapsuckers studied in New Hampshire. While females sometimes equaled them in attentiveness to incubating, brooding, and, for periods, feeding nestlings, males generally performed the larger share of these activities as well as doing most of the excavating and nest cleaning. The females might be regarded as a reserve, exerting themselves to the full when a nest contains a full brood of 4 or more. In a nest with only 1 nestling, on the other hand, as was the case with Nest H, the female left almost all of the care to the male.

This greater role of males may explain differences of behavior in lone males as compared to lone or widowed females. Of 3 lone males, to combine one described by Lawrence (1967) with 2 of mine, 2 succeeded in raising their young, feeding them in normal fashion. Of 3 females that I observed, all fed their young in an inefficient, exaggerated fashion. The nestlings of 2 died, seemingly of starvation. The third lone female succeeded in attracting a new mate who started to feed the nestlings 2 days later (Kilham, in press). A point of comparison was that while one of my lone males and one of Lawrence's attracted new females, these new females, although they came to the territory, showed no interest in the nests. This is perhaps what one might predict, females being on the whole the less domestic-minded. The successful remating, in terms of care of the young, involved a new male.

Lawrence's account (1967) of the nesting of sapsuckers in Ontario differs from mine in a number of respects. One is where (pp. 95–96) she states that of 4 woodpeckers (of which one was the sapsucker) that she studied, none left "their eggs uncovered more than a minute or two at a time or, to be exact, a total of 27 min in 90 hours of observation." Were my observations of much more time (Table 2) unusual? It would not seem so from what other observers have recorded for other picines. Thus, Skutch (1969:469), during 5 hours of observing Red-crowned Woodpeckers (*Melanerpes rubricapillus*), noted that they left their eggs uncovered 86 min or 22% of the time. The restlessness that he describes for this and for the Golden-naped Woodpeckers in the incubation period is almost exactly what I have noted for *S. varius*. Although he only gives times of actually incubating in his table (p. 486) his figures for 4 pairs of *M. chrysauchen* show that they left eggs uncovered for 0, 10, 11, and 24% of the time respectively. Skutch's experiences with Acorn Woodpeckers (*M. formicivorus*) were similar for in one watch of 11.5 hours, he found eggs were left uncovered for 141 min. One can say that all of these species were melanerpine and observed in the subtropics. It is of interest, therefore, that Pynönnen (1939:114), in all-day watching at 2 nests of Greater Spotted Woodpeckers (*Picoides major*) in Finland, found eggs left uncovered for periods totaling 5–6 h for one pair and 4 h for the other. The most restless woodpeckers I have observed were a pair of Hairy Woodpeckers (*P. villosus*) in Lyme. Both the male and female left eggs uncovered up to 30 and 40% of tours on duty on the nest and this was throughout the incubation period, as judged by periods of watching limited to 40–90 min at a time that I made on scattered days, at a distance that was far enough away not to frighten them.

To cite Skutch's account (1969) again there are parallels in nest sanitation between *S. varius* and at least 3 species of *Melanerpes* woodpeckers. He states that Golden-napes "often allow nestling's droppings to accumulate in the hole and then remove them in a spell of concentrated house cleaning." Golden-napes use their nest cavity for roosting after fledging and keep it clean the whole time. On the other hand Golden-fronted (*M. aurifrons*) and Red-crowned woodpeckers, that do not use theirs after fledging, "appear not to clean the nest at all after the young birds can take their meals through the doorway." Sapsuckers appear to be ambivalent in this regard, some pairs ceasing well before and others continuing to carry out feces until the time of nest leaving.

The functions of the loud, persistent vocalizations of nestlings, that could attract predators, is a subject that needs further study. As pointed out by Skutch (1976) they are possibly more important in hole-nesters that cannot be guided by the speed, strength, and color of gaping reactions when feeding young in a darknened nest cavity. The best experiments are seemingly those of von Haartman (1953). He was able to show, by dividing a nest box of the Pied Flycatcher (*Muscicapa hypoleuca*), that the rate at which parents fed their young was not guided by their number but by the clamor raised by the hungriest of them. If birds of temperate zones raise the largest broods possible, then begging cries would seem a device that might insure efficient and constant feeding. Quite opposite to these views, however, are those of Lawrence (1967:125) who states that she "found no evidence of the woodpecker nestlings "chatter notes" having any direct stimulating effect upon parents' feeding rates."

Differences of opinion are, or should be, a stimulus to further studies. If the natural history of sapsuckers or other woodpeckers is to be known with any completeness, it would seem that far more studies are needed by different observers studying them and their nesting habits in different parts of their total range.

SUMMARY

Activities covered in this report extend from excavation through time of fledging of Yellow-bellied Sapsuckers. Males did nearly all of the excavating. When a first excavation failed, one female excavated harder and longer than her mate in starting a new one. Two females were dominant at the nest hole at time of egg-laying. Males started incubating more promptly than some females, but after 4 to 5 days delay, females of 2 nests incubated more than their mates in daylight hours. Eggs were left uncovered 16% of the time. The tasks of brooding and feeding the young were shared by both sexes almost equally. When free of brooding, which lasted for 8–10 days, the combined feeding rate of the sexes doubled almost immediately in 2 pairs. Males did the most of the nest cleaning.

Comparisons are made of feeding rates of parents caring for 1, 2, 3, and 4 young and of the behavior of 2 lone or widowed males as compared to 3 lone females. Both situations brought out the greater role of males. The loud vocalizations of young sapsuckers are considered as having selective value in stimulating parents to a high rate of foraging and feeding of nestlings.

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GENERAL NOTES

Sex differences in alarm responses of wintering Evening Grosbeaks.—Flocked birds probably attract the attention of predators to a greater degree than do solitary individuals. Conspicuous colors, movements, or vocalizations tend to promote flock cohesion while increasing predation risks; thus flocked birds must effect a compromise between the need to communicate among themselves and the need to evade predators (Wiley, Auk 88:881–892, 1971; and references cited therein).

A species illustrating such a compromise is the Evening Grosbeak (*Hesperiphona vespertina*), which occurs in sizable flocks during the winter in several parts of the U.S. The flocks are conspicuous, both visually (due particularly to the boldly patterned plumage of males) and auditorily (due to the grosbeaks' frequent use of loud calls). During a study of winter social behavior in this species, I observed the alarm responses of males and of females in grosbeak flocks. This paper describes some sexual differences in alarm responses which might function to reduce predation in this species.

Methods.—Wintering Evening Grosbeaks were observed from February to May 1976 at Logan, Utah on a 200-m semi-urban wooded stretch bordering the Logan River. Three hundred grosbeaks were banded of an estimated total of at least 700–800 individuals that frequented the study area (Balph and Balph, Bird-Banding 47:340–344, 1976).

Alarm responses within feeding groups of grosbeaks were documented in April and early May at a 0.86 × 0.86 m elevated platform provisioned with sunflower seeds and situated 1.5 m from the nearest cover. The birds were watched through 1-way glass from a blind positioned 0.5 m from the platform.

Counts were made at 15- to 30-sec intervals of the number of males and females present. If, during a given period between counts, the feeding group showed a generalized alarm response in which some individuals adopted a "freezing" stance at the platform and others escaped, a count immediately was made of the number of males and females remaining at the platform. One hundred such instances were recorded.

Additional observations were made of the incidence of distress calls or "squeals" among 189 individuals during trapping and banding operations. Squealing was recorded as present if a bird produced the call one or more times when handled.

Alarm responses within feeding groups.—Evening Grosbeaks feeding in groups at the platform sporadically exhibited fright responses. Such responses appeared sometimes to be caused by the flight overhead of a hawk or shrike or by human activity, although in most instances I was unable to discern an obvious stimulus for the behavior. Typically, the birds suddenly became alert and ceased to eat; then, a fraction of a second later, some or all members of the group flew away, often to nearby trees. Sometimes a bird at the platform gave the *keer* call, which in most contexts functioned as a contact vocalization, just prior to the initial moment of alertness. Escaping birds either were silent or, more often, gave the *bree* call ordinarily associated with agonistic interactions. Occasionally, an escaping bird gave a chirping sound.

Individuals that remained at the platform during a fright adopted a crouched posture and remained motionless and silent for several seconds or longer. Birds freezing in this manner appeared extremely alert and tended to fly away at the slightest fear-producing stimulus. If they did not become further alarmed, they eventually resumed feeding at the platform.

The mean number of males counted at the platform just prior to a fright was 12.8 ($n = 100$, $SD = 6.16$), and of females, 17.7 ($n = 100$, $SD = 6.76$). The pre-fright sex ratio thus was 1.38:1.00 in favor of females. This ratio did not differ significantly from

Table 1

Occurrence of Distress Calls Among Male and Female Evening Grosbeaks at Successive Captures

		Males (n)		Females (n)	
Capture	Previous Behavior	Captured	Calling	Captured	Calling
1	—	87	67	102	93
2	Called at 1	7	3	11	10
	Did not call at 1	2	0	1	0
3	Called at 1 and 2	—	—	1	1
	Called at 1 but not 2	2	0	—	—

the sex ratio of 254 grosbeaks trapped in the same part of the winter (1.31 females to 1.00 males) ($\chi^2 = 0.18$, df = 1, $P > 0.5$).

The mean number of males observed to freeze at the platform during a fright was 1.6 (n = 100, SD = 1.63), whereas that of females was 6.8 (n = 100, SD = 4.36), producing a post-fright sex ratio of 4.30:1.00 in favor of females. In 92 of 100 cases, a greater proportion of females than males exhibited the freezing response; this result differs significantly from chance expectation ($\chi^2 = 70.56$, df = 1, $P < 0.001$). If one compares male to female numbers at the platform before and after the onset of frights, a highly significant difference is again obtained ($\chi^2 = 149.34$, df = 1, $P < 0.001$). Thus, females showed a greater tendency than males to freeze at the platform when alarmed, and males exhibited a greater tendency than females to flee. This difference of behavior appeared also to hold for grosbeaks that became alarmed while resting or feeding on buds in leafless trees, although I did not make quantitative observations of responses in this situation.

Distress behavior of restrained birds.—Evening Grosbeaks that I trapped, banded, and measured often produced squeals when handled. Of 189 individuals for which I recorded the presence or absence of this vocalization at initial capture, 77% of males squealed, whereas 91% of females gave the call (Table 1). A significantly greater proportion of females than males squealed when handled for the first time ($\chi^2 = 7.25$, df = 1, $P < 0.01$). In general agreement with this finding is J. Ogden's (quoted in Norris and Stamm, Bird-Banding 36:83–88, 1965) observation that, of 10 Evening Grosbeaks captured in mist nets, 5 females gave distress calls during removal from the nets, whereas 5 males gave no calls. Parks' (Bird-Banding 16:32–36, 1945; Bird-Banding 18:57–76, 1947) descriptions also suggest that females of this species squealed more often than males when handled.

Twenty-one of the 189 individuals were recaptured one or more times 1–10 days after they were banded. Such birds either repeated the initial response when handled and measured on later occasions or, alternatively, called on the first but not on subsequent occasions (Table 1). Although my sample sizes are too small to permit a meaningful statistical analysis, the fact that several birds squealed at initial capture but not on later occasions, whereas none showed the reverse pattern, suggests that habituation to handling was a factor affecting response frequencies. In all but one case, individuals that called at initial capture but not thereafter were males. It thus seems possible that Evening Grosbeaks differ sexually not only in the propensity to give distress calls at first capture, but also in the tendency to cease responding when handled for a second or third time.

Squealing by hand-held grosbeaks often was accompanied by a visual display in which the bill was opened and the tail spread. Some birds also raised the crest; and occasional individuals spread the wing, maintaining it for several seconds in a horizontally extended position, when I released my hold on one wing. The latter behavior appeared to be more common among vocal females than among vocal males.

Discussion.—Cryptically colored animals may avoid detection by predators by remaining motionless against an appropriate background (reviewed by Alcock, Animal Behavior: an Evolutionary Approach, Sinauer Associates, Inc., Sunderland, Mass., 1975). It seems possible that sex-associated differences in the alarm responses of wintering Evening Grosbeaks are adaptively related to the species' sexual dimorphism in plumage coloration. To me, the plumage of females appears much less conspicuous than that of males against a variety of backgrounds in winter and spring. The sexual difference in visual conspicuousness seems more marked when the birds are stationary than when they are in flight. If the difference is similarly evident to animals that prey upon this species, then female Evening Grosbeaks should benefit more than males by freezing in relatively open situations. Conversely, males should increase their chances for survival by fleeing immediately to cover when alarmed. Males, by fleeing, might secondarily reduce the probability of a predator's detecting exposed, motionless females. One might expect to find similar differences of behavior in males and females of some other bird species showing comparable dimorphism in plumage coloration.

The sexual differences I observed in the distress responses of restrained Evening Grosbeaks seem problematical. One could speculate that these differences bear some relationship to differential alarm responses in free-ranging flocks. Since females apparently rely more extensively than males upon concealment in open situations, they should be more vulnerable than males in the event of detection by a predator. A second line of defense (i.e. squealing) thus might be more important to females than to males. However, an examination of Norris and Stamm's (1965) findings on interspecific differences in the occurrence of distress calls among restrained birds reveals no obvious relationship between cryptic coloration and the tendency to squeal when handled.

In many species, squealing by a captured individual stimulates birds of the same and sometimes of other species to mob the predator, potentially providing the victim with an opportunity to escape (reviewed by Thorpe, Cambridge Monogr. Exp. Biol. 12:1–143, 1961). Free-ranging Evening Grosbeaks did not mob me when I removed squealing conspecifics from traps, although the possibility remains that the birds might mob a predator under different circumstances. In any event, it seems possible that squealing—with its concomitant visual display, which contains several postural elements used intraspecifically in threat—might function in this species to startle or repel a predator and thereby to increase a victim's chances for escape.

Summary.—Observations were made of alarm responses among Evening Grosbeaks wintering at Logan, Utah. When a feeding flock became alarmed, females exhibited a significantly greater tendency than males to freeze rather than to fly to cover. Females also showed a significantly greater tendency than males to give distress squeals when handled. It is hypothesized that sexual differences of response to danger stimuli may be adaptively related to sexual dimorphism in plumage coloration in this species.——MARTHA HATCH BALPH, *Dept. of Wildlife Science, Utah State Univ., Logan 84322.* *Accepted 7 Dec. 1976.*

Nesting of Turkey and Black vultures in Panama.—On 23 March 1976 I found a Turkey Vulture (*Cathartes aura*) nest with 1 young, and a Black Vulture (*Coragyps atratus*) nest with 2 young on a 0.5 ha island in Gatun Lake, Panama Canal Zone. The island is 525 m from the nearest mainland and 275 m offshore Barro Colorado Island. the Smithsonian Tropical Research Institute's biological reserve. The vegetation is young secondary forest about 20 m high with a relatively open canopy and a predominance of palms. The undergrowth is not dense and consists of tree seedlings, vines, and grasses. One-third of the island has been cleared for an experiment and there has been almost daily human activity there since January 1976. Other than vultures, the largest animals regularly encountered on the island are basilisk lizards (*Basiliscus basiliscus*) and marine toads (*Bufo marinus*). One armadillo was seen on the island for a short time. The scarcity of animals which might prey on the eggs or nestlings may make the island a particularly favorable nesting site.

The Turkey Vulture nest encompassed an area of about 1 m^2 under a tangle of grass and brush at one end of the island. Leaves and debris under this cave-like shelter had not been arranged in any way. It appeared that the 24-day-old nestling moved about in the entire area.

The nestling was removed from the nest 8 April 1976 and hand-reared. From photographs and descriptions of the development of a Turkey Vulture (Bent, U.S. Natl. Mus. Bull. 167:18, 1937) I estimated its age on 8 April to be about 24 days. Egg-laying, therefore, was the first week of February for incubation is "almost 40 days" (Coles, Studies in the Life History of the Turkey Vulture, Ph.D. thesis, Cornell Univ., Ithaca, N.Y., 1938) and hatching occurred the week of 14 March. The bird fledged when 70 days old, on 21 May, which age corresponds to that provided by Coles (1938) of 70 to 80 days. The nest site was periodically examined for 4 months after the young had been removed and there was no evidence of a second nesting attempt.

A Black Vulture nest was 35 m from the Turkey Vulture nest. The nest was located at the base of a clump of palms in a small tunnel-like shelter formed by dead palm leaves among the trunks. No nest material appeared to have been brought in or arranged by the adults. Both the Turkey and Black vulture nesting sites were similar in being somewhat concealed from view, providing some shelter from rain, and encompassing about the same area.

The Black Vulture young had apparently left the nest at least 17 days before fledging: no young had been seen after 23 March until 7 April when one flightless young observed near the site was easily captured. By 9 April, however, 2 young and 2 adults were seen on the shore of the island. I believe that the young were fully capable of flight by this time, and that the 4 were the 2 adults and young from the nest on the island, although none had been banded. Subsequent observations reinforced that assumption. Four Black Vultures were commonly observed on the island for 15 weeks after the young had fledged: a tall tree at the edge of the cleared area was a favorite roost. The 4 Black Vultures formed a cohesive group, flying in together to perch in the tree, and always flying off together. The composition of the group was always 2 young and 2 adults; it was unusual to see vultures other than these 4 roosting on the island.

Incubation for Black Vultures has been reported as 38 days, and the young fledge in 80 days from hatching (Stewart, Auk 91:595–600, 1974). Thus, the Black Vultures which had fledged by 9 April probably hatched the first week of February; egg-laying then would have occurred the last week of December 1975.

For at least 5 weeks after fledging the 2 Black Vulture young would beg for and receive food from the adults. The young would vigorously flap their wings, bob their heads, and emit a low-pitched hissing sound. On 26 July, more than 15 weeks after fledging, the young were still begging food but were not fed on the one occasion I observed them. Long post-fledging dependence is also indicated for the Turkey Vulture by the hand-reared young's recognition of and behavior towards me. For 7 weeks after fledging the young Turkey Vulture would, upon my appearance, assume a posture with wings slightly spread and arched downwards, the head lowered, and the tail inclined upwards with the feathers separated. There was much head-bobbing and wing-flapping when food was presented, but no vocalizations. The Turkey Vulture did not behave in this manner if approached or fed by other individuals.

The nesting of Turkey and Black vultures I observed corresponds to the dry season in Panama which is from January to April. Wetmore's (Smithsonian Misc. Coll., 150(1): 160–161, 1965) incidental reports of Black Vulture nesting activity, nestlings, fledglings, and an egg collection also indicate that nesting occurs during the dry season in Panama for this species. His only information on *Cathartes* sp. nesting in Panama is for the Yellow-headed Vulture, *C. burrovianus*, for which he reported 2 young "only recently able to fly" on 14 May 1953. The Turkey Vulture from the nest on the island fledged 21 May.

Vulture nesting activity correspondence with the dry season may be due to several factors. Carrion resources for vultures may be greater during the dry season. However, for frugivorous animal populations at least, highest mortality might be expected at the end of the wet season, during November, December, and January, when fruit abundance is lowest (Smythe, Am. Nat. 104:25–35, 1970). Alternatively, the dry season weather may be more favorable for raising young. The dry season months are windier and drier than the rest of the year and foraging time is likely maximal then. The wet season's rains and calmer weather may make soaring difficult and thus make hunting less energetically efficient. Also, the higher relative humidity and rainfall then might be detrimental to the health and development of the terrestrial young.

I thank Eugene S. Morton for commenting on the manuscript.—LAURIE A. MCHARGUE, *Smithsonian Tropical Research Institute, Box 2072, Balboa, Canal Zone. Accepted 11 Nov. 1976.*

Fulvous Whistling Duck populations in Texas and Louisiana.—Numbers of Fulvous Whistling Ducks (*Dendrocygna bicolor*) declined rapidly in the 1960's apparently from exposure to pesticides applied to rice (Flickinger and King, J. Wildl. Manage. 36: 706–727, 1972). The species was listed as endangered by the Texas Organization for Endangered Species since 1972. However, numbers have increased since 1970 when many rice growers began to voluntarily discontinue the use of aldrin-treated rice seed in Texas and to substitute drill planting for aerial seeding of treated seed in Louisiana. Aldrin treatment of rice seed was suspended by the U. S. Environmental Protection Agency in 1974.

Ground or aerial surveys of Fulvous Whistling Ducks were made at all their traditional concentration areas in 14 southeast Texas counties or 4 Parishes of southwest Louisiana along the Gulf Coast. Counts and estimates were alternated between Texas and Louisiana between 1968 and 1974 when the first late summer estimates were made for both states. Spring and later summer censusing was done in Texas for the first time in 1975. Most spring counts were made from the ground from mid-April through May with the exception of the count in Texas in 1975 (made 15 to 30 April). Late summer birds in both states were estimated from aircraft during mid-September except in Texas in 1975 when a ground count was taken.

In the spring of 1968 only 1123 Fulvous Whistling Ducks were counted in both states

TABLE 1

FULVOUS WHISTLING DUCKS OBSERVED IN TEXAS AND LOUISIANA, 1966–1975

Year	Texas	Louisiana
	Spring[a]	
1966	—[b]	192
1967	519	672
1968	379[c]	744 (1,000)
1969	978	—
1970	—	1,441 (4,000)
1971	—	1,555 (4,000)
1973	(2,000)[d]	—
1975	1,650[c]	—
	Late Summer	
1973	—	(6,000– 8,000)
1974	(15,000)[e]	(8,000–10,000)
1975	6,700	(8,000–12,000)

[a] Counts and estimates of total numbers in Louisiana from J. Lynch, U. S. Fish and Wildlife Service (pers. comm.); [b] (—) = No observations made; [c] Ground and aerial counts made in the rice belt; [d] Estimate for the Texas Rice Belt (from C. Stutzenbaker) *in* Bellrose (The Ducks, Geese and Swans of North America, Stackpole Books, Harrisburg, PA, 1976:75; [e] Estimate of Chambers and Jefferson counties from J. Dunks, Texas Parks and Wildlife Department (pers. comm.).

(Table 1) when the use of aldrin-treated rice seed was at a peak. Following a decline in aldrin use, numbers increased in the spring in Louisiana (1441 in 1970) and in Texas (about 2000 in 1973). There were also fewer Fulvous Whistling Ducks found dead in rice fields in 1970 and 1971 (Flickinger and King, J. Wild. Manage. 36:706–727, 1972) than in earlier years.

During the spring of 1975 largest concentrations in Texas occurred in Chambers and Wharton counties with the peak number of 650 birds in Wharton County on 26 April. The Texas counties of Chambers and Jefferson had concentrations in both spring and late summer. In late summer there was an eastward movement of Fulvous Whistling Ducks into the Port Arthur area from the western part of the rice belt (Flickinger et al., J. Wildl. Manage. 37:171–175, 1973). This may explain the increase in numbers in Chambers and Jefferson counties and their absence in western rice belt counties at this time of year. In late summer of 1974, 15,000 birds were estimated from aircraft during a general waterfowl survey of Chambers and Jefferson counties (J. Dunks, pers. comm.). In 1975, 6700 birds were recorded by ground counts made in late summer. The highest count of 5700 birds was made in Chambers County on 14 September. However, most of the rice country in Chambers and Jefferson counties was not surveyed by aircraft in the late summer of 1975. Therefore, the decrease in late summer numbers in Texas from 1974 to 1975 is probably more apparent than real and does not indicate a sudden decline in the population. From 8000 to 10,000 Fulvous Whistling Ducks were estimated for southern Louisiana in the late summer of 1974 and from 8000 to 12,000 in 1975. The largest number observed (5000–7000 birds) was in Acadia Parish on 15 September.

A reasonable estimate would be that about 17,000 Fulvous Whistling Ducks were in southeast Texas and southwest Louisiana in the late summer of 1975 (7000 in Texas and 10,000 in Louisiana). This should provide a base-line index for future late summer censuses.—EDWARD L. FLICKINGER, *U.S. Fish and Wildlife Service, Victoria, TX 77901*; DAVID S. LOBPRIES, *Texas Parks and Wildlife Dept., Port Arthur, TX 77640*; HUGH A. BATEMAN, *Louisiana Wild Life and Fisheries Commission, Baton Rouge, LA 70804.* *Accepted 14 Jan. 1977.*

Slipper shells, a major food item for White-winged Scoters.—In the winters of 1973 and 1974, large feeding flocks of White-winged Scoters (*Melanitta deglandi*) moved into the New Bedford Harbor region of Buzzards Bay, Plymouth Co., Massachusetts. I collected 28 White-wings and examined their upper digestive tracts. Six individuals did not have sufficient food material in the gullet for analysis. The contents of the 22 individuals analyzed differed from those in the literature and from my own previous observations. Slipper shells (*Crepidula fornicata*) comprised 88% of the bulk organic matter by volume. The remainder of the stomach contents was mostly oyster spat and soft shelled clams. These did not exceed 25% of the bulk in any individual. Cottam (U.S.D.A. Tech. Bull. 643, 1939) reports from an examination of 819 adult White-wings, that ¾ of their food was mollusks, of which bivalves comprised 63% and less than 2% were slipper shells. Scott and Olson (Ecol. 54:996–1007, 1973) found in New Hampshire that 89% of the total volume of food of White-winged Scoters was bivalves and *Siliqua costata* was the dominant food; they recorded no slipper shells.

Trawl and dredge samples from the feeding area revealed a high accumulation of shell. These shell deposits are from shucking operations of local sea and bay scallop industries. Three species of *Crepidula* were attached to the shell deposits; *C. fornicata* was the dominant species. Hoff (Sci. Teach. 38:1, 1971) reported a heavy organic load in the surrounding waters, the primary source of which is untreated sewage from a nearby municipal sewer outfall.

It is apparent that the combination of high concentration of organic nutrients and shell substrate have provided an ideal habitat for slipper shells. These in turn have provided a different food budget for White-winged Scoters in southeastern Massachusetts.—JAMES G. HOFF, *Southeastern Massachusetts Univ., Dartmouth 02747.* *Accepted 16 Jan. 1976.*

Egg movement by a female Gadwall between nest bowls.—Gadwalls (*Anas strepera*) nest commonly on the Woodworth study area located 4.8 km east of Woodworth, North Dakota on the Missouri coteau (Kirsch and Higgins, Wildl. Soc. Bull. 4:16–20). This 1231 ha area is a research station of the Northern Prairie Wildlife Research Center.

On 13 June 1975 a Gadwall nest containing 10 eggs was found at the station headquarters inside an open-topped enclosure measuring 6 m by 6 m and fenced with 5 cm by 5 cm chain link wire mesh. Vegetation at the nest site consisted of smooth bromegrass (*Bromus inermis*) and absinth (*Artemisia absinthium*). This nest was in a corner of the enclosure with the rim of the nest touching the fence. The clutch had been incubated approximately 2 days.

We revisited the nest on 5 July and found that 8 of the 10 eggs had been moved into a new nest bowl on the other side of the fence adjacent to the original one. The other 2 eggs were in the original nest bowl and were cold. Incubation of the 8 eggs in the new nest was about 22 days. We moved the other 2 eggs into the new nest with the remainder of the clutch. Vegetation at this site was comparable to that at the first nest site.

On 7 July all 10 eggs had been moved back through the fence into the original nest and some of the eggs had hatched. Eight ducklings had hatched and left the original nest by 8 July and 2 dead embryos in partially pipped eggs remained in the nest.

A possible explanation of how this egg movement was accomplished has been discussed by Oring (Auk 81:88–89, 1964) who reported that some Pintails (*A. acuta*) and Mallards (*A. platyrhynchos*), but none of 15 trapped Gadwalls, moved their eggs into new nests after a trap was placed over the original nest. The ducks used the ventral surface of their bills to pull the eggs through the trap. This Gadwall may have moved her eggs in the same manner when she returned to her nest from opposite sides of the fence.

The authors thank Kenneth F. Higgins and Harold F. Duebbert for reviewing the manuscript.—ROBERT F. JOHNSON JR., *Dept. of Forestry, Michigan Technological Univ., Houghton 49931* and LEO M. KIRSCH, *Northern Prairie Wildlife Research Center, U.S. Fish and Wildlife Service, Jamestown, ND 58401. Accepted 3 Feb. 1976.*

Foods of western Clapper Rails.—The Colorado River population of the Clapper Rail (*Rallus longirostris yumanensis*) is presently listed as endangered (U.S. Fish and Wildlife Service, United States List of Endangered Fauna, p. 11, 1974). Its presence in fresh-water habitat during the 5-month breeding season and probable migration to Mexican coastal salt water swamps (Tomlinson and Todd, Condor 75:177–183, 1973) are considered unusual for Clapper Rails in general.

In June 1971, Tomlinson and R. L. Todd collected 35 Clapper Rail specimens in the southwestern United States and western Mexico to determine if a racial distinction occurred among the geographically isolated populations. Three separate races (*R. l. yumanensis*, *R. l. rhizophorae*, and *R. l. nayaritensis*) were confirmed from the collection (Banks and Tomlinson, Wilson Bull. 86:325–335. 1974). Because the food habits of these rails were unknown, 32 stomachs (proventriculus and gizzard) were preserved for later food habits analysis. This analysis provides the first insight into the freshwater food habits of *R. l. yumanensis*, and should be useful in future preservation and management considerations. The birds were collected in fresh-water marshes along the Colorado River from Needles, California south to the Delta in Sonora, Mexico and in mangrove (*Avicennia germinans* and *Rhizophora mangle*) swamps from Guaymas, Sonora, to San Blas, Nayarit, Mexico (Table 1). Airline distance from the northernmost to southernmost points is approximately 1800 km. The specimens, including specific data relating to their collection have been deposited in the U.S. National Museum, Washington, D.C.

Each Clapper Rail stomach was wrapped in cheesecloth in the field and preserved in a 10% formalin solution. Analysis was conducted at Arizona State University following procedures described by McAtee (Auk 20:449–464, 1912). The contents of each stomach were separated into ingesta types in a gridded petri dish and examined under a dissecting microscope. Each food type was visually estimated as a percentage of the total content in a particular stomach.

The major foods of Yuma Clapper Rails were invertebrates; little vegetative material was present (Table 2). Crayfish (*Procambarus* and *Orconectes* are the common genera) were the dominant food in 9 of the 10 stomachs from Topock Marsh on the lower Colorado River south to Imperial Reservoir in Arizona and California; the other stomach was empty. Of 2 specimens collected at the confluence of the Gila and Colorado rivers, one contained primarily an introduced fresh-water clam (*Corbicula* sp.) (98%), and the other primarily isopods (97%). Colorado River Delta specimens in Mexico contained a greater variety of food organisms, but the major components were water beetles and fish.

Of the 16 *R. l. yumanensis* stomachs, 9 had crayfish, 11 contained insect fragments, 4 had water beetles, 4 had fish, and 3 contained clams. In addition to the water beetles, other insect matter consisted of small amounts of weevils (3 stomachs), damselfly nymphs (2 stomachs), dragonfly nymphs, grasshoppers, and insect eggs. Spiders, leeches, prawns,

TABLE 1

CLAPPER RAIL COLLECTION SITES

Race	Number of Specimens	Location	Coordinates
Yuma Clapper Rail (*R. l. yumanensis*)			
	4	Topock Marsh and Gorge	34°44′N, 114°30′W
	1	Bill Williams Delta	34°17′N, 114°04′W
	2	Cibola Lake	33°14′N, 114°10′W
	1	Below Cibola Lake in Colorado River	33°11′N, 114°10′W
	1	Martinez Lake	32°58′N, 114°29′W
	1	Imperial Reservoir	32°52′N, 114°28′W
	2	Confluence of Gila and Colorado rivers	32°43′N, 114°33′W
	4	Colorado Delta in Sonora, Mexico	32°02′N, 115°06′W
	16		
Sonora Clapper Rail (*R. l. rhizophorae*)			
	2	Laguna Del Soldado, Guaymas, Sonora	27°57′N, 110°59′W
	2	Bahia Tobari, Sonora	27°05′N, 109°56′W
	2	Topolobampo, Sinaloa	25°38′N, 109°03′W
	6		
San Blas Clapper Rail (*R. l. nayaritensis*)			
	2	Altata, Sinaloa	24°38′N, 107°56′W
	3	Mazatlan, Sinaloa	23°13′N, 106°22′W
	5	San Blas, Nayarit	21°34′N, 105°17′W
	10		
Grand Total	32		

and a small mammalian bone also were found. Vegetative matter consisted of twigs (10% in 1 stomach), 2 legume seeds (1 stomach), and 18 unidentified black seeds (3 stomachs).

All 16 of the *R. l. nayaritensis* and *R. l. rhizophorae* stomachs contained crabs (Table 3). Of the 6 *R. l. rhizophorae* samples, 5 contained 99% or more crab material and one contained 75% pulmonate snail plus 23% crab. The stomach contents of each of the 10 *R. l. nayaritensis* specimens consisted of 89% or more of crab parts. Six morphologically distinct types of crab were differentiated by exoskeleton and chelae in the sample but further identification was not accomplished. Other identifiable items were insect eggs in 2 stomachs and insect fragments in 3. Vegetative matter was slight, consisting of 2 unidentified seeds, each found in a separate stomach. One stomach contained 2 white stones. Esophageal contents from 1 bird (possibly part of a regurgitated casting) consisted of 6 crab legs.

Table 2

Stomach Contents of *R. l. yumanensis* From the Lower Colorado River and Delta[1]

	General Locations of Collection						
	Topock Marsh to Imperial Lake		Confluence of Gila and Colorado Rivers		Colorado Delta		Total Birds Containing Food Items
	% Composition		% Composition		% Composition		
FOOD ITEMS	Average	Range	Average	Range	Average	Range	
Crustacea							
Astacidae (Crayfish)	94.67	80–100					9
Palaemonidae (Shrimp)					.25	0– 1	1
Isopoda			48.50	0–97			1
Insecta							
Hydrophilidae (Water beetles)					56.50	1–80	4
Carabidae (Ground beetle)	0.11	0– 1					1
Unidentified Coleoptera	0.56	1– 5					1
Curculionidae (Weevils)	2.78	5– 10					3
Anisoptera (Dragonfly nymphs)					0.50	0– 2	1
Zygoptera (Damselfly nymphs)	0.11	0– 1			2.00	0– 8	2
Orthoptera (Grasshoppers)	0.11	0– 1					1
Insect eggs	0.11	0– 1					1
Unidentified parts	0.78	1– 6	1.50	1– 2			4
Arachnida (Spider)	0.56	0– 5					1
Hirudinea (Leech)					3.75	0–15	1
Mollusca (*Corbicula*)	0.06	0– 0.5	50.00	2–98			3
Vertebrata							
Unidentified fish					31.75	9–98	4
Unidentified mammal bone	0.06	0– 1					1
Plant matter							
Seeds	0.11	0– 1			2.75	1– 5	2
Twigs					2.50	0–10	1
	100.02		100.00		100.00		
Total Birds Examined	9		2		4		15[2]

[1] Date presented as estimated percentages of total volume of stomach food content.

[2] One additional bird taken at Bill Williams Delta had no food in its digestive tract.

TABLE 3

STOMACH CONTENTS OF *R. L. RHIZOPHORAE* AND *R. L. NAYARITENSIS* FROM MEXICO[1]

FOOD ITEMS	*R. l. rhizophorae* % Composition Average	*R. l. rhizophorae* % Composition Range	*R. l nayaritensis* % Composition Average	*R. l nayaritensis* % Composition Range	Total Birds Containing Food Items
Crustacea					
Brachyura (Crabs)	86.83	23–100	98.40	89–100	16
Mollusca					
Pulmonata (Snail)	12.50	0– 75			1
Insecta					
Eggs	0.17	0– 1	1.00	0– 10	2
Misc. Parts	0.17	0– 1	0.20	0– 2	3
Plant					
Brown seed	0.17	0– 1	.10	0– 1	2
Miscellaneous					
White Stones			.10	0– 1	1
Feathers	0.17	0– 1	.10	0– 1	2
Unidentified black fragments			.10	0– 1	1
	100.01		100.00		

[1] Data are presented as estimated percentages of total volume of stomach food content. Samples included 6 *R. l. rhizophorae* and 10 *R. l. nayaritensis.*

Food selections by birds in our sample were similar to those of other Clapper Rail populations. The major food item of Georgia Clapper Rails (*R. l. waynei* and *R. l. crepitans*) was crabs, supplemented by other invertebrates and the seeds of cordgrass (*Spartina* sp.) (Oney, J. Wildl. Manage. 15:106–107, 1951). Pellet castings by *R. l. crepitans* in Delaware revealed crab exoskeleton and clam shell fragments (Meanley, Auk 79:113, 1962). Foods of western races of Clapper Rails, other than those reported herein, also consisted mainly of invertebrates with a minor amount of plant material. Moffitt (Condor 43:270–273, 1941) reported that the California race (*R. l. obsoletus*) ingested horse mussel (*Modiolus demissus*) as its main food item, with other invertebrates and seeds of cordgrass as supplements. Test and Test (Condor 44:228, 1942) found representatives of amphipods (Amphipoda) in one specimen of *R. l. obsoletus*, and Williams (Condor 31:52–56, 1929) observed this race to feed on clams (*Macoma* sp.). Applegarth (M.A. thesis, Stanford Univ., Standford, Calif; 1938) also listed a variety of invertebrates in the diet of the California birds and stated that this race lives almost entirely upon invertebrates. It was therefore not surprising that the 3 populations sampled in our study also relied heavily on invertebrates, particularly crabs and crayfish. However, we noted several interesting observations relative to food selection. First, despite a great abundance and variety of invertebrate food species in the mangrove swamps of Mexico, the birds sampled there apparently selected crabs in preference to other available foods. In the Colorado Delta (which generally contains brackish water and no crabs), the birds were adaptable and consumed a greater variety of foods. Up stream in the freshwater marshes of the Colorado River (which are relatively limited in invertebrate species and numbers; Grinnell, Univ. Calif. Publ. Zool. 12:15–294, 1914), the rails' principal food was crayfish. Thus, within the limits of this investigation, Clapper Rails were selective, opportunistic, or limited in the variety of foods eaten depending upon habitat type.

On the basis of the available literature (Ortmann, Proc. Am. Phil. Soc. 41(171):267–400, 1902) it is interesting to note that crayfish were absent on the lower Colorado River prior to 1900. In recent years, crayfish have become relatively common through introduction and/or natural expansion. The increase of a major food item, combined with creation of stable marsh habitat behind dams during the same period (Ohmart, et al., Trans. 40th N.Am. Wildl. and Nat. Res. Conf., 240–254, 1975) strongly support a hypothesis suggested by Tomlinson and Todd (Condor 75:177–183, 1973) and supported by Ohmart and Smith (USBR contract no. 14-06-300-2409, Boulder City, Nev., 1973) that *R. l. yumanensis* has since 1904 increased its distribution from the Colorado Delta northward along the Colorado River to approximately Needles, California. Further documentation of early river development and Clapper Rail distribution can be found in Dickey (Auk 40:90–94, 1923), Phillips et al. (The Birds of Arizona, Univ. of Ariz. Press, 1964), and Welsh (Audubon Field Notes 20:590, 1966).

We are grateful to R. L. Todd (Arizona Department of Game and Fish) for his help in securing specimens. Jill B. Leigh and Nancy Stamp aided in the sorting and identification of stomach contents.—R. D. OHMART, *Dept. of Zoology, Arizona State Univ., Tempe, 85201 and* R. E. TOMLINSON, *Patuxent Wildl. Res. Center, U.S. Fish & Wildl. Serv., Laurel, MD 20811.* (Present address RET: *U.S. Fish & Wildl. Serv., P.O. Box 1306, Albuquerque, NM 87103.*) *Accepted 19 Jan. 1976.*

Aggression in foraging migrant Semipalmated Sandpipers.—The comparative study of foraging in young and older birds is a current interest in ornithology (e.g. Orians, Anim. Behav. 17:315–319, 1969), but few accounts assess the specific components that affect foraging efficiency, for example age-related differences in mechanical abilities or differences in social factors (e.g. aggression) related to foraging.

We describe here some social and mechanical aspects of foraging in juvenile and adult Semipalmated Sandpipers (*Calidris pusilla*) which we observed at Plymouth, Massachusetts on 29 and 30 August 1973. Juveniles were easily identified by their juvenal plumage (see Bent, U.S. Natl. Mus. Bull. 142:248, 1927). The observations were made during an especially high tide when prey items, mostly amphipods, were unusually visible, even to us. Semipalmated Sandpipers in Plymouth usually rest during high tides and, except for brief periods during falling tides, they normally locate prey tactually.

Our observations on 29 August were made to compare the frequency of aggression among about 20 adult and 5 juvenile sandpipers. Chasers were usually in a "Tail-up" posture quite similar to what Drury (Fig. 5 in Auk 78:176–219, 1961) likens to Sharp-tailed Grouse (*Pedioecetes phasianellus*) dance postures. Dominant birds in virtually all chases we saw were the individuals that initiated a particular chase. The results (Table 1) are assessed by the same method Hailman (Bird-Banding 46:236–240, 1975) used in his analysis of sparrow aggression and show (1) that juvenile sandpipers were more frequently aggressive than adults ($\chi^2 = 19.88$, $P < 0.001$), but (2) that they were no more aggressive towards adults than towards other juveniles.

Our observations on 30 August were made under conditions similar to those of the 29th, but were directed more toward tallying rates of feeding attempts rather than toward determining social interactions between adults and juveniles. About 45 juveniles and 45 adults were present in the observation area, more than on the previous day. We chose a

TABLE 1

FREQUENCIES OF CHASES AMONG ADULT AND JUVENILE SEMIPALMATED SANDPIPERS FEEDING IN INUNDATED TIDAL WRACK

	Bird chased		
Chaser	Adult	Juvenile	Total
Adult	34[1] (42.88)[2]	5 (10.72)	39 (53.60)
Juvenile	25 (10.72)	3 (2.68)	28 (13.40)
Totals	59 (53.60)	8 (13.40)	67

[1] Observed Frequency.
[2] Expected Frequency.

single bird, either an adult or a juvenile, in either a normal or an aggressive Tail-up posture, and with a stop-watch timed its activities including the number of feeding attempts and aggressive encounters, for 30–120 sec. The time intervals varied because we often lost track of individuals in the melee of other birds. The summarized results (Table 2) show clearly that birds in Tail-up postures initiated chases more often than birds in normal postures, and that birds in normal postures were the victims of chases more often than birds in Tail-up postures. These results were regardless of age. This relationship may explain why the rates of feeding attempts were similar in all 4 possible age/posture groups (Table 2). Because we did not record the ages of birds being chased on the 30th, we can not state quantitatively whether or not there was any change in dominance relationships among juveniles from the previous day. Our impression was that there was little change.

Our intent is to show that in one circumstance, juvenile Semipalmated Sandpipers were more frequently aggressive than conspecific adults and that consequently they dominated adults proportionately more than they were dominated by adults. Thus all young birds are not necessarily submissive to adults while foraging, something which is often assumed. Our efforts to quantify whether or not this aggression resulted in their obtaining more food were inconclusive because we could rarely discriminate between successful and un-

TABLE 2

FEEDING ATTEMPT RATES AND FREQUENCY OF CHASING BY ADULT AND JUVENILE SEMIPALMATED SANDPIPERS FEEDING IN INUNDATED TIDAL WRACK

Age	Posture	No. sec observed	Mean no. of attempts/sec	No. of times chaser	No. of times chased
Adult	Normal	1068	0.50	3	28
Adult	Tail-up	880	0.45	68	8
Juvenile	Normal	960	0.44	4	15
Juvenile	Tail-up	855	0.50	77	8

successful feeding attempts. We noted, however, that aggressive and non-aggressive sandpipers had similar feeding attempt rates.

According to Recher and Recher (Wilson Bull. 81:140–154, 1969) a point is reached when the frequency and intensity of aggression among sandpipers declines as they become more concentrated in an area of abundant food. The adult sandpipers we watched may have reached this point but the juveniles may not have—possibly because they were less efficient than adults (see Recher, Ecology 47: 393–403, 1966) in catching prey and therefore had a higher threshhold for lowering aggression.

We thank D. G. Ainley, J. P. Hailman, and M. A. Howe for their helpful comments. This report is part of the results we have obtained in studies of migratory shorebirds funded by the Migratory Bird and Habitat Research Station, U.S. Fish and Wildlife Service, Contract No. 14-16-0008-687.—Brian A. Harrington and Sarah Groves, *Manomet Bird Observatory, Manomet, MA 02345.* (Present Address SG: *Dept. of Zoology, Univ. of British Columbia, Vancouver, B.C.*). *Accepted 9 Apr. 1976.*

Herring Gull eating bayberry.—Several studies of the Herring Gull (*Larus argentatus*) (Harris, Ibis 107:43–53, 1965; Threlfall, Can. Field-Nat. 82:176–180, 1968; Tinbergen, *The Herring Gull's World*, 1960) have demonstrated the omnivorous and opportunistic qualities of its diet. In addition to the well known animal and garbage components, Herring Gulls consume grasses, grain, and blueberries (*Vaccineum angustifolium*) when available (Threlfall, Nature in Wales 11:67–73, 1968; Davis, Br. Birds 49:400–404, 1956; Haycock and Threlfall, Auk 92:678–697, 1975). This note describes a previously unrecorded vegetable food source.

On 30 August 1975 I observed an adult Herring Gull feeding on the fruit of bayberry (*Myrica pennsylvanica*) at Great Gull Island, Suffolk County, New York. The bird flew to the bush from downwind, lowered its feet and spread them in the upper twigs of the bush, and kept its wings spread so that it was supported by the wind. While in this position the bird bent its head several times and picked berries off the upper twigs. The gull fed in this manner for approximately 2 min and then flew off upwind.

Pellets of either Herring Gulls or Great Black-backed Gulls (*L. marinus*) containing bayberry fruit have been found by visitors to the island in late December and early January (Hays, pers. comm.), but no gull has ever been seen eating the fruit. (Observers are present on Great Gull Island every year from 1 May to at least mid-September.) The fruit is available throughout the year, although least common in late spring and early summer. The unusual feeding technique and scarcity of evidence suggest that for Herring Gulls bayberry fruit is an infrequent food item.

This is contribution No. 43 from the Great Gull Island Project, American Museum of Natural History.

I thank Helen Hays for reading an earlier version of this paper. Work at Great Gull Island is supported by the Linnaean Society of New York and the American Museum of Natural History.—Roger F. Pasquier, *Dept. of Ornithology, American Museum of Natural History, New York 10024.* *Accepted 9 April 1976.*

The Lesser Antillean Bullfinch in the Virgin Islands.—The polytypic Lesser Antillean Bullfinch (*Loxigilla noctis*) occurs throughout the Lesser Antilles (except the Grenadines), from Grenada in the south through Anguilla and Saba in the north and northwest. This species was not observed west of the Anegada passage, a 124 km strait separating the northern Lesser Antilles from the Virgin Islands and Puerto Rico until discovered by Raffaele and William Truesdell, Park Naturalist of the Virgin Islands National Park, in 1971 (Bond, Seventeenth supplement to the check-list of the birds of the West Indies (1956), Acad. Nat. Sci., Phila., 1972). In this note we provide details of the occurrence of the Lesser Antillean Bullfinch and speculate concerning its dispersal to the Virgin Islands.

On 16 April 1971 Raffaele and Truesdell saw either a female or immature male Lesser Antillean Bullfinch .3 km from John's Folly Pre-school in the southeast corner of St. John. The bird, perched in a thicket of dry scrub and cactus, was giving a vocalization consisting of 5 "seeps" occasionally followed by a buzz note. The next morning Raffaele and Truesdell found a bullfinch at the same location. About .4 km to the south they located a pair of these bullfinches; a second pair was found .9 km further southwest on the trail to Kiddel Bay Salt Pond. Thus 5 birds were encountered in the xeric scrubland of the southeast coast. This is reported in summary by Bond (1972).

Dr. Marcus Buchanan (pers. comm.), Director of the Virgin Islands Ecological Research Station on St. John saw 2 male bullfinches flying near Centerline Road above Coral Bay on 18 October 1971. On 16 November, Truesdell located at least 10 individuals (Bond 1972) in the Nanny Point subdivision near where the first female was observed and a Mrs. Learner on 25 November found 2 birds 1.1 km west-northwest of the head of Kiddel Bay Trail.

From 16 January to 5 February 1972 Daniel Roby observed bullfinches on 9 days with a maximum of 15 being observed in a single day. He estimated having seen 40 *L. noctis*, but due to the inaccessibility of much suitable habitat adjacent to that where sightings were made we think that 100 birds is probably a more accurate estimate of the number of bullfinches on St. John at the time.

Roby searched for *L. noctis* throughout the island, including the remote east end, but only found the species in the southeast corner. The greatest concentrations of the Lesser Antillean Bullfinch were on the western side of Ram Hill, on the hill behind Nanny Point, and at the head of Salt Pond Trail. With the exceptions of the sightings by Buchanan and Learner and a pair of females seen by Roby on the east side of Europa Bay Salt Pond (3.2 km westnorthwest of Salt Pond), all bullfinch observations were within 1.5 km of Salt Pond.

Roby noted that the underparts of all closely observed adult male bullfinches were smokey gray. On 7 December 1972 Raffaele collected a female *L. noctis* at the foot of Ram Hill on St. John. This specimen was sent to the Bird and Mammal Laboratories at the U.S. National Museum and was identified by Richard Banks as *L. n. ridgwayi*. The specimen will be deposited in the University of Puerto Rico, Rio Piedras campus collection.

Habitat.—The area around Salt Pond is among the driest on St. John and the vegetation type is referable to the cactus woodland of Robertson (Auk 79:44–76, 1962). This association is characterized by a predominance of columnar cactus (*Cephalocereus royenii*), and the century plant (*Agave americana*); woody plants occur only as low scrub. Except for 2 females feeding by mangroves at the edge of Europa Bay Salt Pond, all perched *L. noctis* were in cactus woodland a short distance from the sea.

Feeding.—Roby observed *L. noctis* feeding on fruits on 6 plant species. Five individuals were recorded feeding on dildo cactus (*C. royenii*). Three fed on barrel cactus (*Cactus intortus*), 2 on common sage (*Lantana involucrata*) and manchineel (*Hippomane mancinella*) (a plant poisonous to man), one bullfinch ate fruits of gumbolimbo (*Bursera simaruba*) and of the bromeliad *Tillandsia fasciculata*. These are all common plants of the cactus woodland which surrounds Salt Pond.

Nesting.—Roby found an active nest containing 2 brown-speckled eggs on 20 January

1972 about .7 km from Ram Head. This nest, placed 1.8 m above the ground in an isolated 2.5 m tall *Opuntia rubescens*, was 23 m from the high tide mark and the cactus was 4 m from the edge of the vegetation. The nest, constructed of dried grass stalks, small twigs, vines, leaves and lined with the soft, silky plant fiber from the dildo cactus, was situated between 2 lobes of the cactus and was well protected from all sides by thorns. This nest measured 16 cm long by 11 cm wide by 17 cm high with an opening on the north side measuring 3 cm high by 5 cm wide. The female bullfinch was observed entering and leaving the nest several times and the male was seen in the vicinity. The pair abandoned the nest before the eggs hatched. Truesdell and Roby found a second nest 200 m south of the first on 29 January again in *O. rubescens.* This nest also had 2 eggs and, again, was close to the sea, about 15 m from the high water mark. Its construction and placement resembled that of the first nest except that its opening faced east. The nest measured 13 cm long by 11 cm wide by 15 cm high. The eggs hatched on 1 February. On 2 February both parents were photographed feeding the young. Occasionally the female entered the nest and brooded the young for a short time. Both birds were quite tame and were easily photographed from a distance of 4 m.

There were several indications that some bullfinches had fledged their young at the time of these observations in late January and early February, while others were just beginning to nest. Roby observed a female with a fully-fledged immature bird following her and gaping for food. On Nanny Point Hill he found a nest placed high in a tall *C. royenii* that was very similar in construction to the 2 active nests. On the west side of Ram Hill, 5 partially completed nests were found in *O. rubescens.* Roby heard male bullfinches singing at Kiddel Bay, the head of the trail to Salt Pond, and 200 m south of the second active nest.

Method of introduction.—Marcus Buchanan observed 2 schoolgirls from Barbados arrive on Tortola with 2 caged male Lesser Antillean Bullfinches on 1 July 1971. Possibly then, the establishment of *L. noctis* on St. John might be the result of an introduction.

James Bond (Nineteenth supplement to the check-list of the birds of the West Indies (1956), Acad. Nat. Sci., Phila., 1974) suggests another feasible mechanism for the transportation of *L. noctis* to St. John is via cruise ship en route to Charlotte Amalie from St. Martin or Antigua. While such a mechanism may be excellent for explaining the arrival of a flocking species such as the House Sparrow (*Passer domesticus*), it has its drawbacks when one considers a territorial species like *L. noctis* that demands trees or brush and is not likely to be found near docks or flying offshore.

There are several factors that support natural colonization by this bullfinch: (1) *Loxigilla n. ridgwayi* occurs on the Lesser Antillean islands of Anguilla, St. Martin, St. Barthelemy, Barbuda and Antigua that lie adjacent to the Virgin Islands. Therefore this race is the most likely of the 9 Lesser Antillean Bullfinch races to have invaded the Virgins. Anguilla and St. Martin, the closest islands in the range of *L. n. ridgwayi* to the Virgin Islands are also the closest of all Lesser Antillean islands (supporting bullfinches) to the Virgins. Saba, the closest source to the Virgins of another race of Lesser Antillean Bullfinch (*L. n. coryi*), is not only farther from these islands (with the exception of St. Croix which is not known to have bullfinches) than Anguilla and St. Martin, but *Loxigilla* is rare on Saba while it is common on Anguilla and St. Martin.

(2) The only islands directly in the path of expansion of *L. n. ridgwayi* from its native islands to St. John are Norman and Peter islands. Both of these have now been reported to support Lesser Antillean Bullfinch populations. Though no bullfinches have been found on St. Thomas nor St. Croix (Murray, Birds of the Virgin Islands, Dukane Press Inc., Hollywood, Fla., 1969; G. A. Seaman, pers. comm.), Anegada (La Bastille and Richmond,

Carib. J. Sci. 13:91–110, 1973), Virgin Gorda and Beef Island (Raffaele, pers. observ.), nor on Tortola (Raffaele, pers. observ.; A. Wetmore, pers. comm.), none of these islands is in the most direct potential route of expansion of *L. n. ridgwayi* from Anguilla or other islands inhabited by this bullfinch. Norman Island lies 8 km due east of Salt Pond, the population center of *L. noctis* on St. John, and is thus directly in the path of any expansion from Anguilla. Peter Island, because of its location 2.2 km northeast of Norman Island is probably less important than that island to any immigration. In May of 1972 Marcus Buchanan received reports of bullfinches inhabiting both Norman and Peter islands.

(3) Hurricane Donna provides a plausible mechanism for the transport of the bullfinch to the Virgin Islands. On 5 September 1960 the eye of hurricane Donna passed directly over Anguilla. At this time the San Juan, Puerto Rico Weather Bureau reported the highest winds above 135 kph extending 135 km in a northeast semicircle and 72 km in a southwest semicircle. Outside these areas were gale force winds ranging from 61–133 kph extending 35 km northeast and 180 km southwest of the hurricane's center. Later that morning Donna passed a short distance north of St. Thomas in the Virgin Islands. Wind gusts up to 108 kph were reported there even before the hurricane. This hurricane which passed directly over Anguilla and through the Virgin Islands could have been responsible for transporting *L. noctis* to the Virgin Islands.

Since 1957, when the thorough study of Robertson (1962) indicated that there were no bullfinches on St. John (Robertson, pers. comm., spent 5 days on the coast from Lameshur to John's Folly and Ram Head), the only other major storm that passed between Anguilla and the Virgin Islands was hurricane Faith in August 1966. This hurricane, however, was weaker than Donna and passed farther to the north of the islands under consideration, striking them with lesser winds (61–133 kph) (Herbert, Weatherwise 20:17–23, 1967). We doubt that Faith's winds would have been strong enough to dislodge bullfinches from Anguilla, and as this hurricane passed relatively far to the north of the Virgin Islands we could expect the Lesser Antillean Bullfinch's invasion to have involved more northerly islands in the group.

(4) The pattern of *L. noctis* distribution in the Virgin Islands when compared to that of human settlement argues for natural expansion rather than human introduction as the means of bullfinch dispersal. If the species had been brought in as a cage bird and had escaped, the probability of such an incident occurring would be greatest near human population centers. The bird would then establish itself in the nearest suitable habitat to these centers. This has been the case in Puerto Rico where of the 11 Ploceidae and Fringillidae found to be recently established on that island the majority have their population centers in or near large cities and appear to be spreading outward from them while only 1 species has done all its colonizing completely removed from a heavily populated metropolitan area.

Biogeography.—Rather than representing a haphazard invasion into an area, the Lesser Antillean Bullfinch's expansion to the Virgin Islands appears to fit a trend if looked at as the expansion of a Lesser Antillean element. Of 13 endemic West Indian genera known from the Lesser Antilles at least 3 have relatively recently expanded to Puerto Rico or the Virgin Islands. Among these are the 2 hummingbirds (*Sericotes* and *Orthorhyncus*), of South American origin (Robertson 1962), and now *Loxigilla.* Also new to these islands is the Caribbean Elaenia (*Elaenia martinica*), an endemic West Indian species (see Robertson 1962). *Margarops*, a fourth West Indian genus that appears to be increasing in numbers on Puerto Rico, is not considered here to be a recent arrival to that island because of other evidence suggesting long residency there (Bond, Eighteenth supplement to the check-list of the birds of the West Indies (1956), Acad. Nat. Sci., Phila., 1973). In contrast to Puerto Rico and the Virgin Islands only a single West Indian genus has undergone a range expansion in recent times anywhere in the Lesser Antilles. That is the case of *Eulampis*, another hummingbird, which has been found in Grenada and Barbados (Bond, Eleventh supplement to the check-list of the birds of the West Indies (1956), Acad. Nat. Sci., Phila., 1966). The expansion of *L. noctis* into the Puerto Rico-Virgin Islands region strengthens the hypothesis suggested by Robertson (1962) that the species arriving there may be part of a contingent that moved through the Lesser Antilles more or less at the same time. Certainly the 3 endemic West Indian genera extending their ranges through the Virgin Islands to Puerto Rico as compared to the 1 for all of the Lesser Antillean islands combined suggests an unusual circumstance that needs an explanation, particularly with respect to the source area and time of initiation of such a dispersal.

Loxigilla noctis is surviving well on St. John and habitat similar to that which the species inhabits there abounds on other nearby islands. We might therefore expect the dispersal of *L. noctis* through the Virgin Islands to Puerto Rico where it may compete with its congener *L. portoricensis*. Should the ranges of *L. noctis* and *L. portoricensis* come to overlap, the interaction of the species should be carefully observed as this might shed light on the extinction of *L. p. grandis* on St. Kitts which at one time coexisted with *L. noctis* there.

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Foraging behavior of the White Ibis.—The foraging behavior of many ciconiiforms is fairly well known. There is a particularly extensive literature on herons (Kushlan, Auk 93:86–94, 1976) and storks (Kahl, Behaviour 27:76–106, 1966; J. Ornithol. 112: 21–35, 1971; Ibis 114:15–29, 1972; Condor 75:17–27, 1973). However, little is known about the feeding behavior of ibises. Most accounts note merely that they probe in the water or on land. Bent (U.S. Natl. Mus. Bull. 135, 1926) reported Audubon's claim that the American White Ibis (*Euducimus albus*) can force crayfish from burrows by placing mud in them, and Vestjens (Emu 73:21–22, 1973) reported that the Australian White Ibis (*Threskiornis molucca*) breaks mussels on stones. The purpose of this paper is to document the various behaviors used by the American White Ibis and to note some of the circumstances in which they are used. I hope that this will provide a foundation for future study of this generally neglected group. Observations reported here were made both in the field and under various experimental conditions on captive birds.

The White Ibis is primarily a non-visual, tactile forager, and most techniques involve placing the partially opened bill in the water or bottom sediment and closing the tip on encountered prey. Ibises often swallow items by thrusting the head downward. Prey can also be worked upwards to the gullet by closing the bill tip since there is a gap between the mandibles midway up the bill when the tips are closed. This may permit backward propulsion of a food item when the bill tips are brought together. The gap between the ibis' bill is similar but not as extensive as that of the Limpkin (*Aramus guarauna*) (Snyder and Snyder, Living Bird 8:117–223, 1969) or the 2 openbill storks (*Anastomus* spp.) (Kahl, J. Ornithol. 112:21–35, 1971). Although it has been hypothesized that this feature is an adaptation for mollusc predation in other birds, particularly catching and extracting snails, the ibis does not extract snails. It is possible that the primary function of the bill gap in all 4 species is to effect a tweezer-like apposition of the bill tips for better grasping of prey as has also been suggested by Wetmore (Howell, Florida Bird Life, Coward-McCann, N. Y., 1932).

The *probe* is the most characteristic and most commonly used feeding behavior. Several types of probing can be distinguished by the depth and rapidity of the stab and the extent of accompanying locomotion. *Shallow probing* is directed to the top or less than 2 cm into the sediment. It may consist of multiple tactile nibbles at the sediment or ground surface. *Deep probing* is the insertion of the slightly open mandible deep into the sediment, under plant roots, or under rocks. A deep probe may consist of multiple exploratory thrusts in the same hole. Several types of movement accompany probing. In *stationary probing*, ibises remain in one place. In *step-probing*, ibises generally alternate a single shallow probe with 2 or more steps. In *multi-probing*, ibises take several steps followed by several shallow or deep probes. Obviously intermediate behavior occurs.

Other feeding behaviors are used less frequently. *Pecking* is the picking up of sighted objects without inserting the bill into the substrate. This is usually used on land. In water, even when prey items are visible, ibises generally use vision only to choose a particular area and then probe non-visually to locate prey. This was demonstrated repeatedly by captive birds in a 10 cm deep pool. *Groping* is holding a widely gaping bill in the water while moving the tip along the bottom. This is similar to the behavior of Wood Storks (*Mycteria americana*). *Head swinging* is moving the partially submerged and gaping bill from side to side in the water. At the termination of each swing, the ibis' bill and head face to one side, with the plane of the dorsal surface of the bill perpendicular to the water. This behavior is similar to that used by spoonbills (*Platalea* spp.) except that spoonbills swing their head and neck from side to side while the dorsal surface of the bill remains at an angle of about 45° to the surface of the water. I have also seen head swinging in the Scarlet Ibis (*Eudocimus ruber*) and Glossy Ibis (*Plegadis falcinellus*), suggesting the behavior is widespread in ibises. Since spoonbills also probe, it is probable that both probing and head swinging are homologous behaviors in the 2 subfamilies and each group typifies a line of adaptation leading to the perfection of one of the feeding techniques.

Although White Ibis foraging behavior is labile and almost any technique may be used in any situation, certain behavior patterns are characteristic of particular habitat conditions. The more usual behavior sequences observed under particular foraging circumstances are shown in Fig. 1. Birds feeding with flocks in shallow open marshes are generally restricted to probing-while-walking behaviors (Fig. 1a). Often the entire flock moves as a loose unit through a feeding location. When movement is fast, as in a tight flock or on land (Fig. 1b), probing is generally shallow. Stationary multi-probing is used especially along the roots of plants (Fig. 1c) and around and under other objects in the water. Deep probing is characteristic of feeding in locations with soft, drying mud and little surface water (Fig. 1d). Birds feeding alone in deeper water (Fig. 1e, f) use a succession of techniques such as deep probing and groping. Figure 1g is a particularly varied sequence of a lone bird feeding in deep water and around a rock. Exploration around and under the rock occupied much of the birds' time. Head swinging was restricted to deep, open water (Fig. 1e, g) and was often performed after observing an-

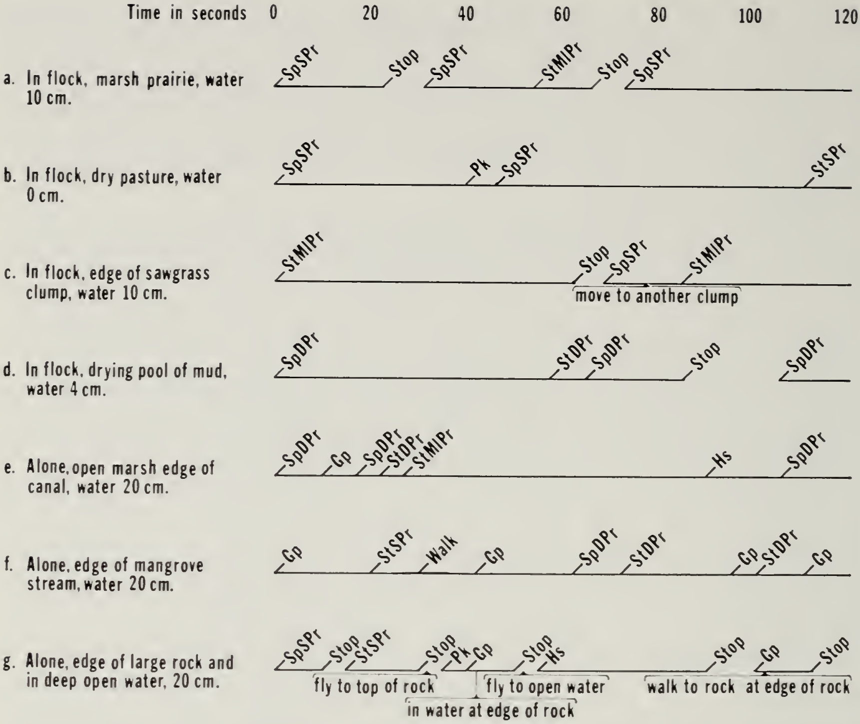

FIG. 1. Ethogram of feeding behavior of White Ibis in various circumstances. Abbreviations: Sp-SPr = step-shallow probing, St-SPr = stationary-shallow probing, Sp-DPr = step-deep probing, St-Dpr = stationary-deep probing, St-MlPr = stationary-multiple deep probing, Pk = pecking, Gp = groping, Hs = head swinging.

other bird head swinging. In the sequence of Fig. 1g, the ibis flew to within 2 m of a foraging Roseate Spoonbill (*Ajaia ajaja*) before beginning to head swing.

These sequences illustrate the nature of ibis foraging behavior. Foraging is generally restricted simply to probing, groping for and picking up objects, usually without specific visual cues. Variability in behavior is primarily a matter of speed of movement and water depth. Yet within the narrow constraints imposed by morphology, a number of subtle behavioral variations are formed by combinations of probing and locomotor movements that can be used to explore various microhabitats for prey. Thus the feeding behavior of the White Ibis is characterized by use of relatively few primary techniques but a number of subtle variations that permit tactile foraging in any location shallow enough to allow walking or standing. The adaptable repertoire available suggests the White Ibis could obtain a wide variety of prey but specializes on those types easily caught by its non-visual techniques (Kushlan and Kushlan, Florida Field Nat. 3:31–38, 1975). Ibis feeding behavior, as presently understood, is less diverse than that of many herons and storks, lacking aerial components and making no special use of feet or wings. Future studies of the White Ibis and comparative work on other species may reveal additional components and complexity.—JAMES A. KUSHLAN, *Dept. of Biology, Univ. of Miami, Coral Gables, FL* (Present address: *U.S. National Park Service, Everglades National Park, Homestead, FL 33030*). *Accepted 14 Mar. 1976.*

Birds of five families feeding from spider webs.—Burtt et al. (Wilson Bull., 88: 157–158, 1976) observed a Cedar Waxwing (*Bombycilla cedrorum*) removing specks from 2 spider webs in the top of a dead tree. They suggested that the waxwing was removing insect prey that had become entangled in a possibly abandoned web. Since reports of web-feeding are scarce in the literature, Burtt et al. (1976) suggested that opportunities for web-feeding might be rare. Because of their hovering abilities, hummingbirds appear to be pre-adapted for web-feeding, and, indeed, the only literature reports we have found come from the family Trochilidae (Wolf, Condor 72:1–14, 1970; Bent, U.S. Natl. Mus. Bull. 176:377, 1940; Bullock, 1825, in Bent, op. cit., 431). Therefore, we thought it important to report our observations on web-feeding in species of 5 avian families, and in 1 species to compare web-feeding with gathering of web material, possibly for use in a nest. The first 4 species mentioned were observed by R.B.W. in Mexico, the last by J.P.H. in Madison, Wisconsin.

On 26 March 1973, a nesting Fawn-breasted Hummingbird (*Amazilia yucatanensis*: Trochilidae) pecked repeatedly at a vertically-oriented spider web in an area of dry deciduous forest 16 km south of Xpujil, Campeche. The bird hovered in front of the web and darted forward several times, touching the web with its bill on each occasion. Whether or not the bird removed insects from the web could not be determined because of poor light. The bird did not appear to be grasping web materials, nor did it begin nest-building after it left the spider web.

On 16 March 1974, a Blue Bunting (*Cyanocompsa parellina*:Fringillidae) pecked at an orb-weaver (Family Araneidae) web located about 50 cm off the ground. The bird flew up from a perch 10 cm above the ground and hovered near the spider web. The bird pecked several times at the web and then returned to its perch near the ground. The bird repeated its actions 3 times, the third time directing its pecks toward a second web adjacent to the first. Whether the bird was taking insect prey or small spiders could not be determined. This sequence occurred about 200 m from the first observation.

In December 1974, at the Chicanna Archaeological Zone, 8 km west of Xpujil, Campeche, another Blue Bunting was observed dismantling a spider web about 3 m from the ground. The bird approached the web along a twig, grasped a strand of the web and pulled. In pulling, the bird assumed an upright posture with the long axis of the body perpendicular to the perch and the head held perpendicular to the body axis. The bird struggled with the web for 15 sec and finally broke off the strand and flew away. The action of web-gathering appeared substantially different from the pecking motions described above.

Another instance of web-feeding occurred at Chicanna on 17 July 1975 while a White-bellied Wren (*Uropsila leucogastra*:Troglodytidae) was foraging in a tree 4 m above the ground. The bird was moving rapidly from twig to twig, actively foraging by pecking at twigs and hawking insects. At one point, the bird pecked twice at a twig, turned, and delivered 2 pecks to a spider web, and then moved away. The web which the bird pecked appeared abandoned and had a large amount of vegetable or animal matter entangled in it.

A Yellow-green Vireo (*Vireo flavoviridis*:Vireonidae) also pecked at a spider web while foraging at Xpujil on 5 July 1974. The bird was foraging 10 m up in a 13-m tree at the edge of a clearing. The bird grasped a speck in a spider web with its bill, pulled forcefully for a moment, and then swallowed. The bird then wiped its bill twice and moved away.

On 11 May 1975, a Yellow-rumped Warbler (*Dendroica coronata*:Parulidae) hovered in front of a vertically-placed spider web attached to the tips of branches high in a tree, plucked one prey item from the web, and flew off. There were no perches convenient to the web as in the case of the Cedar Waxwing reported by Burtt et al. The web had 13 remaining prey items visible in it and despite many warblers of several species foraging in this tree and others nearby, no other bird fed from or even inspected the spider web in the 10 min after the feeding instance.

Our observations suggest that web-feeding is more widespread than the paucity of literature on the subject suggests. Perhaps observers have overlooked it or assumed that it was already so well known that it was not important to mention it. It may be significant that 3 of the 4 tropical species were observed web-feeding during the breeding season, when a need for higher protein intake may occur. Hummingbirds in particular are not well adapted for capturing insects, but their hovering abilities make it possible for them to secure protein by cleptoparasitism from spider webs.—ROBERT B. WAIDE AND JACK P. HAILMAN, *Dept. of Zoology, Univ. of Wisconsin, Madison 53706. Accepted 1 May 1976.*

Winter nest microclimate of Monk Parakeets.—Monk Parakeets (*Myiopsitta monachus*) have a broad distribution in South America where their range extends from tropical Bolivia and Brazil well into the temperate regions of Argentina (Bull, Wilson Bull. 85:501–505, 1973; Olrog, Las Aves Sudamericanas, Universidad Nacional de Tucuman, Argentina, 1968). While the species normally encounters a wide range of local climates, in North America it survives winters which are more severe than those of its native range (Bump, U.S. Fish and Wildl. Serv., Bureau of Sport Fisheries and Wildlife, Wildlife Leaflet No. 496, 1971). Among psittacids Monk Parakeets are unique in building large enclosed nests composed of interwoven twigs. (Forshaw, Parrots of the World, Doubleday and Co., Inc., New York, 1973). Unlike most birds Monk Parakeets occupy their nests throughout the year. The role of enclosed nests in contributing to the maintenance of a favorable microclimate has been demonstrated for several species (Ricklefs, *in* Avian Energetics, R. Paynter, ed., Publ. Nuttall Ornithol. Club 15:152–297, 1974). Tolerance of low winter temperatures in this species may be improved by the use of these stick nests for nighttime roosts. In this paper we investigate the possibility that during the winter the nest of the Monk Parakeet contributes to energy savings by creating a favorable microclimate.

Methods.—Measurements of air temperature (Ta) and nest temperature (Tn) were made at a nest which had been constructed by a breeding pair in the upper corner of a large (4 × 3 × 2 m) outdoor flight cage. The nest was situated approximately 10 cm below the cage roof, but otherwise exposed on all sides. The nest (Fig. 1) was 0.5 m long, 0.3 m deep and 0.3 m wide. At the time of study it was occupied by a mated pair.

Temperatures were measured with 20-gauge copper-constantan thermocouples and were recorded at intervals of 2 min with a Honeywell recording potentiometer (model 112). The uncertainty of measurement did not exceed 0.2°C. Ta was recorded from a thermocouple placed 5 cm from the back of the nest. Tn was recorded from thermocouples implanted at several locations within the nest, but concentrated around the inner nest chamber (Fig. 1). An additional thermocouple was positioned on the floor of the inner nest chamber such that it was in contact with the birds when they occupied the nest. This probe signaled when the birds entered or left the nest.

Measurements were made during 10 days in January and February usually from 16:00

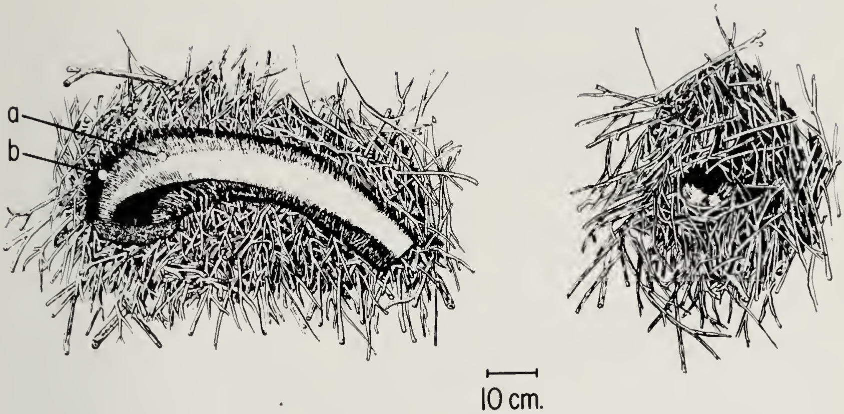

FIG. 1. Representation of the Monk Parakeet nest seen in longitudinal section (left) and on end (right). Points marked *a* and *b* correspond to the position of the thermocouples represented in Fig. 2 by the dots and solid line respectively.

until 09:00 of the following day. Wind velocity was obtained from records of the university meteorological station located approximately 100 m from the nest.

Results.—The birds entered the nest at various times during the day for short periods, especially during inclement weather. They also entered the nest around 17:30 (½ h after sunset) and remained in the nest until approximately 06:30 (½ h before sunrise) the following day. While the birds were in the nest, temperatures within the inner chamber generally exceeded Ta; temperatues within the tunnel never exceeded Ta. This reflected the birds' position within the nest.

Fig. 2 illustrates a typical record of night time Ta and Tn. Early in the night Tn's were only slightly above Ta. However, with time the difference between Tn and Ta increased. The increase in Tn over Ta during the early morning hours corresponded with a decrease in wind velocity as shown in Table 1. The maximum temperature difference (Tn-Ta) observed on any night was 4.6°C. The mean Ta calculated during the time the birds were in the nest was –5.65°C while the mean nest temperature (calculated as

TABLE 1

WIND VELOCITY AND THE GRADIENT BETWEEN NEST TEMPERATURE AND AIR TEMPERATURE

Time of day	Wind velocity[1], m/sec		T[2], °C	
hours	maximum	minimum	maximum	minimum
1700–1950	8.5–11.6	1.8–3.1	1.0	–0.1
2000–2250	8.0– 8.9	1.8–2.7	1.4	0.0
2300–0150	5.4– 8.0	1.8	2.0	0.1
0200–0450	3.6– 5.8	0.4–0.9	3.3	0.1
0500–0750	3.1– 4.5	0–0.9	3.0	0.8

[1] Ranges for values determined over 10 min intervals.
[2] Range of values for the difference between nest temperature and air temperature in Fig. 2 while birds occupied the nest.

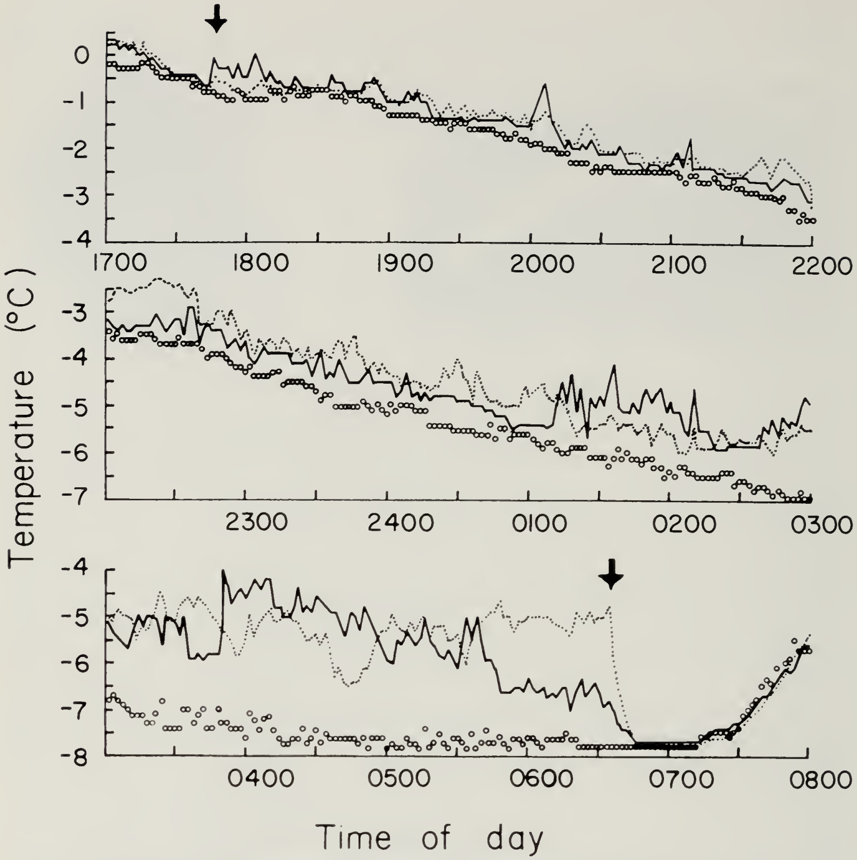

FIG. 2. Relation of air temperature (circles) and nest temperatures (line and dots) to time of day. Arrows indicate time when birds entered and left the nest.

the mean of the 2 thermocouple temperatures recorded within the inner nest chamber) was 3.89°C. Thus on the average Tn exceeded Ta by 1.76°C.

Discussion.—The nest examined in this study was relatively small. As Monk Parakeets nest gregariously, nesting assemblages may contain up to 20 inner chambers, weigh 200 kg, and measure 2m or more across (Forshaw 1973; Roscoe, et al., N.Y. State Fish and Game J. 20:170–173, 1973). Despite this fact, temperatures near the inner chamber of the nest were as much as 4.6°C above Ta, and on a typical night exceeded Ta by an average of 1.76°C. It seems probable that temperatures would be even more moderate in larger nests which should be better insulated. Additionally, since winter nests may be occupied by both adults as well as the juveniles of the previous breeding season (pers. obs.), even higher temperatures might be anticipated.

Although nest temperature was higher than air temperature, a major advantage of using the nest as a winter roost might be in reducing radiant heat loss, since heat loss to the cold night sky may represent an appreciable fraction of the total heat loss (Schmidt-Nielsen, Oxford Univ. Press, New York, 1964; Webster, J. Appl. Physiol. 30:684–690, 1971). By ameliorating the effects of wind, particularly in large nests, convective losses also may be reduced.

The minimum energy savings resulting from elevated nest temperatures can be estimated from the relation of oxygen consumption (VO_2) to Ta of Monk Parakeets (Weathers and Caccamise, Oecologia 18:343–358, 1975). Below 25°C VO_2 of Monk Parakeets increases linearly with decreasing Ta at a rate of 0.099 ml O_2 g^{-1} hr^{-1} $°C^{-1}$. The energy savings attributable to the nest is the product of the excess of Tn over Ta and this factor. Taking the average Tn – Ta to be 1.76°C then

$$\text{Energy Savings} = (1.76°\text{C}) \times (0.099 \text{ ml } O_2 \text{ g}^{-1} \text{ hr}^{-1} \text{ °C}^{-1}) = 0.174 \text{ ml } O_2 \text{ g}^{-1} \text{ hr}^{-1}.$$

The resting metabolic rate of Monk Parakeets measured at night and in the thermal neutral zone is 1.17 ml O_2 g^{-1} hr^{-1} (Weathers and Caccamise, 1975). Thus the mean energy savings for the night depicted in Fig. 2, based on the difference between Tn and Ta, represents 15% of the standard metabolic rate. Expressed as the difference in predicted metabolic rate at –5.65°C versus –3.89°C the energy savings is 3.7%. This value does not take into account the effect of the nest in reducing radiant heat loss and therefore should be considered a minimal estimate of the energetic advantage of using the nest as a winter night-time roost.

We thank Helen Mozdic and Peter Alexander for technical assistance, and Mr. Charles Wagg of the Division of Plant Industry, New Jersey Department of Agriculture who was instrumental in obtaining the birds.

This report is a paper of the Journal Series, New Jersey Agricultural Experiment Station, New Brunswick, New Jersey.—DONALD F. CACCAMISE AND WESLEY W. WEATHERS, *Dept. of Entomology and Economic Zoology and Dept. of Environmental Physiology, Rutgers, The State Univ. of New Jersey, New Brunswick 08903* (Present address WWW: *Dept. of Avian Sciences, Univ. of California, Davis 95616*). *Accepted 17 Feb. 1976.*

Snake predation on Bell's Vireo nestlings.—Bent (U.S. Natl. Mus. Bull. 197: 260, 1960) found that cats and cowbirds were the Bell's Vireo's (*Vireo bellii*) worst enemies; he makes no mention of snakes. However, Mumford (Wilson Bull. 64:231, 1952) and Barlow (Univ. Kansas Publ. Mus. Nat. Hist. 12:291, 1962) both suggested snake predation as a cause of nest losses. Nolan (Condor 62:241, 1960) implicated the black rat snake (*Elaphe obsoleta*) and black racer (*Coluber constrictor*) as nest predators based on their abundance in the scrub habitat he studied. This note documents 3 observations of snake predation on nestling Bell's Vireos in Douglas County, Kansas.

On 14 June 1974, about 08:45, I heard the scolding notes of a pair of Bell's Vireos and several Dickcissels (*Spiza americana*) and Northern Yellowthroats (*Geothlypis trichas*) near a dogwood (*Cornus drummondii*) where I had discovered a vireo nest 3 days earlier. I reached the nest in time to see a black rat snake (*E. o. obsoleta*) with a vireo nestling in its mouth climbing quickly off the nest limb to the ground. The nest, which previously held 4 nestlings, was empty. This pair of vireos built a new nest about 10 m from the old site and laid a clutch of 3 eggs.

On 25 June 1975, about 10:00, I heard scolding notes of a pair of Bell's Vireos in the vicinity of a small dogwood. I located the nest on the southeast corner about 38 cm from the ground and observed a red-sided garter snake (*Thamnophis sirtalis parietalis*) on the supporting limb of the nest with its head in the nest engulfing the back half of a very young nestling. It dropped to the ground as I pulled back a branch for a closer look, and as I attempted to grab the snake, it dropped the live but bleeding nestling and escaped. I returned the nestling to the nest, but when I checked the nest again some 10 min later the nestling was missing. Best (Auk 91:169, 1974) found that snakes would return for the remainder of the nest contents when disturbed. This pair of vireos renested about 15 m from the old site and successfully fledged 3 young.

On 27 June 1975, I heard mobbing calls from several species of birds near a Bell's Vireo nest. As I approached the dogwood where the nest was located I saw a black rat snake slipping away through the grass. I killed the snake and found that it had eaten the 3 Bell's Vireo nestlings from the nest.

Bell's Vireos nest very close to the ground and it is not surprising that snakes are important predators on them. Black rat snakes are good climbers, regularly take birds as prey (e.g., Jackson, Wilson Bull. 82:329–330, 1970), and can often be located by mobbing calls of birds (Fitch, Copeia 1963:649–658, 1963). Although red-sided garter snakes are not regarded as climbers they occasionally take nestling birds as prey (Fitch, Univ. Kansas Publ. Mus. Nat. Hist. 15:493–564, 1965).

My thanks to Ivan Boyd of Baker University, Baldwin City, Kansas for permission to use the Baker Wetlands Research Area and to Richard F. Johnston for his comments on the manuscript.—CALVIN L. CINK, *Museum of Natural History and Dept. of Systematics and Ecology, Univ. of Kansas, Lawrence 66045. Accepted 12 Jan. 1976.*

Crow predation on Black-crowned Night Heron eggs.—Corvids prey on the eggs of many species of birds. They feed on some eggs at nest sites and fly off and cache others at a distance. Descriptive and experimental data on crow predation has come from work in gull colonies located on flat ground with high visibility because the vegetation is sparse and low (e.g. Tinbergen et al., Behaviour 28:207–321, 1967). However, Fish (*Corvus ossifragus*) and Common crows (*C. brachyrhynchos*) also prey on the eggs of herons, egrets, and ibises that nest in dense tree colonies where nests are not as visible from the air (Milstein et al., Ardea 58:171–255, 1970; Meanley, Wilson Bull. 67:84–99, 1955; Dusi and Dusi, Wilson Bull. 80:458–466, 1968). No estimation of actual predation rates or descriptions of crow–heron interactions from heron and egret colonies are available. In this note we report on interactions between Black-crowned Night Herons (*Nycticorax nycticorax*) and Common and Fish crows observed in 5 heronries in southern New Jersey from 1973 to 1975. Data were collected in 3 Cherry (*Prunus* sp.) and Poison Ivy (*Rhus toxicodendron*) tree colonies of Black-crowned Night Herons, Snowy Egrets (*Egretta thula*), and Glossy Ibis (*Plegadis falcinellus*) on Little Beach Island, Brigantine National Wildlife Refuge; and in 2 *Phragmites* (with scattered *Iva* and *Juniperus* bushes) colonies of Black-crowned Night Herons, Snowy Egrets, Common Egrets (*Casmerodius albus*), Cattle Egrets (*Bubulcus ibis*) and Glossy Ibis on Big Heron and Islajo islands near Atlantic City (see Adams and Miller. EBBA News 38:103–107, 1975 for description).

All 5 heronries examined had at least 1 active crow nest. Two of the 3 heronries on Little Beach Island had cache nests (used only to store food items), located near the active nests. These contained heron eggshells, the unbroken eggs of night heron, Clapper Rail (*Rallus longirostris*) and Glossy Ibis, diamondback turtle (*Malaclemys terrapin*) eggs and hatchlings, and a dead Glossy Ibis chick. We often observed crows eating the numerous bird and turtle eggshells that were scattered on *Spartina* mats in the grassy areas near the heronries.

We systematically searched the tree areas on the northern end of Little Beach Island and found 2 inactive heronries each with an inactive crow nest, but no other crow nests. Similarly, crow nests were only located in the heronries (in *Juniperus*) on Islajo and Big Heron islands.

Heron egg success was determined in 1 heronry on Little Beach Island by marking all eggs and checking nests every other day. In 1974 the heronry contained 22 Black-crowned Night Heron nests, 6 Snowy Egret nests, and 1 crow nest. From a blind we observed crows taking all of the eggs in 5 and some of the eggs in 2 night heron nests. Egg loss at 5 other nests was attributed to crows when shells with peck holes were found. No other aerial predators were observed in this colony. We also observed crows carrying night heron eggs. We observed no egg loss in Snowy Egret nests. In 1975 this colony contained 21 night heron nests, 6 Glossy Ibis nests, 2 Snowy Egret nests, and 1 Fish Crow nest. In 1975 only 10% of the eggs were eaten compared to 36% in 1974. In both years there was an active crow nest, but in 1975 the nest was deserted halfway through the night heron incubation period. This crow nest was only 1 m above a night heron nest, and the heron pair might have caused the crow's desertion.

Corvids were the only aerial predators we observed in any of the heronries. Common Crows were seen most often. We observed 1 Blue Jay (*Cyanocitta cristata*) take and eat a Black-crowned Night Heron egg.

We observed Black-crowned Night Herons from blinds for 50 hours each year. Night herons react to crows in several ways: (1) an incubating bird remains silent on the nest when a crow flies over, (2) a night heron standing near its uncovered eggs (less than 3.5 m) walks quickly down to its nest and resettles when a crow approaches, (3) a night heron standing more than 3.5 m from its uncovered eggs flies to the nest and settles when a crow approaches and (4) a night heron whose mate is incubating either ignores a crow, flies out of the heronry squawking, or aggressively moves toward a crow while vocalizing. Crows were successful in taking eggs only when night herons failed to return quickly to their nests, when an incubating bird left before its mate returned, and before incubation began. Usually night herons did not actively chase or attack crows although night herons did supplant crows sitting near night heron nests 20% ($n = 25$) of the time. On 2 occasions we saw night herons chase and mob crows flying over the heronry located in *Phragmites*. The night herons did not dive-bomb or attack the crow, but flew very close to it.

Crows were observed flying slowly over areas known to contain heron nests, and swiftly over other areas. Once crows descended into the trees within the heronry, the night herons squawked until the crow left.

Although nestling Black-crowned Night Herons actively and pugnaciously defend their nests (this study; Teal, Wilson Bull. 77:257–263, 1965), adults do not overtly attack crows or other predators near their nests. Other herons such as Snowy and Cattle egrets seemed far more aggressive. Thus one advantage of nesting in mixed species colonies may be the anti-predator behavior of other species. For example, the senior author, working at Agassiz National Wildlife Refuge in northwestern Minnesota (1969–1971) observed Black-crowned Night Herons nesting in cattails with Franklin's Gull (*Larus pipixcan*). Whenever the gulls changed the location of their colony, the night herons also deserted the old location and nested in the new colony. When predators (weasel, skunk) approached the colony, the night herons remained on their nests and the gulls mobbed the predator.

This research was funded by grants from Sigma Xi (to D.C.H.) and the Research Council of Rutgers University (to J.B.) and MNIH grant 16727 (to Colin Beer).—JOANNA BURGER, *Dept. of Biology, Livingston College, Rutgers Univ., New Brunswick, NJ 08903, and* D. CALDWELL HAHN, *Institute of Animal Behavior, Rutgers Univ., Newark, NJ 07102.* *Accepted 8 Apr. 1976.*

ORNITHOLOGICAL LITERATURE

Evolution and the Diversity of Life: Selected Essays. By Ernst Mayr. Belknap Press of Harvard University Press, Cambridge, Mass., 1976: ix + 721 pp. $20.00.—In this book Ernst Mayr presents 47 essays on various topics in evolutionary biology originally published in many books and journals between 1940 and 1974, though most are from the past 2 decades. Some of the essays have been shortened, have had the references updated, or have been adapted by the addition of new comments clearly distinguished from the original version. Two have been translated into English. The essays are divided into 9 sections, their titles and the number of essays in each being: (I) Evolution (9 essays); (II) Speciation (7); (III) History of Biology (6); (IV) Philosophy of Biology (4); (V) Theory of Systematics (4); (VI) The Species (5); (VII) Man (1); (VIII) Biogeography (9); and (IX) Behavior (2). For each section Mayr has written a brief introduction placing the topic in historical context and assessing his own contribution to it. Many of the essays deal directly with birds and will be of special interest to ornithologists; these include "Bird speciation in the tropics," "History of the North American bird fauna," "Inferences concerning the Tertiary North American bird faunas," "The origin and history of the Polynesian bird fauna," "Fragments of a Papuan Ornithogeography," "The ornithogeography of the Hawaiian Islands," and "The nature of the colonization of Birds." Most of the essays do not deal directly or principally with birds, but with general aspects of evolution and systematics that are applicable to ornithology as well as other branches of evolutionary biology. This is a valuable collection of essays, many of which are otherwise available only in specialized libraries. For anyone interested in the evolutionary aspects of avian biology, this book is indispensible.—Robert J. Raikow.

Ecology and Evolution of an Andean Hummingbird (*Oreotrochilus estella*). by F. Lynn Carpenter. University of California Press, Berkeley, California, 1976: 106 pp., 8 black-and-white plates, 14 text figs., 11 tables. $2.50.—Probably more than any other avian group, hummingbirds are presently serving as vehicles for testing ecological-evolutionary theory. The attention is well deserved. The ease with which they can be observed and captured, their territorial tendencies and dependency of spatially and temporally restricted nectar sources, and the great degree of species' sympatry, are all attributes that make them a convenient group to study. Surprisingly, however, there are only 2 monographs on individual species; one by F. Gary Stiles on the behavioral ecology of *Calypte anna*, and the recent one considered here. Carpenter continues the trend set by Stiles—dependence on long-term systematic study, thorough documentation, and insistence that the way to understand the evolution of a species is through its extant ecology.

Carpenter follows the activity of *Oreotrochilus estella* through 2 wet seasons and 1 dry season in southern Peru and northern Chile. *O. estella* is one of only a handful of resident hummingbird species living above 4000 m, though species literally swarm on the slopes and in the lowlands below. Carpenter set out to identify the morphological, behavioral, and ecological adaptations that are integrated into the life history strategy of *O. estella* and which allow it to exploit this climatically rigorous and vegetatively sparse habitat. Hummingbirds seem to be more specialized and less variant in morphology, physiology, and behavior than most other avian groups, thus Carpenter has selected this particular species as the one most likely to be "aberrant" and show striking differences in these categories from "typical" tropical or temperate species.

The monograph is organized into 5 major sections: (1) morphological adaptations, (2) behavioral adaptations (foraging and roosting), (3) reproductive adaptations, (4) territorial adaptations, and (5) energetics. In the first section adaptive value of large size, dull coloration of both sexes, and large foot size, characteristics unusual in hummingbirds, are discussed. Coloration is seen as an antipredator device peculiar to a grassland habitat totally devoid of trees, and the large size of both sexes ($\bar{x} = 8$ g) is believed related to increasing energy use efficiency. Large foot size is explained as an adaptation to vertical roosting on canyon and cave walls.

In the second section behaviors associated with these unique roosting and foraging habits are discussed in the context of the climatic and biotic factors that have determined the evolution of morphological adaptations. Carpenter suggests that cave and rock roosting is an adaptation for avoiding nocturnal predation and for protection against ambient winter night temperatures which sometimes approach 0° C. Foraging technique at flowers is shown to involve significantly less hovering than in other hummingbirds, but much more perch feeding, an adaptation Carpenter sees as an energy-saving response to high altitudes where thin air produces a large energy demand for hovering. Pollen feeding by *O. estella* on the only winter blooming hummingbird-flowered plant, *Chuquiraza spinosa*, is discussed as a probable coevolutionary pollination relationship in which the plant is more reliably pollinated by *O. estella* at this time of year than by more externally temperature-influenced insects.

Section 3 deals with the selection of nest sites, construction of nests, the phenology of nesting, and nesting success. Most nests are constructed under rock overhangs, are well insulated, and occur near the richest nectar sources. Carpenter argues that these features protect the nestlings from severe weather and nest predators, and account for the high nesting success compared to other hummingbirds. Because such sites are limited, competition for nest sites was intense and was believed to account for the evolution of an aggressive female territoriality associated with the nest site in which both male and female conspecifics are usually vigorously repulsed (Section 4). The aterritorial males appeared to be subdominant to females, and males visit females on territories and display and attempt to mate with them, the reverse of what occurs in all other hummingbird systems described to date. Carpenter believes this atypical arrangement is forced by the need for females to occupy gorges and construct nests there. Because, incidentally, the richest nectar sources are also found in these areas, males are forced out onto open hillsides where food is dispersed and scarce and therefore not dependable. The larger size of males is also seen as related to food supply: larger body size is believed to result in more efficient linear flight between distant food sources.

In section 5 an energetics model of feeding territoriality is generated for *O. estella* by measuring resting and torpid metabolism, estimating cost of linear and hovering flight, then computing time and energy budgets for both sexes in summer and winter. Winter is seen as the critical time of year when most mortality occurs despite a very physiologically efficient torpidity system finely tuned to the daily winter ambient temperature regime.

An integrative concluding discussion section recounts the morphological, physiological, and behavioral adaptations that allow *O. estella* to exploit the high Andes, discusses the possibility of a taxon cycle in *O. estella* and other high Andean species, and concludes with a discussion of evolution and colonization at high altitudes. Topics covered include numbers of trochilid species in high altitude vs. low altitude environments, the relation between competition and speciation in high altitude hummingbird species, and the magnitude and speed of evolutionary change to life at high altitude.

The monograph is well written in a crisp, easily read style. Jargon is kept to a minimum. so the interested layman will be able to glean much from each section. Figures and tables are kept simple and are effective in helping to grasp textural explanation. Statistical analysis is straightforward.

Most major contentions are well argued. There is effective integration of field observations and laboratory experimentation, particularly regarding torpidity. The choice of this "aberrant" species for investigation was a good one and Carpenter generally makes a strong case for the major hypotheses that the peculiar adaptations of *O. estella* have been forced by the climatic and physical factors characteristic of the altiplano and, secondly, that hummingbirds, usually regarded as a highly specialized and adaptively limited group, can evolve adaptations which allow them to exploit unusual and climatically rigorous environments.

The work is not without weaknesses. In my opinion there is excessive speculation throughout, particularly in the first section (morphological adaptations). Arguments regarding body size differences between *O. estella* and other hummingbirds and explanations for sexual dimorphism in *O. estella* are protracted and overextended. Occasionally, major arguments are based on very small sample sizes.

Conceptual confusion also sometimes occurs. Early on, with little evidence, winter mortality is identified as the most important population limiting factor and implicitly regarded as ultimately limiting. Later, the introduced winter blooming *Eucalyptus* is belived to have decreased winter mortality, but this is not regarded as important because at this point Carpenter tells us that ultimate limitation occurs through nest site scarcity. In another section, he says that "the nesting stage is still probably the most vulnerable of the whole life cycle," but no data are offered in support. Still later in the energetics section the species' winter energetics strategy is pictured as extremely efficient and finely tuned. If so, one wonders why winter mortality occurs to the extent that it supposedly does. The reader is left guessing what Carpenter really does believe ultimately limits the population.

Arguments in the concluding discussion also are flawed. The relationship of trochilid species diversity at high vs. low altitudes is simplistic and arguments marshalled to explain the reason for low diversity at high altitude are confused, e.g., "rigorous" environment is poorly defined and seemingly confused with "stressful," and it is not clear whether it is the "rigor" of the environment or the lack of evolutionary time that is the main explanation for the low diversity. Further, though the effect of speciation rate on diversity is considered important, the importance of extinction rates of species in high elevation environments is not even mentioned, an unexpected oversight for one who argues earlier for the presence of a taxon cycle in *O. estella* and related high-altitude congeners.

In general, however, this study is a valuable addition to our increasing knowledge of hummingbird systems and is one of the few to date that provides an overview of the ecology and evolution of a single species. Serious students of hummingbird ecology will find it very useful.—DAVID L. LYON.

CROWS OF THE WORLD. By Derek Goodwin, illus. by Robert Gillmor. Cornell University Press, Ithaca, New York, 1976: vi + 354 pp., 3 color plates, many line drawings and distribution maps. $28.50.—This is a reference guide to the family Corvidae. Most of the book (286 pages) is devoted to individual accounts of each of the 116 species of corvids. In each account there is a detailed description of the species, followed by discussions of field characters, distribution, feeding and general habits, nesting, voice, and display and social behavior. For each species there is also a range map. Those familiar with the range descriptions given in most check-lists (e.g. Khorasan, the Dasht i Lut desert and Persian Baluchistan) will appreciate this visual aid. For most species a line drawing is also provided. Although some of these illustrations are rather poorly reproduced, they add a new dimension to a work of this kind. Readers are usually forced to choose between books that provide many color photos and plates but do not give much information on the birds depicted, or those that provide detailed information with little visual reinforcement. This book provides an excellent compromise between these formats.

The species-by-species analysis of the Corvidae is one of the most comprehensive studies of the vast amount of information that has been recorded concerning this family. In his introduction, Goodwin states that, "one of the book's purposes is to indicate what is not known" about various members of this family. By reading the description and synopsis of the behavior and biology of each species, and then reviewing the references that are listed immediately following the discussion of each bird, the reader becomes aware of the gaps in the information concerning that form. It is probable that these analyses may stimulate readers who are in a position to record observations on some forms to do so, and not disregard the birds with a paraphrase of Aesop's "It's only a crow and that signifies nothing!"

The first chapter discusses taxonomic nomenclature and mechanisms of speciation. For those familiar with these concepts there is little new information, but the chapter should prove helpful to readers not well-versed in these areas. Fig. D.1. is a dendrogram showing the "presumed relationships of the corvine genera." The author does not give data or references that could enable the reader to quickly interpret the meaning of this "phylogeny" or determine the basis by which it was constructed.

The next 2 chapters deal with the adaptive radiation and adaptive characters, and the plumage and coloration of the Corvidae. They provide information that will help the reader to better understand the descriptions given in the species accounts. Chapter 4, on behavior, is longer and more detailed than the preceding chapters. This is understandable considering the vast amount of information that has been recorded on the complex behavioral patterns of the Corvidae. Goodwin has ably summarized much of this information and presents it in a well-organized, easy to read form.

The author states, "In the species section forms believed to be most closely related to each other are placed together in so far as this is possible within the confines of linear arrangement." Although most readers will find the author's arrangement for the most part acceptable, I feel that he should have included a list of the references or observations that were used in constructing this sequence. The book concludes with indexes of common and scientific names.

Crows of the World is a well-written and informative book that provides a well-organized mass of information on all 116 species of Corvidae. It would be a useful addition to any ornithological library.—STEPHEN R. BORECKY.

COLLECTED PAPERS IN AVIAN PALEONTOLOGY HONORING THE 90TH BIRTHDAY OF ALEXANDER WETMORE. Edited by Storrs L. Olson. Smithsonian Contributions to Paleobiology, No. 27, Smithsonian Institution Press, Washington D.C., 1976: xxvi + 211 pp.—Alexander Wetmore has done more to revitalize avian paleontology during the past half century than any other person, and this volume is a remarkable testament to the vigor and excitement of the field today. Festscrift volumes have not been popular recently, at least in this country, which may not be a bad thing because they are often collections of major papers by minor authors, or minor papers by major authors; assemblages of journal rejects rescued from the bottom drawers of file cabinets. Such is decidedly not the case with this volume. An outstanding group of workers has presented a collection of always interesting and often exciting reports on a variety of topics. Though the book opens with brief "appreciations" of Wetmore's work and influence on the field by S. Dillon Ripley and Jean Delacour, and a scientific biography of Wetmore's work by Storrs L. Olson, it is the papers themselves that offer the finest testament to the role that Wetmore has played in stimulating many workers to enter and explore the field. This is further demonstrated in the acknowledgements of Wetmore's influence by various authors, and by the number of new taxa that they have named in his honor.

More than just a collection of fine research reports, this volume is also a summary statement of the present state of avian paleontology. For this reason, rather than try to review all of the papers separately, I will take this opportunity to assess the strengths and weaknesses of the field, and its current role in avian biology, at least as I percieve it from the viewpoint of an interested nonparticipant in the field.

Paleontology in recent years has shifted from an emphasis on the description of new forms, as important as that continues to be, to an analysis of the significance of its findings in terms of evolutionary theory. Thus it has become more closely associated with biology and less with geology than was formerly the case, a trend that is recognized in the increasing use of the term paleobiology. In this context its greatest potential contributions to ornithology would seem to lie in three general areas: (1) the origin of birds and of their peculiar adaptations, especially for flight, (2) analysis of the phylogeny of the higher categories of birds, and (3) clarification of the role of birds in the evolution of ecosystems through time. I will consider the field as exemplified by the present collection of papers in relation to these three areas.

The problem of the origin of birds has been reexamined by several workers in recent years, following several decades during which Heilman's thecodont theory went unchallenged. Of the several ideas recently suggested for avian origins, John Ostrom's theory of an origin from the coelurosaurian dinosaurs has been the most convincing. In this volume Ostrom uses his intimate knowledge of the anatomy of *Archeopteryx* to speculate on some of the anatomical changes that must have occurred between *Archeopteryx* and modern birds so as to make powered flight possible. The main interest centers on the coracoid and its changes in form that were apparently associated with a conversion of the action of the supracoracoideus muscle, converting it from a depressor of the wing to an elevator, thus making possible the recovery stroke of powered flight.

The toothed birds of the Cretaceous are reexamined in two papers. Philip D. Gingerich assesses the significance of these birds to avian phylogeny. He argues that *Hesperornis* did indeed have teeth, and also a paleognathous palate. This leads him into a consideration of the ratite problem, and he argues against Cracraft's theory that the ratites are monophyletic because (among other reasons) the paleognathous palate is considered to be a primitive condition among birds rather than a derived state. Larry D. Martin and James Tate Jr. provide a detailed description and analysis of *Baptornis*, a diving bird closely related to the better-known *Hesperornis*.

In order to understand both the phylogeny of birds and the evolution of faunas, it is obviously important to know at what periods in time the various groups occurred, and especially when they first appeared. Fossils are the source of this information, and many useful data have been provided by avian paleontologists, including several important contributions in this volume. Nevertheless, the overall picture is subject to frequent reevaluation and must be regarded with a certain caution owing to the frequency with which specific fossil forms are reallocated to different higher taxa. In the present volume, for example, Alan Fedducia reassigns the genus *Neanis*, previously considered to be the oldest known passeriform, to the order Piciformes. Feduccia and Larry D. Martin discuss *Uintornis*, which was originally placed in the Picidae, then the Bucconidae, then shifted to the Cuculiformes. They return it to the Piciformes, but in a new family Primobucconidae. Storrs L. Olson shifts *Protornis* from the Alcedinidae to the Momotidae, thus giving this presently New World family an Old World history. Charles T. Collins moves the extinct family Aegialornithidae from the Apodiformes to the Caprimulgiformes. Reallocations of this sort are not uncommon in the avian paleontological literature. It is unclear whether this is because the often fragmentary remains are ambiguous, or because earlier workers were less rigorous in their studies than more recent investigators. However, in some cases, including those in this volume, it seems that new interpretations follow upon the analysis of larger and better samples than those available to earlier workers. This is an important problem because the whole picture of avian phylogeny, to the extent that paleontology contributes to it, depends on the accurate recording of the occurrence of different groups in time and space, and unexpected discoveries may have a profound effect on our ideas of the history of particular groups. This is clearly illustrated by Storrs L. Olson, who presents us with Motmots in Europe and Todies in Wyoming.

Another important problem is how to interpret fossil forms that are intermediate in characteristics between living taxa. "Intermediate" in this context means that the fossil forms are mosaics of characters, some shared with one taxon and some with another. Pierce Brodkorb describes a new form, *Alexornis*, that shares some characteristics with the Bucconidae (Piciformes) and some with the Momotidae (Coraciiformes). Pat Vickers Rich and David J. Bohaska describe the oldest known owl, *Ogygoptynx*, as intermediate between the Tytonidae and Strigidae. What can such forms represent phylogenetically? The usual solution is to suggest that the intermediate is some sort of "link" between the later taxa, perhaps ancestral to both of them. The problem of interpretation arises in part at least, from a failure to analyze the meaning of the individual characters, rather than just listing and totalling them. Rather, they should be interpreted in terms of the directions of evolution of evolving characters within the larger taxa; some "similarities" may then be found to be primitive character states, and some derived. If phylogenetic affinities are hypothesized only on the basis of the latter, much of the confusion from conflicting evidence could be eliminated. Of course there is the problem that many of the characters used in avian paleontology are minor variations in bony knobs, projections, grooves, etc., easily subject to convergence and difficult to analyze cladistically with much confidence. Still, it might be worthwhile to try.

Several papers provide descriptons or reinterpretations of fossil birds and early avifaunas, and contribute to an increased understanding of the ecological roles of birds at various times and places in the past. Among the most significant are studies by Alan Feduccia and Larry D. Martin on Eocene Piciformes, and by Storrs L. Olson on Oligocene Coraciiformes. It is suggested that these groups were the dominant small land birds in these epochs, and that the ascendency of the Passeriformes to their current dominance may not have occurred until Miocene time. Among the analyses of more restricted areas, Oscar Arredondo's review of the Pleistocene predatory birds of Cuba presents a remarkable picture of giant eagles, owls, and vultures analyzed in terms of their ecological relationships with the contemporary mammals. Joel Cracraft analyzes the Moas of New Zealand and demonstrates how an adequate fossil record can be subjected to detailed mathematical analysis. He presents a story of adaptive radiation in these giant flightless birds, and also provides a new classification in which many fewer species are recognized than were admitted by earlier workers.

Other noteworthy studies in this volume include reviews of the Lower Miocene swifts by Charles T. Collins, of the Pleistocene pied-billed grebes by Robert W. Storer, of a Pleistocene avifauna of Ecuador by Kenneth E. Campbell, Jr., and of the Paleogene birds of Asia by E. N. Kurochkin. Descriptions of a new Miocene osprey by Stewart L. Warter and of a new Miocene flightless auk by Hildegarde Howard are also included. The final paper, by G. Victor Morejohn, brings us to Recent times with the discovery in California Indian middens of bones from the flightless duck *Chendytes lawi*, previously known from Pleistocene remains.

Altogether, this volume demonstrates that avian paleontology is alive and well, and making important contributions to several areas of systematic ornithology, though it is also troubled by some of the philosophical and methodological problems faced by systematics generally. Students of avian biology owe a debt of gratitude to Storrs L. Olson for his work in organizing this outstanding collection of reports in avian paleontology.—ROBERT J. RAIKOW.

A GUIDE TO EASTERN HAWK WATCHING. By Donald S. Heintzelman. Pennsylvania State University Press, University Park & London, 1976: 99 pp., maps, charts, and black-and-white photos. Cloth $8.95, paper $5.95.—Following brief written descriptions of each species, there are sections on field equipment, migration seasons, mechanics of hawk flights, and hawk lookouts. For each state or province there is information on hawk-watching localities, giving the quality of spring and fall observations, a description of the area, and directions for reaching it. Areas covered include the Great Lakes region and Eastern Canada, New England, the Middle Atlantic States, and the Southern Appalachian States. The book ends with appendices listing raptor conservation organizations, sample field data forms, as well as a short bibliography and index. The heart of the book consists of some 70 plates of raptors in flight; most of these are photographs but a few are line drawings. These will aid the observer in identifying flying birds. There are no illustrations in which different species are shown together for rapid comparison, but such are available in other books such as Peterson's field guides, to which the present volume should prove a handy supplement.—ROBERT J. RAIKOW.

THE BIRDS OF THE LIGONIER VALLEY. By Robert C. Leberman. Special Publication No. 3, Carnegie Museum of Natural History, Pittsburgh, PA, 1976: 67 pp., many line drawings, 6 color plates, numerous photographs. $5.00.—This is an unusually handsome regional list. The Ligonier Valley lies in Southwestern Pennsylvania between the westernmost ridges of the Allegheny Mountains; the area covered is about 100 square miles. Following brief introductions to the area and its ornithological history, the bulk of the book is devoted to species accounts giving the abundance and seasonal occurrences of all birds reported from the area. The line drawings by Carol H. Rudy are attractive and lifelike, illustrating many of the species discussed. H. Jon Janosik has contributed 6 outstanding paintings of locally observed forms, including a seldom-pictured immature Kirtland's Warbler. Unfortunately some of the brilliance of the original plates has been subdued by the printer. The Ligonier Valley is an exceptional birding area, and anyone interested in exploring it will find this book an attractive and useful aid.—ROBERT J. RAIKOW.

BIRD FLIGHT PHOTOGRAPHY. By Roger F. Cram. Creative Arts Photography, P.O. Box 642, Hiram OH 44234: 35 pp., line drawings. $3.95.—Uncomplicated instructions for amateur bird photography using only simple and inexpensive equipment. Order directly by mail.—R.J.R.

ANALYSIS OF VERTEBRATE POPULATIONS. By Graeme Coughley. John Wiley & Sons, New York, 1977: ix + 234 pp.—This is a detailed guide to a study of the mechanics of population biology. Chapters are devoted to The Population; Age, Abundance; Rate of Increase; Dispersal; Fecundity; Mortality; Relationship between Parameters (calculation of r, birth rates, death rates, etc.); Mark-Recapture; and Population Analysis in Management. The first 3 chapters are so cursory as to be of little value, but from Chapter 4 (Abundance) onward this text becomes an interesting "how to" book for a study of basic population parameters. Many statistics, formulae and indices are given, and the level of the math is algebra or less. Great pains were taken to avoid even a hint of calculus (e.g. the fundamental growth equation, $dN/dt = rN$ is only given in its algebraic form, and the differential is not even mentioned). Nevertheless, the mathematics are presented logically and lucidly. This work is valuable in that it pulls together methodological techniques and criticisms for most population parameters. By avoiding complicated mathematics the volume has value to beginning students, specialists and field workers in conservation and game areas. This useful book should form a part of the library of most population biologists, particularly those interested in the analysis of field data and in various techniques of obtaining the data.—MICHAEL A. MARES.

MY RECIPES ARE FOR THE BIRDS. By Irene Cosgrove & Ed Cosgrove, Doubleday & Co., Inc., New York, 1976: 31 pages, paper cover. $2.95.—A handy collection of recipes for bird feeders designed to attract various species, with helpful advice on the design and placement of feeders.—R.J.R.

ANNOTATED CHECKLIST OF THE BIRDS OF ONTARIO. By R. D. James, P. L. McLaren, and J. C. Barlow. Life Sci. Misc. Pub., Royal Ontario Museum, 100 Queen's Park, Toronto, Canada, 1976: 75 pp., paper covers, 2 maps. $2.50.—Status, breeding status, distribution, frequency, dates of occurrence, and egg dates for 427 species.—R.J.R.

A GUIDE TO BIRD-WATCHING IN MALLORCA. By Eddie Watkinson. AB Grafisk Formgivning, Stockholm; Available from M. Philbrick, PO box 83, Vashon, WA 98070; no date given: 56 pp., paper covers, many maps. $3.90.—Not a guide to the birds, but to finding them. Detailed maps and instructions on many local areas, with information on how to get there and what birds to expect at any season, along with helpful advice on local customs, laws, transport, and so forth.—R.J.R.

CONSERVATION COMMITTEE REPORT

Falconry: Effects on Raptor Populations and Management in North America

Falconry can be defined as the sport of hunting with trained raptors. Historically, falconry referred to the training and use of falcons in hunting but now the term is used to describe the use of all raptors trained to take prey. Because of recent declines in population levels of some species of raptors such as the American Peregrine Falcon (*Falco peregrinus anatum*), (Hickey 1969, Cade and Fyfe 1970), Cooper's Hawks (*Accipiter cooperii*) (Snyder et al. 1973), and use of falcons in entertainment (i.e. Atlanta Falcons Football Club and Air Force Academy Falcons Sports), concern has been expressed since the early 1960's about both the future of falconry as a sport and its impact on raptor populations. With listing of the American Peregrine Falcon as an endangered species on 8 March 1969 by the U.S. Fish and Wildlife Service, interest in the welfare of most species of raptors increased. Stringent controls and regulations on taking raptors and on the sport of falconry were instigated in many states in the early 1970's. The Supplementing Agreement to the Convention for the Protection of Migratory Birds and Game Mammals with Mexico in 1972, and subsequent drafts of proposed federal falconry permit regulations created controversy and conflict among falconers, environmental groups, state conservation agencies, and the U.S. Fish and Wildlife Service. The Conservation Committee of the Wilson Ornithological Society undertook this review of the sport of falconry, impacts of removing raptors from the wild, and the final form of federal falconry permit regulations (Federal Register 41(10):2237–2240, 41(37):8053) issued in February 1976.

FALCONRY

The earliest records of falconry are from Mongolia and Egypt (about 2000 B.C.) where it probably originated not as an art or sport but as a method to secure food. The use of trained falcons for hunting evolved into an art and sport which reached its peak popularity in the Middle Ages. From the 8th to the 17th century, falconry flourished in Europe where the type of raptor permitted correlated with social class. After the Middle Ages, interest in falconry declined, perhaps because of firearms development and changes in social order (Nye 1966).

Falconry developed slowly in North America, probably because it was not typical of immigrant peoples or appropriate to pioneer life. By the early 1900's, interest slowly increased, stimulated by R. L. Meredith and an article in the *National Geographic Magazine* in 1920 by Louis Agassiz Fuertes (Nye 1966). As the result of efforts by Meredith and others to stimulate interest in falcons and falconry, the art and sport grew such that, by the late 1930's, over 100 falconers were active in the United States. Growth of falconry was slow in the 1940's and 1950's but greatly increased in the 1960's and early 1970's when there were an estimated 1500 active falconers. This can be partially attributed to increased publicity and legalization of the sport. In 1964 the U.S. Fish and Wildlife Service permitted the use of trained raptors in the taking of migratory game birds. A survey of states and Canadian provinces and territories by the Conservation Committee revealed that 6 of 11 provinces and territories responding and 34 of 47 states responding allow falconry. Supported by the federal regulations in 1976, the tradition of taking raptors for falconry and the "sport" have been solidly established by law.

The Environmental Assessment prepared by the U.S. Fish and Wildlife Service (1976) on the proposed federal falconry regulations states that about 2769 falconry permits had been issued by 29 states in 1974 and projects that 5900 falconers will be licensed in 1980 if all 50 states were to allow falconry. This estimated 2-fold increase may be realized because of previously unlicensed falconers applying for licenses, better law enforcement, and increased awareness of the sport.

The Conservation Committee doubts the projected increase will occur. Falconry requires proper facilities, hard-won expertise, long hours, and dedication. We estimate conservatively that fewer than half of the about 2700 permittees presently licensed are active falconers. The remainder keep raptors, perhaps due to the novelty or supposed glamour of the activity. Administration of federal and state regulations on training, experience, facilities, testing, record keeping and restrictions on the species of raptor allowed is such that license applications will not rapidly increase. Indeed, we estimate that the increase may approximate 40% by 1980 or about 5% per year.

STATUS OF RAPTOR POPULATIONS

The Environmental Assessment of the proposed federal falconry regulations lists 18 species of raptors of "importance" to falconry in North America, but only 6 species, including the Red-tailed Hawk (*Buteo jamaicensis*), Goshawk (*Accipiter gentilis*), Harris Hawk (*Parabuteo unicinctus*), American Kestrel (*Falco sparverius*), Prairie Falcon (*F. mexicanus*) and Peregrine Falcon represent most used at the present. Red-tailed Hawks are certainly the most used in North America.

The status of any wildlife population may be evaluated in 3 general ways: (1) complete annual counts, (2) development of an abundance index in some stage of the life cycle, or (3) a life-equation approach which provides an indirect evaluation of the population's condition. These approaches are not new and fall within the general outline presented by Leopold (1933:139).

A complete count of a raptor population is difficult or impossible unless the area is small and few reliable long-term data are available. Indices of abundance based on counts of fall migrants are available but are confounded by weather, numbers of observers, changes in counting sites, etc. We have relied primarily upon the life-equation approach to evaluate the status of selected raptor populations. A *recruitment standard* was estimated for most species discussed based on models. Knowledge of some parameters used in the models may be excellent but others are poorly understood. Nevertheless, recruitment standards, the long-term average production rate per breeding-age female required to maintain a stable population, have been estimated (Henny 1972; Henny and Wight 1972). The number of young fledged per successful nest, based primarily on banding records, provides a long-term index of production but does not reveal, of course, population decline since young are banded only at existing nests. Finally, production rates based on intensive short-term nesting studies were compared with the long-term recruitment standards. The importance of pesticides as a factor in population declines of raptors used in falconry was kept in mind in the review of available data on raptor populations.

Considerable progress has been made in the last decade demonstrating the relationship between population declines of several species of raptors useful for falconry and pesticide contaminants. Soon after Ratcliffe's (1967) initial report of eggshell thinning in British Peregrines and Sparrowhawks (*Accipiter nisus*), similar thinning was discovered in North American Peregrines (Hickey and Anderson 1968), here associated with high levels of DDT and its metabolites, especially DDE. Measurements of the eggs of many other species of raptors were soon made, and reductions in eggshell thickness were found in several, especially Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks and Prairie Falcons (Anderson and Hickey 1972). Other species important in falconry, such as the Goshawk and Red-tailed Hawk, which feed primarily on mammals, were shown to be much less involved in the shell-thinning problem than species which feed heavily on birds.

Peregrine and Prairie Falcons.—The correlation of DDE in egg contents and thin eggshells has been clearly established for Peregrines (Cade et al. 1971) and Prairie Falcons (Fyfe et al. 1969; Enderson and Wrege 1973). Enderson and Berger (1970) showed that fledging success is inversely correlated with thin-shelled eggs in Prairie Falcons. Despite obvious correlations among DDE residues, eggshell thinning, and reproductive failure in some raptors, it is difficult to establish that these events are in fact the prime cause of population decline of such species as Peregrines (Hickey 1969). A major argument has been that DDT and its metabolites were not abundant enough to account for declines apparent by 1950. Peakall (1974) cleverly demonstrated that DDE was present in amounts accounting for pronounced shell-thinning in Peregrine eggs in California as early as 1948 by extracting residues from shell membranes of museum eggs and comparing the levels with more recent eggs for which the egg contents had also been analyzed.

A major circumstance to be remembered is that pesticide contamination or population declines of Peregrines and Prairie Falcons have not been uniform throughout the range of these species in North America. Prairie Falcons declined 34% in occupancy of territories in western Canada with the reduction being concentrated in 4 of 6 areas studied (Fyfe et al. 1969), but one report (Enderson 1969) and several unpublished accounts from the Rocky Mountain region reveal they are normally abundant and reproducing well. Peregrines disappeared as a breeding bird in the eastern United States, but are not declining and are not significantly contaminated with DDE in the Aleutian Islands (White et al. 1973).

Peregrines in North America, except for those in the Aleutian Islands, are experiencing reproductive difficulties due to DDE, and the threat is probably greater to this species than any other. Even in the Queen Charlotte Islands, British Columbia, Peregrine eggs contain about 3 times the DDE residues found in Aleutian Peregrine eggs (White et al. 1973). Fewer pairs nested in the Queen Charlottes in 1970 than in 1960 (Nelson 1970). Elsewhere in North America, populations are generally declining or steady with some reproductive difficulty apparent. In the Rocky Mountain region from northern New Mexico to Montana, 14 pairs fledged only 3 young in 1973 (Enderson and Craig 1974). In 1974 only 10 of those pairs could be found, but they reproduced well despite thin-shelled eggs. In 1975 only 7 of the original 14 pairs could be found and fledging success was poor. A few pairs are known to persist in western Texas (G. Hunt, pers. comm.) and in California. It is probably true that only between 20 and 30 pairs of Peregrines were known to nest in the contiguous United States in 1975.

American Kestrel.—The status of the American Kestrel in North America was reviewed by Henny (1972). The number of young banded per successful nest in the Northeast provided a crude index to production. The mean number banded per nest was 3.92 young for 1925–45, 3.92 for 1946–59, and 3.63 for 1960–68. The data for the latter period suggest a 7% decrease in young fledged per successful nest. Hackman and Henny (1971) also suggested a slight population decrease in the East. Lincer and Sherburne (1974) found relatively high levels of DDE in the eggs of Kestrels breeding near Ithaca, New York, and felt pesticides were being obtained in the wintering grounds in the southeastern United States.

The Environmental Assessment of the proposed falconry regulations mentions a recent increase in eastern populations, perhaps due to DDT bans. Kestrel eggshells were thinned 10% by one application of DDT at .84 kg per ha on 172,800 ha in the 1974 DDT-Tussock Moth Spray Program in the Pacific Northwest (Henny et al. 1976, unpubl. report). This was accompanied by a 5-fold increase in residue levels of DDT and its metabolites in the eggs over those from controls 30–50 km from the spray area.

Red-tailed Hawk.—The Red-tailed Hawk nests throughout much of North America and few reports of Red-tailed Hawk population declines appear in the literature. Furthermore, Henny and Wight (1972:246) report no significant change in average production per successful nest during the DDT era in North America. They concluded that reproduction is balancing mortality rates in the populations. Unlike other raptors, counts of migrant Red-tailed Hawks at White Marsh, Maryland during the 1950's and early 1960's also remained stable (Hackman and Henny 1971). Anderson and Hickey (1972) found eggshell thinning exceeding 9% in 5 Montana eggs, but other eggshells from the United States were near normal.

In recent years a number of short-term nesting studies of Red-tailed Hawks have been conducted. The observed production rates have approximated the long-term production standard estimated by Henny and Wight (1972). A six-year study (1966–71) in Saskatchewan showed production slightly in excess of that believed required (Harris 1971), while a 3-year study (1967–69) in Alberta showed a population declining slightly (Luttich et al. 1971). Orians and Kuhlman (1956) reported slightly above normal production in Wisconsin in 1953–55, while Gates (1972) reported production slightly below normal in east-central Wisconsin in 1962–64. Similarly, Seidensticker and Reynolds (1971) reported below-normal productivity and 10.9% shell thinning during a 2-year study (1966–67) in south-central Montana. A more recent study (1971–72) in southwestern Montana, however, shows normal production (Johnson 1975). Production in southern California in 1973 appeared to be excellent in an area where man was not interfering with nesting (Wiley 1975). Annual production rates are variable, depending upon local conditions, but the results of the short-term studies in the pesticide era reveal the species is reproducing normally.

Cooper's Hawk.—Accipiters experienced eggshell changes about twice as great as the buteos (Anderson and Hickey 1972) paralleling the reported declines of Cooper's Hawks and Sharp-shinned Hawks in eastern North America (Spofford 1969, Hackman and Henny 1971, Snyder et al. 1973). Young banded per successful nest in the Northeast was taken as a crude index to production (Henny and Wight 1972). The mean number banded was 3.53 young for 1929–45, 3.08 for 1946–48, and 2.67 for 1949–67. More recently, calculations for 1968–74 show an improvement to 3.36 young (Henny, unpublished data). These findings accompany the contention of the Environmental Assessment that Cooper's Hawks have increased in the East during recent years.

PROBLEMS ASSOCIATED WITH MANAGEMENT OF RAPTOR POPULATIONS

Major problems associated with management of raptor populations include contamination of food chains by pesticides, loss of habitats necessary for foraging and nesting, and man-caused mortality (White 1974). Unlike the role of contaminants in declines of some species of raptors, losses of nesting habitat, suitable foraging areas, and prey species are less well documented (White 1974, Braun et al. 1975) but may be important locally. Disturbance of nesting sites by photographers, banders, and the general public can reduce hatching and fledging success (Fyfe and Olendorff 1976). Alteration of nesting sites by nuclear tests has had similar results (Stahlecker and Alldredge 1976). Shooting increases mortality of raptors despite nearly complete legal protection from this source. With increased awareness of values of raptors and enforcement of regulations, losses of all birds of prey through shooting appear to be low compared to earlier periods. Man-caused mortality by vehicles, electrocution, trapping, poisoning, and egg collecting appears to be low and stable at present although data are lacking for definitive statements. These causes undoubtedly are responsible for some mortality but actual impacts on overall populations are unknown.

The Environmental Assessment of the proposed federal falconry regulations documented little mortality of raptors trapped and transported for purposes of falconry. In a survey of British falconers, Kenward (1974) estimated that from 11 to 53% of raptors taken as nestlings, depending upon species, died in the first year of captivity. The survey further indicated that between 50 and 93% of the trained raptors were eventually lost or released. Similar data are not available for North America but it can be safely assumed that deaths of birds taken as nestlings, especially by inexperienced people, are quite high and may exceed those values reported by Kenward (1974).

Cade (1968) estimated that from 25 to 50% of the annual production of Gyrfalcons (*Falco rusticolus*) in Iceland was exported under strict regulations for falconry each year for several centuries with no noticeable impact upon the breeding population. Blood (1968) reported that removal of about 12 nestling Peregrines annually from 1952 to 1967 from the Queen Charlotte Islands did not appear to adversely affect breeding Peregrine populations. Exploitation rates of raptors for falconry appearing in the Environmental Assessment suggest that less than 0.5% of any species population is taken annually. If first-year mortality rates of most raptors in the wild approximate 40 to 60% (Shor 1970, Luttich et al. 1971) and most raptors taken for falconry are first year birds, it is obvious that removal of raptors from the wild for falconry at even double the present levels could not be responsible for regionwide population declines.

Recently, interest in management of raptors has increased, primarily the result of concern about local populations. Olendorff and Stoddart (1974) give an excellent statement of management possibilities for grassland raptors, including the likely possibility of increasing nesting sites by providing man-made structures. Perhaps the largest and most successful attempt in providing artificial nesting sites was conducted in Michigan in 1967 where 43 nest platforms were constructed for Ospreys (*Pandion haliaetus*). The majority of the platforms became occupied in later years and pairs using them experienced lower nestling mortality than pairs using the dwindling supply of natural sites (Postupalsky and Stackpole 1974). In an area in California, the total number of Osprey nests producing young was increased by 37% over the previous 3 years after artificial nest platforms were erected (Garber et al. 1974). R. Fyfe (pers. comm.) has shown that Prairie Falcons nest readily in holes dug in dirt banks where none existed before.

The most massive effort to restore reduced or extirpated populations is now underway for the Peregrine. There are several options available and all are difficult. Population recovery of Peregrines could be effected by 3 means: (1) reduce DDE contamination through limiting or prohibiting the use of DDT, (2) artificially increase the production of young, and (3) reduce mortality rates. Reducing levels of long-lived pesticides in the environment, especially outside of the United States, will be difficult and will necessitate international cooperation. Artificial increase of fledging rates could be effected by manipulating eggs in nests in the wild or by manipulating young which have been bred in captivity. For example, first clutches from nests in the wild could be removed and artificially incubated and second clutches will be produced. Further, eggs or young can be placed into the nests of wild Peregrines. This was done successfully in Colorado in 1973 and is perhaps the best technique as long as wild nesting pairs can be found. Peregrine eggs or young can be put in the nests of other species. It has been shown that hawks can successfully fledge Prairie Falcon young (R. Fyfe, pers. comm.). In some regions the Prairie Falcon would presumably be a suitable foster species, but possible adverse effects of "imprinting" by young Peregrines on their adult foster parents have not been determined. Young Peregrines can be released to the wild in the absence of adults by allowing them to fledge from a protected place and by supplying food until they are independent. This procedure has already been used successfully by H. Meng and by Cornell University in reintroducing captive-produced Peregrines in the eastern United States, avoiding the possibility of "imprinting," and can be used where no adult Peregrine pairs are present. The third means involves the techniques of falconry. Qualified falconers could take wild Peregrine nestlings, train them to hunt and release them after the first or second winter. Good falconers keep a higher percentage of young birds alive than occurs in the wild and perhaps twice as many could be released as would be expected to naturally survive (Cade 1974). Certainly there are many falconers capable of handling Peregrines successfully, but the scheme would require careful organization and so far there is little information relating to survival rates of trained falcons.

There is little doubt that rehabilitation of Peregrine populations south of Canada will consist mainly of the release of captive-bred birds produced by a few large breeding projects. Smaller projects have thus far served to provide reservoirs of the appropriate subspecies and have been useful in developing some of the necessary techniques. People proficient in falconry have clearly been crucial in the progress made in breeding falcons in captivity and are certain to be indispensable to further population rehabilitation efforts.

A major concern relates to the intentional or accidental release of exotic Peregrines in North America. One school contends only the form originally occurring in the area should be flown or released there. The other extreme contends that Peregrines are all substantially similar and that natural selection will determine the genetic attributes of any wild population, regardless of its origin. The argument is academic for the eastern United States since no captive stock of that former population exists and any Peregrines introduced there forming a viable population may well be better than no Peregrines at all. In the West, adequate captive stocks originating in the wild are being bred so that enzootic birds may be re-stocked. In any event, Peregrine populations in temperate North America will be to a major degree artificial in that they must be managed as long as DDE remains the dominant adversary.

Recent success of the Cornell program for captive breeding of Peregrines indicates that production of 250 young Peregrines per year from captive sources is possible by 1980. While some young produced will be retained for eventual captive breeding, many will be available for reintroduction. It is also likely that captive bred falcons will be eventually available to falconers. Since most of the present stock of breeding Peregrines in captivity was obtained on loan from falconers, it is logical for them to expect to receive some of the progeny. Regulation of the disbursement and final disposition of captively bred raptors will be a major problem until firm understandings supported by appropriate legislation are reached.

PERSPECTIVE

Interest in falconry is expected to increase at a slow rate because of more stringent regulations at the federal, state, and provincial levels and because of the difficulty in maintaining and training captive birds. No appreciable impact on wild populations of any species is anticipated because species or subspecies listed as endangered cannot be legally used for falconry. Falconry will continue with the more common species such as Red-tailed Hawks and American Kestrels because other species are more difficult to acquire. Present official attitudes of most states and provinces surveyed reflect little apprehension that falconry is unmanageable or a drain on raptor populations. Some states and provinces believe that regulation of falconry is inordinately expensive in time and money because of demands of the few practitioners.

SUMMARY

The art of falconry in North America, practiced by a few individuals for many years, attracted little attention until the 1960's. Presently about 2800 falconers are licensed in the United States with less than one half considered to be active. While interest in this art is expected to increase, we believe growth will be slow, probably 5 to 10% per year, due to rigorous demands on time and equipment required and restrictive regulations.

Many different species of raptors have been used in falconry. Presently 6 species are commonly used, especially the Red-tailed Hawk and American Kestrel. Present evidence suggests that only 2 races of the Peregrine Falcon are threatened in North America, and declines may have occurred in local populations of other species. Declines in populations of Peregrines are attributed to pesticide contamination of food chains. Apparent declines in other populations of raptors are also attributed to pesticides and locally to changes in land use and possibly indiscriminate shooting. Removal of raptors from wild populations for falconry has not had documentable adverse effects except possibly at local nesting sites. Continuation of the art of falconry under the framework of the recent federal regulations is not expected to have measurable impacts on region-wide populations. Management of raptors is poorly developed and relatively unexplored. Captive breeding of raptors holds much promise for production of birds both for re-establishment and as a source of birds for falconry. Falconers have contributed much to the continued improvement of the Cornell University Peregrine program in terms of breeding stocks and technique development.

RECOMMENDATIONS

1. Additional data are urgently needed for the monitoring of changes in raptor populations over large areas. This may entail the development of new census techniques and establishment of national or continental surveys.
2. Falconry is a legitimate art and has a place in wildlife management and conservation. The art should not be popularized.
3. The federal falconry regulations should be adopted immediately by all states as they represent the initial step in uniform regulation of falconry and the taking of raptors. The Conservation Committee does not see the need for placing Great Horned Owls (*Bubo virginianus*) under the falconry statutes.
4. It is crucial that a practical banding or tattooing system for permanently identifying individual captive raptors be immediately established since enforcement of falconry regulations will be exceedingly difficult without it.
5. Any species of raptor bred in captivity, including properly accounted for and marked endangered species, should be allowed for falconry. The effect will be to encourage captive breeding and will reduce dependence on wild populations.
6. Properly accounted for and marked birds used in falconry should be allowed free interstate transport provided proper state and federal permits have been obtained.

ACKNOWLEDGMENTS

We acknowledge the contribution of the personnel of state and provincial Conservation Agencies who responded to the questionnaire survey. Several individuals greatly facilitated the Committee by making data available which improved our knowledge of falconry and raptors. Specifically, our appreciation and thanks are extended to J. L. Ruos of the U.S. Fish and Wildlife Service and R. M. Stabler of Colorado College.

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Heinz Meng
Alva G. Nye, Jr.

ORNITHOLOGICAL NEWS

HAWK MOUNTAIN RESEARCH AWARD

The Board of Directors of Hawk Mountain Sanctuary takes pleasure in announcing an annual award of $250 for support of raptor research. The Hawk Mountain Research Award will be granted annually to a student engaged in research on raptors (Falconiformes).

To apply, students should submit a description of their research program, a curriculum vitae, and 2 letters of recommendation by 31 October 1977 to: Mr. Alex Nagy, Hawk Mountain Sanctuary Association, Route 2, Kempton, PA 19529.

A final decision will be made by the Board of Directors in February 1978.

Only students enrolled in a degree granting institution are eligible. Both undergraduate and graduate students are invited to apply. Projects will be judged competitively on the basis of their potential contribution to improved understanding of raptor biology and their ultimate relevance to conservation of North American hawk populations.

COLONIAL WATERBIRD GROUP MEETING

The Colonial Waterbird Group, organized during the Wading Bird Conference at Charleston, South Carolina last October 1976, will hold its first annual meeting on 21–23 October 1977, at Northern Illinois University, in DeKalb. The conference will include paper sessions, subgroup meetings (surveys, conservation, etc.) and an important business session. Any person wishing to present a paper on an aspect of research or management of pelicans, cormorants, herons, ibises, gulls, terns, alcids or other colonial waterbirds should submit a single page abstract no later than 15 August 1977 to the National Audubon Research Department, 115 Indian Mound Trail, Tavernier, FL 33070. Additional information on the conference will appear in the mid-summer CWG newsletter, or may be obtained by writing the above address.

REQUESTS FOR ASSISTANCE

Shorebird color-marking.—In 1977, the Canadian Wildlife Service will again be carrying out extensive banding and color-marking of shorebirds in James Bay. Last year, over 12,400 shorebirds were captured during July and August resulting in over 580 reports of color-marked birds in eastern North America and South America. Much valuable information on migration routes is being obtained and observers are again asked to look out for and report any color-dyed *or* color-banded shorebirds that they may see. Reports should include details of species (with age if possible), place, date, color-marks, and if possible, notes on the numbers of other shorebirds present. For color-dyed birds, please record the color and area of the bird that was dyed. For color bands and standard metal leg bands, please record which leg the bands were on, whether they were above or below the "knee," the colors involved, and the relative position of the bands if more than one was on a leg (e.g., right leg, blue over metal etc.). All reports will be acknowledged and should be sent to Dr. R.I.G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1A 0E7.

International Shorebird Surveys, 1977–78.—A cooperative International Shorebird Survey scheme was started in 1975 to obtain information on shorebird migration and to identify and document areas of major importance. This scheme has been highly successful, with much very valuable information on shorebird distribution and migration coming from contributors throughout eastern Canada and the U.S.A., the Caribbean Islands, and Central and South America. Information from the scheme will be valuable in assessing requirements for the future protection and conservation of the birds and their habitat. In 1977 we are anxious to continue and extend the scheme in as many areas as possible. Any observer who may be able to participate in regular survey counts of shorebirds during spring and autumn migration periods, as well as during the winter in shorebird wintering areas. are asked to contact one of the undersigned. Occasional counts from observers visiting shorebird areas on an irregular basis would also be most welcome.

For areas in Canada: Dr. R.I.G. Morrison, Canadian Wildlife Service, 2721 Highway 31, Ottawa, Ontario, Canada K1A 0E7.

For areas in the U.S.A., Caribbean Islands, Central and South America: Brian A. Harrington. Manomet Bird Observatory, Manomet. MA 02345, U.S.A.

Wing-tagged Laughing Gulls.—Juvenile Laughing Gulls have been wing-tagged with green or orange and green wing tags (and with metal leg bands) in Barnegat Bay. New Jersey to study behavior. migration. habitat selection. and survival rates. The tags are round (5 cm in diameter) and numbered. Please report all sightings to Bird Banding Laboratory, Office of Migratory Bird Management, Laurel. MD 20811. Please include date, time, location, color of tag, and number of the tag if possible. Information may also be sent to Joanna Burger, Dept. of Biology. Livingston College. Rutgers University. New Brunswick. NJ 08903.

Bird-strip mine and bio-indicator literature wanted.—A bibliography on birds found on strip mines and the use of birds as bio-indicators of the quality of the environment is being compiled for the Institute of Mining and Minerals Research in Kentucky. Anyone wishing to submit published or unpublished articles, reports, theses, etc., to be included in the bibliography should send them to: Pierre N. Allaire, Dept. of Science and Mathematics, Lees Junior College, Jackson, KY 41339.

Needed: Egg date records for Purple Martins (Progne subis).—Please send date on which each martin pair at colony laid its 1st egg. Age of each pair (adult or subadult) if known and yearly total of martin young raised at colony also would be helpful. If dates represent 2nd nesting attempts or 2nd broods, please indicate. Records for as many years as possible are needed. Each contribution will be acknowledged.—Charles R. Brown, 2601 Turtle Creek Drive, Sherman, Texas 75090.

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THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

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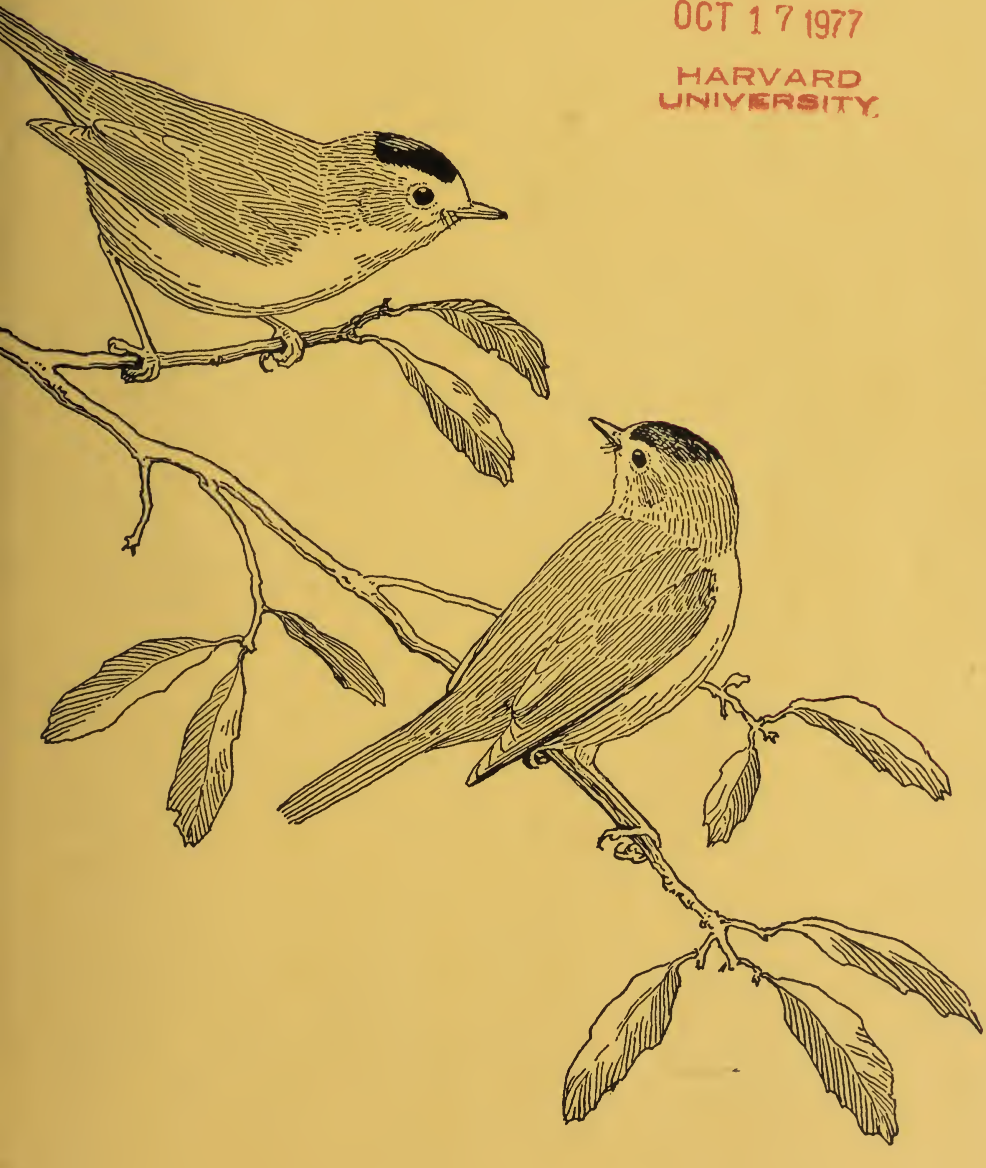

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NESTING HABITAT OF BACHMAN'S WARBLER—A REVIEW

Robert G. Hooper and Paul B. Hamel

Bachman's Warbler (*Vermivora bachmanii*) is on the verge of extinction; no populations are known. Recent systematic searches in widely separated parts of its range failed to locate nesting birds (Stevenson 1972, pers. comm., Hamel et al. 1976). The 2 most recently published sightings were apparently of transient birds as each was seen only once (Imhof 1973, American Ornithologists' Union 1975). Most observations of the bird were made in the late 1800's and early 1900's when little attention was given to habitat. Often habitat descriptions were ambiguous and thus, misleading when considered alone. By comparing the varied descriptions collectively, a clearer conception of the warbler's habitat evolves. Much of the information on the nesting habitat of Bachman's Warbler is unpublished and generally not known to exist. We reviewed published and unpublished descriptions of habitat in order to better identify the most likely breeding areas.

REPORTS OF NESTS

We know of 40 nests of Bachman's Warbler that have been found. Some mention of habitat was made in the account of 32. Eleven of these descriptions were published. The remaining 21 habitat descriptions were found in the field notes of A. T. Wayne which are on file at the Charleston Natural History Museum. We examined Wayne's notes from 1901, when he rediscovered the bird in South Carolina (Wayne 1901), to 1928 when he apparently stopped taking notes. We believe the set of field notes is complete (A. E. Sanders pers. comm.); but, Wayne did not record 3 of the nests in his notes. Observations on the same nest were often made on different days; however, Wayne apparently collected all Bachman's Warbler nests he found and recorded the names of persons to whom he sent them. This information along with radically different habitat descriptions allowed accurate determination of the number of nests located. Wayne found at least 35 nests in I'On Swamp, near Charleston, South Carolina, between 1906 and 1919.

←

Bachman's Warbler (*Vermivora bachmanii*), male above and female below. Watercolor and acrylic painting by Sidney A. Gauthreaux, Jr.

Widmann (1897, 1899) reported 2 nests from Missouri. One nest was reported from Kentucky (Embody 1907) and 2 from Alabama (Holt 1920, Stevenson 1938). A nest from Georgia originally reported as that of Bachman's Warbler (Arnow 1908) was later attributed to Swainson's Warbler (*Limnothlypis swainsonii*) by Wayne (1912). Burleigh (1958) credited the Georgia nest to Bachman's Warbler but we accepted Wayne's judgment. With the exception of records of Barnes (1954), Dawn (1958), and Chamberlain (1958), we disregarded sightings of the bird when a nest was not found. In these cases a male was observed throughout much of the nesting season and was apparently on territory even though presence of a nest or female was not confirmed.

RESULTS AND DISCUSSION

The swamp habitat.—All Bachman's Warbler nests were found in low, wet forested areas. The 35 nests Wayne found in South Carolina were in the headwater swamp and adjacent wet flats of I'On Swamp. The other 5 nests were in bottomland forests along coastal plain rivers. Twelve of the descriptions of nest sites mentioned water, but as water levels fluctuate rapidly in both headwater swamps and bottomlands, the lack of water at other nest sites is of unknown significance. Also, it is possible that Wayne failed to record in his brief notes the proximity of water to some nests.

Descriptions of the overstory vegetation near Bachman's Warbler nests were poor. Wayne (1907) said of the area where his first 6 nests were found, "The trees are chiefly of a deciduous character, such as the cypress, black gum, sweet gum, tupelo, hickory, dogwood, and red oak. In the higher parts of the swamp short-leaf pines [probably *P. taeda*], water oaks, live oaks, and magnolias abound." At least some of the other nests Wayne found were in different parts of I'On Swamp up to 2.4 km from the site of the first nests. However, no further reference was made to the overstory trees. Widmann (1897) described the forests of the St. Francis River basin but failed to associate the site of his nest discovery with any particular forest community. Embody (1907) found, "The tulip tree, sweet and black gums, sycamore, elm and various oaks occur in abundance." He, too, was talking of the bottomland not the actual nest site. Holt (1920) said, "The burn (where the nest was located) was surrounded by the virgin swamp growth of *Pinus taeda*, *Magnolia virginiana*, *Pieris nitida*, *Ilex coriacea*, *Persea* and other hydrophytic vegetation." Stevenson (1938) mentioned that elm (*Ulmus alata*) and cherry (*Prunus serotina*) were near the nest.

I'On Swamp, the headwater swamp where Wayne found 35 nests, is a complex of forest communities. Non-alluvial headwater swamps occur in the interstream areas of the lower coastal plain where poorly developed drainage patterns and depressions impound rainwater and seepage. Wet flats are the better drained areas bordering the swamps (Stubbs 1966). The deep water areas in the headwater swamps are forested with swamp tupelo (*Nyssa sylvatica* var. *biflora*) and bald cypress (*Taxodium distichum*) with almost no understory. Shallower areas support pond cypress (*T. ascendens*) and swamp tupelo with an impoverished understory, again offering little potential for nesting habitat. The next drier zone is forested by the sweet bay (*Magnolia virginiana*)—swamp tupelo—red maple (*Acer rubrum*) association that often has a moderate to dense understory. Slightly drier sites, the wet flats, support sweet gum (*Liquidambar styraciflua*), willow oak (*Quercus phellos*), numerous other hardwoods and scattered loblolly pine (*P. taeda*). Drier sites support other hardwood associations that grade into loblolly pine sites. The driest areas are forested in longleaf pine (*P. palustris*). All of these conditions occur in I'On Swamp. Stands of the sweet bay—swamp tupelo—red maple association and the wet flats seem the most probable areas where Wayne found nests.

Current flood plains, also called first bottoms, are dissected by former stream channels that create sloughs, which are generally the last part of the bottom to dry. Sloughs are forested by bald cypress and water tupelo (*N. aquatica*) stands that, because of the inhibiting effect of long standing water, have poorly developed shrub layers and thus, are probably poor habitat for the warbler. The remainder of the first bottoms and the slightly higher former flood plains or terraces are forested by some 70 species of trees (Putnam et al. 1960) including those listed by Widmann (1897), Embody (1907), Holt (1920), Stevenson (1938), and Barnes (1954). The drier portions of the first bottoms and wetter areas of the terraces seem to best fit the descriptions given by those workers.

It appears that Bachman's Warbler used the portions of the river bottoms and headwater swamps that were inundated for relatively short periods compared to the lowest and wettest areas. The territory in a longleaf—loblolly pine stand (Dawn 1958, Chamberlain 1958) was the most radical deviation from the use of such areas; however, nesting was not determined. In view of all nests being found in swamps and bottomlands, there is little reason to believe that pine stands were of much importance to the bird as nesting habitat.

Seral condition of the overstory.—Only twice was reference made to virgin or primeval condition of the forest (Wayne 1907, Holt 1920). Because the area was surrounded by virgin forest, it is important that the site of the nest Holt (1920) found had undergone disturbance: "The nest was . . . in a small burned-over area covered with a thin, new growth of blackberry briers." Wayne spoke of the primeval swamp in which he worked as having an understory that was "chiefly cane, aquatic bushes, and swamp palmetto, while patches of blackberry brambles and thorny vines are met with at almost every step." The patches of blackberry (*Rubus* spp.) are evidence that disturbance had occurred in the overstory: these are relatively shade intolerant plants that appear to grow best in full sunlight. In hardwood stands, cane (*Arundinaria tecta*) develops into thick patches following disturbance to the overstory (Hughes 1957). In the case of virgin forests, the disturbance to the overstory would have been due to natural mortality of the trees.

The description by Widmann (1897) of the area in which he found a nest also indicated disturbance: ". . . two acres of blackberry brambles . . . medley of half-decayed and lately felled tree tops . . . steaming under a broiling sun. . . ." Stevenson (1938) found a nest ". . . in a thicket between two branches of an unused logging road . . ." indicating an opening in the overstory.

There is no evidence that the swamp where Wayne (1907) found his nests was virgin forest. A study by D. B. Urbston and D. R. Mudge (pers. comm.) of former land use patterns in I'On Swamp indicated only 6% of the swamp hardwood forest was over 30 years old in 1900–1920. The swamp had been cultivated extensively for rice, the practice of which declined rapidly after 1865. Outlines of the former fields show clearly on aerial photographs and dikes are prominent landscape features.

There is evidence that Wayne found some of the nests in abandoned rice fields. The year prior to his initial nest discovery in 1906, Wayne wrote to Brewster (1905), "I have at last found a breeding ground of Bachman's Warbler. The locality . . . is very swampy and was originally a rice field, but is now covered with a dense forest of deciduous trees with innumerable patches of low bushes and blackberry brambles." Of his discoveries in 1906 Wayne (1907) wrote, ". . . I made a special effort to find the nest and eggs of this rare warbler, and knowing that the birds which I had seen and did not molest in 1905 would return to the same swamp to breed the following spring, I determined to devote my entire time with the hope of finding a nest." Thus, Wayne's first 6 nests and several later ones were probably in or on the edge of former rice fields that were undergoing natural reforestation. His statement of primeval swamp most likely referred to the tough working conditions and not to the seral stage of the forest. Although a thinned or sparse overstory is implied, it is not clear what range in tree densities the warbler used.

Understory conditions.—Several species of understory plants were found repeatedly supporting or concealing nests (Table 1). All identified species, with possible exception of supplejack (*Berchemia scandens*) and American

TABLE 1

FREQUENCY OF UNDERSTORY PLANTS IN DESCRIPTIONS OF NEST SITES OF BACHMAN'S WARBLER

Species	Wayne	Widmann	Embody	Holt	Stevenson	Total
Cane	14		1		1	16
Palmetto (*Sabal minor*)[1]	8					8
Gallberry (*Ilex coriacea*)[2]	8					8
Unidentified shrub	6					6
Unidentified vine	3					3
Greenbrier (*Smilax* spp.)	7					7
Blackberry	3	2	1	1	1	8
Grape (*Vitis* spp.)	2				1	3
American holly	1					1
Supplejack	1					1
Fetterbush (*Lyonia lucida*)	1					1
Number of nests	27	2	1	1	1	32

[1] May include *S. palmetto.*
[2] May include *I. glabra.*

holly (*Ilex opaca*), form dense thickets when the overstory is open. As discussed in the previous section, the overstory appeared to be open, and a relatively dense understory was implied. Additional evidence of the density of the understory was given by Wayne who used the terms "dense swamp," "dense thicket" and the like 11 times and mentioned that 4 nests were in a "tangle" of cane and vines. Embody (1907) also referred to a tangle of cane. Holt (1920) found a nest beside a path that had been cut through a blackberry patch. Thus, the idea of a dense understory is reinforced. The mean height of 29 nests was about .6 m and the range .3 to 1.2 m suggests that the understory was dense from near ground level to 1 m or higher. Dense understories are ephemeral, perhaps explaining the disappearance of the bird from known nesting sites in the time when it was still relatively abundant. To us, the range in density of the understory that the warbler used for nesting is one of the largest gaps in knowledge of its habitat.

Another poorly defined factor is the size of the thicket chosen for placement of the nest. Widmann (1897) spoke of a 0.8 ha patch of blackberry but area is difficult to estimate without practice. We have found experienced observers tend to overestimate distance and area in stands with a dense understory. Therefore, we feel Widmann could have overestimated the size of the opening in which he found the nest. The thicket in which Stevenson (1938) found a nest was less than .02 ha. Other records do not shed light on this question.

SUMMARY

Between 1897 and 1919, 40 nests of Bachman's Warbler were found in the Southern Coastal Plain. Thirty-five were in headwater swamps and adjacent wet flats in South Carolina and 5 were in bottomlands along rivers in Missouri, Kentucky and Alabama. From descriptions of nesting habitat at 32 of the sites, it appears the bird used the portions of the bottomlands and headwater swamps that were inundated for relatively short periods compared to the lowest and wettest areas. The sweet bay—swamp tupelo—red maple association of the headwater swamps, the sweetgum—willow oak association of the wet flats and the bottomland hardwoods of the first bottoms and terraces form the complex of plant communities most probably used as nesting habitat. The overstory of areas chosen for nesting appeared to have been subjected to disturbance, either natural or man caused, that stimulated development of a relatively dense understory of shrubs, palmetto, and cane. Many of the nests found in South Carolina could have been in or on the edge of abandoned rice fields that were undergoing secondary succession.

ACKNOWLEDGMENTS

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MORPHOLOGICAL VARIATION IN NORTH AMERICAN PINE GROSBEAKS

Curtis S. Adkisson

The Pine Grosbeak (*Pinicola enucleator*) is a resident of the taiga of North America from Newfoundland to the Bering Sea, and southward in the western mountains to California, Arizona, and New Mexico. Within this range it shows geographic variation in size (Jenks 1938). The breeding range of one population in California and another in the Queen Charlotte Islands are isolated from the other populations. The limits of the forms described from the taiga are only approximately known.

In this paper I present an analysis of morphological geographic variation in this species. In another paper I will describe the geographic variation in calls and songs, and attempt to use data from morphological and vocal variation to draw some conclusions about the patterns of evolution in North American Pine Grosbeaks.

METHODS

I analyzed morphological variation using measurements of 9 characters from study skins: wing length (chord); upper mandible length (distal end of nostril to tip); lower mandible length (1, middle of ramus fork to tip; 2, exposed proximo-lateral notch at the corner of mouth to tip); lower mandible width at widest point; bill depth; tarsus length (outer side of proximal joint to the base of the toes); and tail length (base of the central pair of rectrices to tip of the longest rectrix). Weight was used in the analysis when available from specimen labels.

In addition to these measurements, age, sex, plumage color, and comments of the collector were recorded. Only breeding-season adults were used in the analysis. Those taken before 1 May and after 15 August were excluded on the grounds that they might be migrants.

Data were collected from 487 specimens from throughout the species' range in North America and analyzed with analysis of variance and regression programs written by the Statistical Research Laboratory of the University of Michigan. Regression analysis and scatter plots were used to test for clinal variation. In addition, product-moment correlation coefficients were computed to test for possible concordance in all characters.

RESULTS

Data are presented for 9 morphological characters of birds within the following regions: the taiga from Newfoundland to western Alaska; coastal Alaska; the Queen Charlotte Islands; California; and the Rocky Mountains to northern British Columbia (Fig. 1, Table 2). I subdivided the range of the species to correspond to previously described subspecies' ranges. Each of these regions appeared to contain separate, isolated populations, judging by

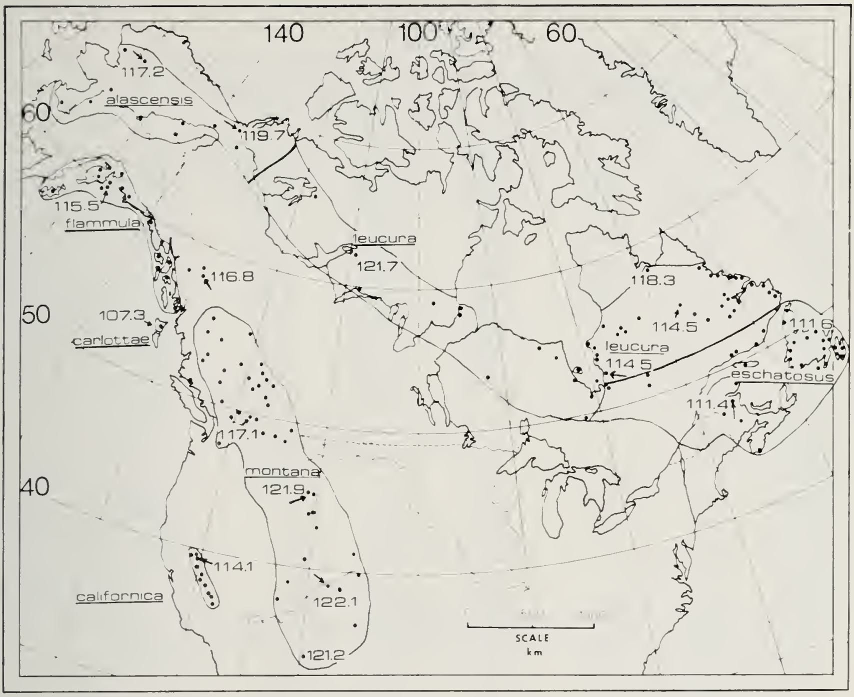

Fig. 1. Map of the breeding range of North American Pine Grosbeaks. Dots indicate localities where birds used in this study were collected. Wing lengths are included for several isolated localities and for certain 2° blocks (arrows point to locality in center of the block). The wing length average for Newfoundland includes 5 neighboring 2° blocks. Subspecific names and ranges (delineated by lines) are from the A.O.U. Check-List (1957).

the literature (Cowan 1939, Rand 1946, A.O.U. 1957) and by the geographic origin of available specimens. In addition I divided the species' range into 2-degree blocks, and computed character means for each block containing 5 or more birds, making it possible to look for trends in variation over large areas. This technique proved of only limited use, since few of the blocks contained enough birds. Wing length means for some blocks are included in Fig. 1.

Analysis of variance for the above regions shows significant geographic variation for all 9 characters (all $p < .0001$). Linear product-moment correlation coefficients of the means of each population indicate that variations in wing and tail lengths are positively correlated, as are the bill measurements. Table 1 gives a correlation matrix for the large Newfoundland sample. Weight data from most areas are unavailable. Only the Rocky Mountain sample has

TABLE 1

CORRELATION MATRIX FOR 8 SIZE CHARACTERS IN PINE GROSBEAKS FROM NEWFOUNDLAND

	Tail	Tarsus	Upper Mand.	Lower Mand. 1	Lower Mand. 2	Mand. Width	Bill Depth
WING	.787***	.111	.149	.220*	.205*	.233*	.176
	(100)[1]	(101)	(98)	(99)	(99)	(99)	(55)
TAIL		.004	.098	.138	.119	.217*	.149
		(100)	(97)	(98)	(98)	(98)	(54)
TARSUS			.104	.031	.105	.215*	.138
			(98)	(99)	(99)	(99)	(55)
UPPER MAND.				.572***	.522***	.314**	.159
				(97)	(97)	(96)	(53)
LOWER MAND. (1)					.697***	.403***	.047
					(97)	(97)	(53)
LOWER MAND. (2)						.268**	.221
						(97)	(54)
MAND. WIDTH							.328**
							(55)

*, **, *** Significance levels for correlation coefficients: .05, .01, .001, respectively.

[1] Sample sizes in parentheses.

a sufficient number of weights for correlation analysis, and in this population weight and wing length are positively correlated ($r = .341$, $n = 31$, $p < .058$).

Pine Grosbeaks vary clinally in the Rocky Mountains and in the taiga. Nevertheless it is useful for comparisons to provide sample statistics, for subregions of the taiga as well as for the other regions, for each of the 4 least correlated size characters used in this study (Table 2). From these data the following generalizations can be made. The longest bills are found in coastal Alaska, the shortest in the Alaskan taiga. The narrowest bills are found in the California population followed by those of the eastern taiga and the Queen Charlottes. Bill depth and width are greatest in the taiga west of Hudson Bay and least in California and the Queen Charlottes. Wing length is greatest in the western taiga and the Rocky Mountains, and least in the Queen Charlottes and eastern Maritime provinces. The tarsus is longest in coastal Alaska birds, closely followed by that of some birds from the taiga and Rocky Mountains, and is the shortest in birds from the Queen Charlottes. The populations of the Maritime provinces, California, Queen Charlottes, and coastal Alaska are all very distinct. Birds from the coast of Alaska in turn can be distinguished from those of the interior region using all size characters except bill width and depth.

TABLE 2

PINE GROSBEAK SIZE DATA FOR 8 NORTH AMERICAN REGIONS

	Wing Length (ad. males) (mm)			Tarsus length (mm)		
	N	x̄	S.D.	N	x̄	S.D.
Maritime Provinces	70	111.68	2.298	134	22.30	0.600
Labrador Peninsula	31	115.16	3.072	73	22.51	0.780
Taiga, Ont. to NWT	17	119.57	3.305	40	22.50	0.630
Alaskan Taiga	16	118.66	2.673	24	22.37	0.712
Coastal Alaska	6	115.23	2.331	25	22.54	0.803
Rocky Mountains	56	118.00	3.395	124	22.44	0.802
Queen Char. Islands	7	107.53	3.333	23	21.39	0.706
California	15	114.19	1.354	30	22.08	0.821

	Upper Mand. Length			Lower Mand. Width		
	N	x̄	S.D.	N	x̄	S.D.
Maritime Provinces	130	11.37	0.484	132	9.35	0.340
Labrador Peninsula	73	11.40	0.505	70	9.78	0.340
Taiga, Ont. to NWT	40	11.69	0.647	37	10.04	0.369
Alaskan Taiga	25	10.96	0.622	25	10.19	0.318
Coastal Alaska	25	12.08	0.544	25	10.14	0.353
Rocky Mountains	124	11.83	0.633	122	9.66	0.307
Queen Char. Islands	22	11.36	0.402	22	9.50	0.286
California	29	11.45	0.418	28	8.70	0.352

The most interesting patterns of variation occur in specimens from the taiga from Newfoundland to western Alaska, and the northern Rocky Mountains. Birds taken from the Maritime provinces and the Gaspé Peninsula of Quebec form a homogeneous population for each of the size characters. Comparison of 2° block means from this area shows no differences. Wing length of birds from this area is among the smallest for the species. However, on the Labrador Peninsula small birds indistinguishable from those of Newfoundland, and much larger birds, have been collected. The largest and smallest adult males differ in wing length by 15%. Most of the birds taken on the Labrador Peninsula north of about 54°N are inseparable from those of the taiga population west of Hudson Bay, while most of those taken from near the St. Lawrence River to about 52°N are inseparable from Maritime provinces birds. Regressions on latitude for wing and tail lengths in adult males are significant ($p < .001$). Figure 2 reveals no evidence of discontinuities in the cline of wing length in the Labrador Peninsula sample. There is no well-defined pattern of variation in other size characters, nor is there any east-west variation in the birds of the Maritimes, Labrador, and Quebec.

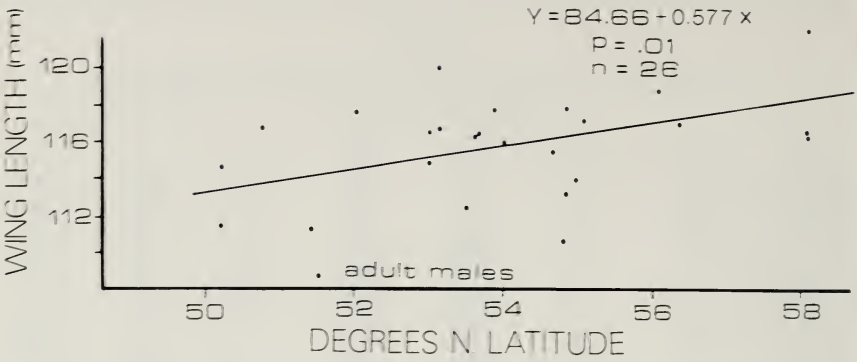

FIG. 2. Plot of wing length on latitude in Quebec and Labrador.

West of Hudson Bay, the Pine Grosbeaks are among the largest in this species. The region from Moosonee, Ontario, to Great Slave Lake is poorly collected, but a trend toward larger body size appears to begin in northwestern Ontario (Ft. Albany). The longest-winged birds were taken near Great Slave Lake (110°W), and from there to western Alaska (160°W), there is a trend toward shorter wings. While there is little variation in tarsus and bill width measurements, regressions of wing length, and bill length and depth on longitude from Great Slave Lake to western Alaska are significant ($p < .05$, $p < .001$). Figure 3 contains plots of wing length and bill length on longitude. The change in bill length in the western half of the taiga is on the order of 10%. There is less than 3% change in bill depth and wing length. Thus, birds taken along the Kobuk River in western Alaska average shorter bills ($p < .05$) than birds taken at Great Slave Lake, but many intermediate birds have been taken between these localities.

Pine Grosbeaks of the Rocky Mountain region also show clinal variation. Regression of size characters on latitude for the entire Rocky Mountain region revealed decreasing size northward in wing, tail, and tarsus lengths, and in bill length, width, and depth. Figure 4 contains plots of wing (adult males), tarsus, and upper mandible lengths, and lower mandible width on latitude. The wing length cline appears not to be a simple linear function, since it levels out around 48°N. Within B.C. there is little change in wing length, and bill width and depth increase slightly (slopes not significant) to the north. Specimens from the southwestern localities in B.C. (Lytton, Lillouet, Rossland) have shorter wings than are found anywhere else in the Rocky Mountain region (Fig. 4, specimens with wing lengths < 116.0 mm, 48°–51°N).

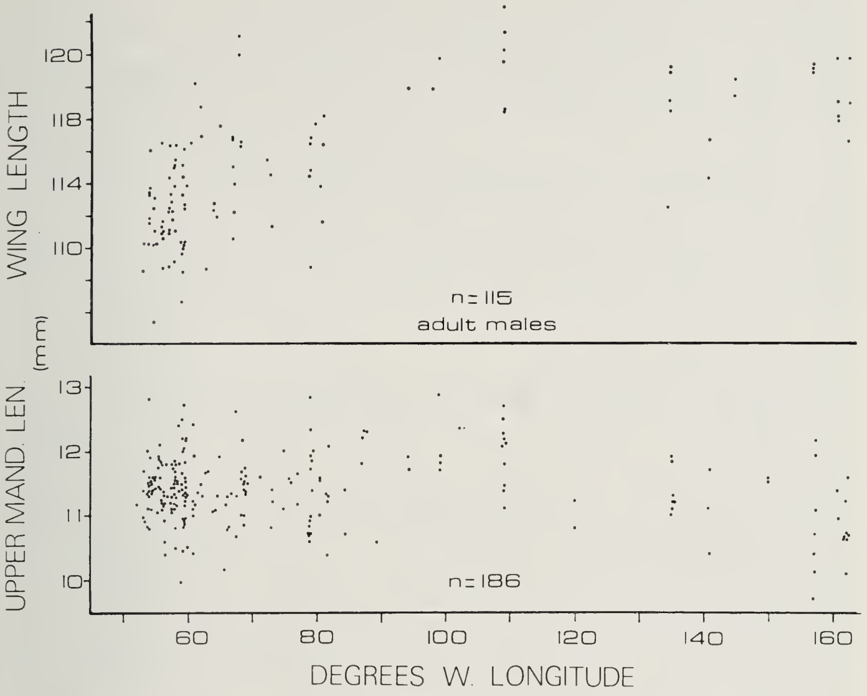

FIG. 3. Plots of wing length and upper mandible length on longitude in the taiga from Newfoundland to Alaska.

The northern part of British Columbia presents an especially interesting problem since Pine Grosbeaks appear (Fig. 1) to breed from the montane region throughout coastal Alaska. Five birds taken along the Stikine River near Telegraph Creek were reported (Swarth 1922) to resemble those of coastal Alaska. These specimens are indeed inseparable from birds taken on Chichagof Island or in Prince William Sound, and differ from recent specimens from Dease Lake, just 60 km to the east, in having shorter wings, longer bills, and darker plumage. Similarly, birds from Cassiar and Dease Lake differ from coastal Alaska birds in having longer wings ($p < .01$, $n = 21$ females and gray males) and shorter bills ($p < .001$, $n = 33$ of both sexes). As stated above, Cassiar area birds do not differ significantly in any of the size measurements from birds collected in the southern half of B.C. and Alberta.

Age and sex variation.—There is secondary sexual dimorphism in size in all populations examined. Analysis of variance for size characters in Maritime

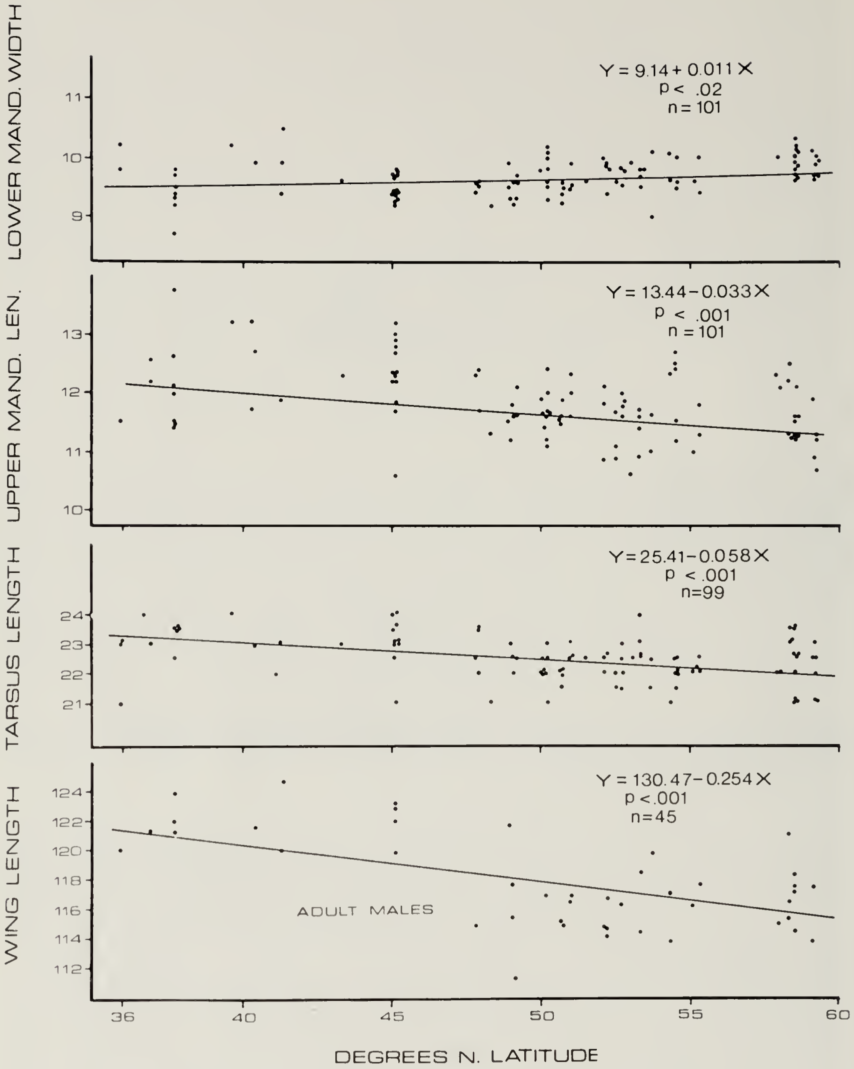

FIG. 4. Plots of wing length, tarsus length, upper mandible length, and lower mandible width on latitude in the Rocky Mountains, New Mexico to northern British Columbia.

provinces birds, the largest sample in this study, showed that of 8 skin characters, adult males and females differed only in wing and tail lengths. In the U.S. Rocky Mountains sample, which contains weight data adequate for comparisons, males were consistently heavier than females ($p < .01$, $n = 26$).

Age and sex variation in plumage color is well known in this species. Adult males have red body plumage, and first year males are usually indistinguishable from females in possessing gray body color with yellow crown and rump. In addition, a few gray males and females of unknown age have bronze or reddish crown and rump color.

In addition, there is a pronounced age dimorphism among males. First year, gray-plumaged males have shorter wings and tails than adult red males ($p < .001, n = 97$) by an average of 3% in the Maritime sample. There are no differences in the other characters. Other regions, though less well sampled, are similar in this respect. Thus yearling males and females are very similar in all characters.

Geographic variation in plumage color.—Adult male body color within each population is highly variable, and is sufficient to swamp out differences claimed by Todd (1963) and others to exist between most continental populations. For example, a sample of 56 adult males from Newfoundland varied in color between yellowish-orange and dark red. I have noticed similar variation in wild birds of the taiga and Rocky Mountains. Pine Grosbeaks molt in August and September and sometimes disperse immediately toward the wintering grounds. Adult male specimens taken in fall and winter in Quebec, Ontario, Michigan, and the Great Plains are decidedly pinker than those collected anywhere on the breeding grounds. Microscopic examination of feathers shows that the difference in hue arises from wear of the pigmentless barbules at the tips of the red feathers. Attempts to establish the subspecific identity of winter specimens using plumage color (Gabrielson and Jewett 1940, Jewett et al. 1953) apparently failed to take feather wear into account.

There are, however, 2 populations in which this plumage is consistently distinctive. On the Queen Charlotte Islands males are a dark brick red in contrast to the lighter carmine red of most populations. In males from the Alaska panhandle, the plumage contains more orange than is found in that of interior Alaska birds. Curiously, adult males from Anchorage and the Kenai Peninsula, otherwise similar to Alaska panhandle birds, have red plumage similar to Rocky Mountain and taiga birds (5 specimens, pers. observ. in the field, and photographs). In addition, adult males from California appear to have more orange in their plumage than is found in males from most other regions. Average population differences in hue of red among the populations might be revealed with spectographic techniques, but hue of red can be of limited use in identifying the origin and population affinities of a given specimen.

As noted, female and first-year male plumages are very similar within all populations, but Queen Charlotte Islands and coastal Alaska birds of this plumage are also distinctive. In the former there is a pronounced olive-green cast to the plumage, and in the latter, except in Kenai Peninsula birds, the gray is much darker than in the interior population. Microscopic examination of individual feathers from these populations showed that dark gray feathers have more pigment granules in the barbules. The greenish cast in the plumage of Queen Charlottes birds is due to the presence of a pale yellow pigment in the feather barbs, and in males the darker red is the result of a concentration of a dark pigment in the barbules at the feather tips. In other populations there is no pigmentation in these barbules.

DISCUSSION

The Pine Grosbeaks of the taiga vary clinally, but unevenly. Throughout the Maritime provinces the birds are uniform in size and proportions. North of the St. Lawrence River the only change is toward larger body size (longer wings and tail) in the north. Both Griscom (1934) and Todd (1963) insisted on the occurrence of 2 distinct populations, *P. e. leucura* and *P. e. eschatosus* in the Labrador Peninsula, despite Austin's (1932) observation that the birds merely increase gradually in size to the north. I examined specimens seen by previous workers, and many more collected since 1950, and agree with Austin that it is impossible to separate birds of the region into 2 populations. Todd (1963) argued that the southern limit of the large grosbeaks extended from the Straits of Belle Isle to southern James Bay, a boundary fitting closely the one between dense boreal forest and the sparse transitional zone between forest and tundra described by Rowe (1957). In the absence of breaks in the body size cline, however, any effect of this described difference in the forest on Pine Grosbeaks is at best hypothetical. Either of 2 explanations may account for the observed clinal change in body size: natural selection has favored greater body size in the north, or there is secondary contact between previously isolated populations, with considerable intergradation in this region. In the latter case, small birds adapted to thick boreal forest may have invaded the peninsula from the south and east, with large birds moving from the northwest around James Bay to occupy sparse forest in northern Quebec and Labrador. That body size also appears to increase over the same latitudinal range to the northwest, between James Bay and Great Slave Lake, supports the former explanation. Variation in vocalizations, to be discussed in another paper, is consistent with a theory of 2 colonizations of the peninsula after the last glacial recession (Adkisson 1972).

As noted above, only wing length varies in the poorly-collected region between James Bay and Churchill, Manitoba, increasing to the west. Between the central taiga (95° to 115°W) and the Mackenzie delta, wing length increases, but varies little further to the west. Over this region bills become notably shorter. This region is so poorly collected that one cannot determine how gradually or abruptly these changes occur. From a taxonomic point of view, it is interesting that the cline for smaller bodies and shorter bills is first noticeable well within the described range of *P. e. leucura.*

Both of the clines of increasing wing length of taiga Pine Grosbeaks begin in northern Ontario and Quebec near the tip of James Bay. But the clinal decrease in bill length to the northwest is not repeated to the north on the Labrador Peninsula. In both examples, clinal variation in this measure of body size is consistent with Bergmann's rule, and the trend for shorter bills to the northwest, with Allen's rule. Indeed, colder average January temperatures (1945 to 1971) are found to the west in Canada (Ottawa, –10.9°C; Moosonee, Ont., –20.2°; Churchill, Man., –27.6°; Yellowknife, NWT, –28.6°; Aklavik, NWT, –32.1°; Hare and Thomas 1974). Fort Yukon, Alaska, averaged –28.1°C for January between 1931 and 1952 (U.S. Weather Bureau 1953). The lack of bill variation in the northeastern taiga is consistent with data indicating that winters are milder here than in the Northwest. For example, the January mean temperature at Sydney, N.S., is –4.4°; at Natashquan and Quebec, P.Q., –11.8°; at Goose Bay, Labrador, –16.3°; and at Ft. Chimo, P.Q., –23.4°. Thus, winters are colder to the north in the Labrador Peninsula, but not as cold as in the Northwest Territories (Hare and Thomas 1974). The decrease in wing length between Great Slave Lake and Alaska similarly implies a milder climate, yet the shortest bills are found in the westernmost populations, and winters in interior Alaska are similar to those at Yellowknife, NWT.

Clinal variation in the Rocky Mountains may have a different explanation. Clines of decreasing weight, and wing, tail, and tarsus lengths approximately parallel the decreasing altitudes toward the north at which the preferred Pine Grosbeak habitat is found. In Colorado and southern Utah, Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) occur between 2400 m and tree line at about 3000 m. The birds, in my experience, are most abundant above 2500 m in moist valleys, and on forested mesas. All New Mexico specimens were taken at 2500 m or above. At Togwatee Pass in northwestern Wyoming, I found the birds to be common at 2100 m to 2300 m. In Alberta, at Banff National Park, I found grosbeaks at 1500 m near Moraine Lake. Specimens from central and northern B.C. were taken at less than 1000 m.

While the trend of decreasing wing length to the north is uneven, the data points apparently not fitting a sample linear regression on latitude (Fig. 4), there is a strong association with breeding locality altitude. Those Rocky Mountain specimens with altitude data show a strong positive correlation with altitude for weight, and wing, tail, tarsus, and bill lengths (all $p < .02$). Wing length and altitude are correlated in a sample of 31 females and young males ($r = .7522$, $p < .001$) and 19 adult males ($r = .6695$, $p < .001$) from this region.

For intraspecific comparisons wing length tends to become greater at higher altitudes (Hamilton 1961, James 1970). Two prevalent theories seek to explain this effect: cold winter temperatures would favor larger bodies for heat conservation (in the original sense of Bergmann's rule; see James' discussion); and reduced air pressure selects for greater wing surface (Moreau 1960). James (1970), however, showed that wing length in 8 species of birds is most highly correlated with wet bulb temperatures, which combine both temperature and humidity effects. James points out that the known increase in evaporative water loss at higher altitudes could account for altitudinal changes in bird bodies. My own data support her argument. I have no data on winter temperature in grosbeak habitats in the Rocky Mountains, nor do I know exactly where the birds winter, but I suggest that the altitudinal limit of the spruce-fir forest is related to climate, and that Pine Grosbeaks in this forest throughout the Rockies face similar weather conditions. The most parsimonious explanation for the association of body size and altitude is that increased evaporative water loss at higher altitudes selects for larger bodies at all seasons. Analysis of measurements from other sedentary Rocky Mountain species, and of weather from high altitude localities, would help clarify further the relationship between altitude and body size in homeotherms.

In the other isolated western populations, there is no evidence of intrapopulation variation. In California, for example, there is no hint of latitudinal variation in the north-south oriented Sierra Nevada. It is possible, however, that larger samples from more localities could reveal some variation. The morphology of California birds bears no obvious relation to trends in populations from the Rocky Mountains or elsewhere. Rocky Mountain birds are at least 10% larger than any California birds, and the narrowness and shallowness of the bill in California birds is unique within this species. If California birds were more widespread we might find variation as in Rocky Mountain birds, but they are apparently largely restricted to the red fir (*Abies magnifica*) forest (ca. 1700 m) over a distance of 500 km in the Sierra Nevada, mainly on the western slope (Ray 1912, pers. obs.). In 1970 I observed at least 6 pairs near Devil's Postpile National Monument (Madera

Co.) for 10 days. In a mixed forest of red fir, Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*P. contorta*), I found the birds virtually ignoring the pines, only perching in them occasionally, while using the firs constantly for food, nesting, and during maintenance activities. There are no spruces in the range of the California form (Little 1971). In view of its unique bill proportions, a comparison of its food habits with those of other populations seems justified. In summary, therefore, it is not possible now to predict or fabricate its morphology by extending any known cline from any other part of the species' range. My preliminary explanation for the small size of this form, by comparison with Rocky Mountain birds, is that it is found at much lower elevations, at similar latitudes, in a generally warmer mountain range.

Similarly, the Queen Charlotte population is morphologically homogenous, and seems isolated in its own unique environment. With the exception of one winter specimen from southwestern B.C., no grosbeaks of the nearby mainland approach Queen Charlotte birds in any characteristic, nor are there known clines, which if extended, could predict its extreme smallness and darkness. Newfoundland birds, also occupying a cold, moist island habitat, approach the size of Queen Charlotte birds, but less than 10% of a sex or age class are as small, and none is as dark. In spite of reports that "*carlottae*" breeds on the mainland and Vancouver Island (Rand 1943), the specimens ($n = 3$) on which these speculations are based fall within the color and size ranges of Alaska panhandle birds, and may be birds that bred following a winter irruption.

In forested coastal Alaska, many areas where the birds should occur have never been sampled, and sample sizes from several localities are small. However, there is no evidence of intraregional variation. Nor is there evidence of continuous distribution and clinal variation between (1) coastal and interior Alaska north of the Alaska Range, and (2) coastal Alaska and interior B.C. Swarth's (1922) birds from Telegraph Creek, B.C., may represent either an unusual occurrence or possibly a logical extension of the breeding range of *flammula*. In the latter case, at most 40 km would separate 2 very different populations, as I noted earlier. Possibly there is introgression in this region, but in the absence of specimens I suggest that coastal Alaska and northern B.C. birds have allopatric ranges.

In light of the known morphological variation in Pine Grosbeaks, past confusion over the subspecific identity of birds collected in winter (see comments and citations in Sutton 1948) is understandable. In most years there is a limited movement to the south from the taiga. In nearly all winters they are common around Canadian cities and in northern New England

(Godfrey 1966, Forbush 1927). At irregular intervals they move south in large numbers as far as New Jersey, Ohio, and Kansas, but not all populations irrupt in the same winter. There is little concordance between northeastern and northwestern irruptions. Support for this statement has appeared in many issues of American Birds. For example, in the winter of 1973–74 the northwestern U.S. and British Columbia experienced an irruption of unprecedented size, while the birds were scarce in the central provinces and in the northeast (Arbib 1974). Montane populations apparently undergo only a slight altitudinal migration. In California, Pine Grosbeaks have never been recorded outside the Sierra Nevada (Grinnell and Miller 1944), and in Colorado they are seldom seen below the limits of pine forest (Bailey and Niedrach 1965). Specimens of Pine Grosbeaks taken in winter in Kansas and Missouri have been referred to the taiga form, *P. e. leucura* (Ely 1961, Rising 1965).

In order to understand more fully the movements of this species, specimens and tape recordings should be obtained from every irruption. A combination of morphological and vocal characters should make it possible to determine the approximate geographic origin of the birds in most instances (Adkisson, unpublished data).

Even if trinomial classification is retained as a convenience, defining the limits of the subspecies is arbitrary in many cases (Mayr 1963, Simpson 1961: see also discussion in Lidicker 1962). Whether or not one believes subspecies to be incipient species, to recognize them where there is neither isolation nor evidence of discontinuous variation serves neither taxonomy nor evolutionary biology. I follow Mayr (1963) in allowing subspecific distinction for any isolated population differing in certain morphological characters from others. The geographical isolates of *P. enucleator* considered here already have this status. I attempted to apply the 97% rule (Amadon 1949) and found that single-character comparisons among the isolates failed. In fact, only the longest-winged (western taiga) and shortest-winged (Queen Charlotte Islands) populations can be separated using the formulas in Amadon's paper. However, I find that specimens of each of the isolates can easily be identified using all characteristics described in this paper. I have less success separating all specimens of the Rocky Mountain and taiga populations in this way.

Each of the isolates possesses a unique combination of characteristics. The western-most ones (*californica*, *carlottae*, and *flammula*), occupy relatively small ranges, and I detect no intrapopulation variation (except color of adult males in *flammula*). Rocky Mountain birds (*montana*) are clinally variable, and there appears to be a hiatus in range between northern B.C. and central

Yukon Territory and Alaska. In my opinion, each of these 4 populations should continue to have subspecific status.

In the taiga, however, the birds appear to occur continuously from coast to coast. *P. e. alascensis* was originally separated from other taiga grosbeaks mainly on the basis of a shorter bill and larger body (Ridgway 1898). However, I have shown that these characters vary clinally in the taiga, and recommend that *alascensis* be considered a synonym of *leucura*.

P. e. eschatosus, described on the basis of small size (Oberholser 1914), can be applied to birds from the Maritime provinces of Canada. But equally small birds also occur in southern Quebec, and from there to tree line, wing and tail lengths increase gradually. On this basis I suggest that *eschatosus* be synonymized into *leucura* also. I prefer to adopt the system of Owen (1963) in which clinal variation is acknowledged, as opposed to arbitrary subspecific categories.

Accordingly, *P. e. leucura* should be applied to all Pine Grosbeaks in the taiga, from Newfoundland to western Alaska. Future checklists should contain a note on its variation, in the manner described in Owen's paper. We thus recognize that, in the absence of geographical barriers, regional variation in selection pressures can give rise to continuous morphological variation, and the different characters need not vary concordantly. In fact, *montana*, recognized since 1898, is nearly as variable as the newly-defined *leucura*. The distinctiveness of *flammula, carlottae, montana*, and *californica* may be related to their being set apart in apparently different environments.

SUMMARY

There is significant morphological variation in North American Pine Grosbeaks. Variation in wing length and bill length in birds of the taiga is clinal. Beginning in the southern Labrador Peninsula, body size increases to the north and to the northwest. Variation in all characters is clinal in the Rockies. Body size becomes smaller to the north, and is highly correlated with the altitude of breeding localities. There is no evidence of clinal variation elsewhere.

The largest birds occur in the taiga of northern Quebec and Labrador, and west of Hudson Bay to western Alaska, and in the southern Rocky Mountains. Small birds occur in the Canadian Maritime provinces, and in California, but the smallest are in the Queen Charlotte Islands. Bills of western taiga birds are short, deep, and wide, especially in comparison with the long, wide bills of coastal Alaska birds, and the extremely narrow bills of California birds.

It is suggested that there is no basis for the recognition of 3 subspecies in the taiga, and that one name, *P. e. leucura*, should be applied to the clinally variable, continuously distributed form.

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BREEDING SUCCESS AND NEST SITE CHARACTERISTICS OF THE RED-WINGED BLACKBIRD

Donald F. Caccamise

In many species of birds the process of nest site selection results in a general consistency in the qualitative characteristics of the nest site within particular habitats. It would seem that such consistency would have developed through a depression in reproductive success in those individuals acquiring nest sites of somewhat inferior quality. Within the normal range of nest site characteristics individuals acquiring nest sites with particularly advantageous characteristics or combinations of characteristics would be more successful reproductively than individuals not acquiring such sites. Selection would operate to maximize reproductive output by optimizing the nest site selection process.

The purpose of this study was to identify potentially important nest site characteristics of a species, to quantify these, and then to assess the relationships between these characteristics and reproductive success.

I selected Red-winged Blackbirds (*Agelaius phoeniceus*) for this study because: (1) their nesting habits provide a broad range of nest site characteristics which can be quantified; (2) they are colonial, thereby providing large numbers of nests within relatively small areas; (3) there is a considerable body of literature available on this species.

STUDY SITE AND METHODS

The study site was on a tidal salt marsh in southern Ocean County, New Jersey. Typically on these marshes, the lower elevations are dominated by 2 grasses (*Spartina alterniflora, S. patens*) which form expansive stands interrupted only by numerous potholes and creeks. At successively higher elevations, with concomitantly less tidal inundation, 3 shrub species appear that are used for nesting by Red-wings. These are, in order of increasing elevation, *Iva frutescens* (marsh elder), *Baccharis halimifolia* (sea myrtle), *Myrica pensylvanica* (bayberry). These shrubs generally are transitional between the low grass dominated marsh and the higher tree dominated upland areas. The study tract was along a dead end road that extends about 7 km onto the marsh. Because soil was added to the marsh surface in order to construct the road, this narrow strip of land is at a slightly higher elevation than the surrounding marsh. This increased elevation provides suitable habitat for the establishment of dense shrub stands along the edges of the road. It is in these roadside shrubs that the Red-wings nest.

I located, numbered, and subsequently observed nests through the course of the nesting season. Surveys were conducted on alternate days from 15 May–25 July 1973, with changes in nest conditions or contents assigned to the day intermediate to the visits. Nest site characteristics for each nest were measured following fledging of the young. These included nest height, total vegetation height at the nest, vegetation height

TABLE 1

COMPARISONS OF MEAN NEST SITE CHARACTERISTICS AMONG PLANT SPECIES USED AS NEST SUBSTRATE

Nest site characteristic	*Baccharis halimifolia* (78)[1]	*Iva frutescens* (106)	*Myrica pensylvanica* (13)
Vegetation height (cm)	179 (3.0)[2]	165 (2.2)	243 (7.5)
Nest height (cm)	135 (3.3)	112 (2.0)	182 (7.0)
Vegetation cover (cm)	44 (1.4)	54 (1.7)	61 (7.0)
% Cover	76.4 (1.57)	68.6 (1.27)	84.1 (4.50)

[1] Sample size.
[2] Standard error.

above the nest (vegetation cover) and distance to the nearest neighboring Red-wing nest. Since none of the nests was built in emergent aquatic vegetation, height measurements were made from ground level. To quantify the density of the vegetation over each nest I photographed the sky directly above the nest from the nest height using a 50 mm lens on a 135 mm single lens reflex camera. The negatives were projected onto a grid of 10 vertical and 10 horizontal lines. The 100 points resulting from the intersection of these lines composed the sample. The percentage of the total points covered by images of vegetation was taken as an index of vegetation density over the nest and is hereafter referred to as the percent cover. This process was repeated twice (each from opposite sides of the nest) for each nest with the mean value taken as the best estimate. Nest sites were mapped on aerial photographs of the study site and these were used to construct an index of nest density. For this I drew a circle including 1810 m^2 centered around each nest and used the number of nests included within that circle as the index. Because a number of nests and/or the supporting vegetation were lost or damaged before nest site characteristics could be measured, some nests could not be included in the analyses. The Student's *t*-test was used to analyze the results.

RESULTS

Breeding success and nest site characteristics.—Measurements of nest site characteristics are summarized in Table 1. These data are separated according to the plant species in which the nests were located. Comparisons among plant species for each nest site characteristic were significant in all but 2 cases. These exceptions occurred in vegetation cover between *Iva* and *Myrica*, and in percent cover between *Myrica* and *Baccharis*. Both comparisons involved *Myrica* for which there was a relatively small sample. In comparing the 3 plant species used as nest substrate, the relative magnitudes were the same for both vegetation height and nest height. The vegetation cover over the nest for the shortest shrub, *Iva frutescens*, was statistically indistinguishable from the tallest shrub, *Myrica pensylvanica*, but it was statistically greater than the intermediate shrub, *Baccharis halimifolia*. The percent cover for *Iva frutescens* was significantly less than the other 2 plant species which were not significantly different from each other. In *Iva*, which

Table 2

Breeding Success Relative to Nest Height

	Nest height (cm)										
	<100	100–109	110–119	120–129	130–139	140–149	150–159	160–179	180–199	>199	Total
No. nests	15	21	23	22	15	14	9	5	8	4	136
No. eggs	47	61	72	69	45	44	28	17	28	14	425
No. hatched	39	46	53	55	36	26	19	12	17	8	311
Hatched/egg	0.83	0.75	0.74	0.80	0.80	0.59	0.68	0.71	0.61	0.57	0.73
No. fledged	24	28	28	34	25	17	14	9	9	4	192
Fledged/hatched	0.62	0.61	0.53	0.62	0.69	0.65	0.74	0.75	0.53	0.50	0.62
No. successful nests	10	11	13	15	12	8	6	3	5	2	85
% successful	0.67	0.52	0.56	0.68	0.80	0.57	0.67	0.60	0.62	0.50	0.62

provides the least dense vegetation cover, nests were constructed further from the surface of the plant and closer to the ground than were nests in the other 2 shrubs.

I compared the relative levels of breeding success among nests in these 3 shrub species. There were no significant differences in clutch size, brood size, nor the number of young fledged per nest. Notwithstanding the rather distinctive nest site characteristics of the 3 shrub species used as nest substrate, there was no evidence that breeding success was related directly to any of these differences.

Nests were categorized according to the magnitude of each measured nest site characteristic. Ratios of the number of young hatched to the number of eggs laid (H/E) and the number of young fledged to the number of young hatched (F/H) within each category were used as an index to breeding success.

In Table 2 these indices along with the constituent data are presented relative to the height of the nest above the ground. There was a general decrease in the H/E ratio with increasing nest height. The F/H ratio increased steadily from the lower nest heights to the 160–179 cm nest height category after which breeding success decreased. A linear regression of the H/E ratio to nest height was significant (Fig. 1a); however, a simple relationship was not apparent for F/H ratio versus nest height (Fig. 1e).

The H/E ratio and vegetation height (Table 3) were negatively correlated indicating a general decline in hatching success with increasing vegetation height (Fig. 1b). There was, however, no obvious relationship between the F/H ratio and vegetation height (Fig. 1f).

Direct relationships between percent nest cover and nest density and the H/E and F/H ratios were not evident (Fig. 1c, d, g, h).

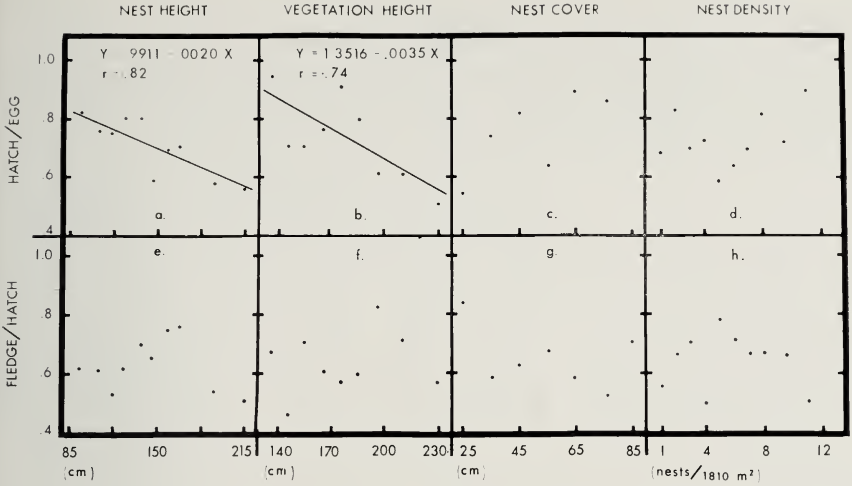

FIG. 1. Relationships between hatching and fledging success and nest site characteristics.

Mortality and nest site characteristics.—The 3 greatest sources of mortality to eggs and nestlings during this study were predation, abandonment, and death-in-nest (Caccamise 1976). Predation includes losses of both eggs and nestlings. Losses ascribed to abandonment include nest desertion and also apparent abandonment resulting from death of the adult. Losses from death-in-nest represent primarily nestling starvation, although a small percentage of losses in this category likely result from sources such as overcrowding

TABLE 3

BREEDING SUCCESS RELATIVE TO VEGETATION HEIGHT AT THE NEST

	Vegetation height (cm)									
	<140	140–149	150–159	160–169	170–179	180–189	190–199	200–219	>219	Total
No. nests	7	11	20	19	27	14	9	12	17	136
No. eggs	22	34	57	60	90	37	28	40	57	425
No. hatched	21	24	40	45	83	29	17	24	28	311
Hatched/egg	0.95	0.71	0.70	0.75	0.92	0.78	0.61	0.60	0.49	0.73
No. fledged	14	11	29	27	47	17	14	17	16	192
Fledged/hatched	0.67	0.46	0.72	0.60	0.57	0.59	0.82	0.71	0.57	0.62
No. successful nests	5	5	14	10	19	9	6	8	9	85
% successful	0.71	0.45	0.70	0.53	0.70	0.64	0.67	0.67	0.53	0.62

TABLE 4

Comparisons of Mean Nest Site Characteristics Among Nests Incurring Mortality (M) and Nests Not Incurring Mortality (S) From the 3 Greatest Sources of Nesting Mortality

	Sources of Mortality								
	Abandonment			Death-in-nest			Predation		
Nest Site Characteristics	M(31)[1]		S(135)	M(48)		S(64)	M(39)		S(97)
Nest height (cm)	120	N.S.[2]	127	128	N.S.	123	136	N.S.	126
Vegetation height (cm)	174	N.S.	176	174	N.S.	176	185	*	173
Vegetation cover (cm)	53	N.S.	50	48	N.S.	50	50	N.S.	50
% Cover	72.7	N.S.	72.7	70.0	N.S.	70.5	75.5	N.S.	72.5
Distance to nearest nest (m)	15.3	N.S.	17.8	12.4	*	19.7	21.7	N.S.	16.4
Nest density (nests/1810 m^2)	4.8	N.S.	4.1	5.0	*	3.6	4.0	N.S.	4.2

[1] Sample size.

[2] Level of significance attained using Student's *t*-test; N.S. not significant; * significant at the 0.05 level.

and/or nest eviction. Since death-in-nest refers only to nestlings, those nests which did not successfully hatch young were not included in these comparisons.

For each nest site characteristic I compared nests incurring losses with those nests not incurring losses from each source of mortality (Table 4). Analyses indicated that nests incurring losses attributed to the death-in-nest category were characterized by a significantly smaller mean distance to the nearest nest and a significantly greater nest density. Also nests with losses to predators were in shrubs significantly taller than nests without such losses. None of the other comparisons were significant.

DISCUSSION

For the Red-winged Blackbird there have been many attempts to relate nest site characteristics to various measures of breeding success (Meanley and Webb 1963, Goddard and Board 1967, Holcomb and Twiest 1968, Robertson 1972, Holm 1973). In reanalyzing the nest height data from several of these studies and others, Francis (1971) found that some of the differences in breeding success, as related to nest height, were in fact not significant. He further suggested that the greater nesting success reported by Holcomb and Twiest (1968) in the higher nests, although significant, may have been related to differences in nest substrate rather than nest height.

In my study, nest site characteristics differed markedly for nests placed in the 3 plant species used as nest substrate. Additionally, as there were differences in the occurrence of the 3 shrub species according to the marsh elevation, the nests in these shrubs also reflected the differences in habitat distribution among the shrubs. However there were no detectable differences in breeding success among nests located in the 3 different plant species. Therefore it would seem that the differences in nest site characteristics specifically related to the differences in growth form among these plant species did not directly affect breeding success.

It is not clear why hatching success (H/E) decreased with increasing nest height and with increasing shrub height. Since nests incurring losses to predators were located in shrubs significantly taller than nests not receiving such losses (Table 4), it would appear that the nests in tall shrubs were more susceptible to losses to predators. While predation was not the only factor contributing to the differential hatching success, differences in predation pressure probably were important.

The reasons why relationships similar to those for hatching success did not apply between fledgling success (F/H) and nest height or vegetation height are obscure. However there is a major difference between eggs and nestlings in that eggs exhibit no behavior while nestlings do. Thus nestling behavior could affect predation as well as other sources of mortality.

Both measures of nest density indicated that nests incurring losses in the death-in-nest category were in areas of significantly greater nest density than nests not incurring such losses. In the current study the manifestation of nestling starvation was similar to descriptions of Red-wing nestling starvation appearing in the literature (Robertson 1973). Often starvation was noted initially when a nestling appeared somewhat smaller than its siblings, showing an increasing size disparity over a period of several days and eventually either disappearing or being found dead in the bottom of the nest.

At my study site territories of 1 to several females were maintained along the road borders in the dense stands of shrubs. Most foraging was done off the territories often along the numerous creeks and potholes common in the grass dominated areas of the marsh. It seems unlikely that the greater indices of nest density for nests incurring mortality from nestling starvation (Table 4) were related to overexploitation of food resources in high density areas. This is because the distance between areas of high nest density and low nest density was generally small compared to what might be considered the potential range in which a female could effectively forage. Orians (1961) pointed out that the amount of food obtained by a female on the territory is inversely related to the size of the territory; however, he also suggests that "it is doubtful whether food *per se* is the *proximate* factor by which territory size is regulated." Since nest dispersion at my study site was a linear array of nesting clumps along the road margin, each female had access to a large area of undefended marsh in which to forage. Considering the very large size of the foraging area relative to the number of Red-winged Blackbirds in this colony, it seems unlikely that food abundance would be significantly reduced only in the foraging areas used by females from areas of high nest density.

Alternatively, the one factor that always increases directly with nest density is the potential for intraspecific interactions in the vicinity of the nest. In areas of high nest density there would be considerable opportunity for such interactions while in areas of low nest density there would be very little opportunity. Female Red-winged Blackbirds, when in polygamous associations with a single male, will defend territories within the male's territory (Nero 1956; Nero and Emlen 1951). Thereby they exert an active role in determining the number of females able to breed in a specific territory (Orians 1961, Holm 1973).

Robertson's results (1973), indicating similar levels of starvation between low density upland areas and high density marsh areas, could be interpreted as mitigating against the possible role of aggression in nestling starvation. However, his results are based on averages over separate colonies or groups of colonies. Because these broad comparisons were designed to contrast habitat differences they ignore variations between individual nests. Such individual nest site characterizations are the basis for my study.

Since aggressive interactions between females seem to fill an important role in the mating system of the Red-winged Blackbird, excessive levels of aggression in areas of high nest density could impair the female's ability to nourish her young. Whether this would be sufficient to increase nestling starvation is open to conjuncture. However, the contribution of intraspecific aggression in determining breeding success certainly merits further study.

SUMMARY

Breeding success was assessed and nest site characteristics were measured in a colony of Red-winged Blackbirds nesting on a tidal salt marsh. Breeding success was not directly related to the plant species used as nest substrate, vegetation height over the nest, or density of cover over the nest. However, negative correlations were found between hatching success and both nest height and height of the shrub used as nest substrate. Nests incurring losses from nestling starvation were characterized as being in areas of significantly greater nest density than nests not incurring such losses. Also significant differences were evident in vegetation height between nests incurring predation and nests not incurring predation.

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FORAGING BEHAVIOR OF THE EASTERN BLUEBIRD

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Avian foraging behavior is known to vary intraspecifically with habitat (Root 1967), weather (Lunk 1962:15), season (Ligon 1973), prey availability (Morton 1967), and from one population to another (Ligon 1968). Few studies, however, have examined the variety of factors influencing predatory behavior of a single species. I found the Eastern Bluebird (*Sialia sialis*) a good subject for such an investigation because this species forages in relatively open areas and is conspicuous from a distance. Moreover, bluebirds employ a variety of foraging tactics (Bent 1949:247) but typically use a lookout perch to locate prey on the ground (Preston and McCormick 1948, Krieg 1971); several parameters of the perch-feeding technique (perch height, predator-to-prey distance) can easily be quantified. In this paper I describe predatory behavior in the Eastern Bluebird and examine the effects of several environmental variables on bluebird foraging.

METHODS

Study area.—Observations were made in Macomb Co., southeastern Michigan (42°48′N, 82°59′W) during 1972 and 1973. The bluebird nesting period extended from late March to early August (Pinkowski 1975a) and most observations were made during the nesting season. Fifty nest boxes were available in the study area and bluebirds nested in these as well as in natural cavities (Pinkowski 1976a). In Michigan most bluebirds migrate south in winter; spring migrants first appear in early March with a peak arrival period occurring between 20 March and 20 April.

Six pairs of bluebirds were randomly observed at all times of the day, under all types of weather conditions, and in various stages of the nesting cycle. The bluebirds foraged in old fields (Fig. 1) characterized by hawkweed (*Hieracium* sp.), vetch (*Vicia* sp.), sheep sorrel (*Rumex acetosella*), goats-beard (*Tragopogon major*), cinquefoil (*Potentilla* sp.), daisy fleabane (*Erigeron philadelphicus*), oxeye daisy (*Chrysanthemum leucanthemum*), and various grasses. This is a low-growing, perennial sere that appears late in field succession in Michigan (Beckwith 1954). Common foraging perches were tree limbs and branches (especially if dead or defoliated, with oaks, *Quercus* sp., commonly employed), fence posts, boulders, and coarse weed stalks such as mullein (*Verbascum* sp.) and evening-primrose (*Oenothera* sp.). Foraging bluebirds were watched from a distance without disturbance and the presence of an observer did not alter their behavior in any way (cf. Krieg 1971:5).

Measurements.—Several parameters were measured on a foraging sequence, including the type of foraging tactic employed. A short "drop" to the ground (the "flydown" described for *S. sialis* by Goldman 1975) was most common. Measurements made on feeding drops were: perch height (vertical distance of the bird above the ground), drop base (ground level distance from a point immediately below the take-off perch to the landing location), hypotenuse of the resulting triangle (predator-to-prey distance), and

FIG. 1. View showing the old field flora with scattered trees and shrubs in the southeastern Michigan study area.

distance between consecutive feeding perches (measured for birds moving along fencerows having predetermined distances between fence posts). Not all perches resulted in the bird locating prey and not all drops resulted in prey capture. A perch was considered successful if a drop was made from it (prey was sighted but not necessarily captured) and a drop was considered successful if food was obtained. The latter was often impossible to determine with certainty, especially if small prey were pursued.

Each observation period lasted 1–2 h. Temperature was recorded in the field at the beginning and end of each observation period and the average value was assumed for all observations made during the period. Percentage of sunshine was obtained for each observation period by noting the proportion of time that shadows were cast. Wind speed could not be measured by instrument because the birds often foraged in valleys or behind wind breaks where wind speed was quite different than elsewhere. I estimated wind speed at a foraging site according to the effect of wind on feeding perches and foraging bluebirds. Light winds were those not causing noticeable movement of perches (tree limbs and weed stalks) and approximated actual speeds up to 5 km/h. Moderate winds (5 to 20–30 km/h) caused perch movement but did not interfere with foraging. Strong winds (over 20–30 km/h) caused at least some perches to move rapidly and be unacceptable as lookout posts.

Statistical procedures.—Percentages were examined for significant differences by a t-test for the equality of percentages (Sokal and Rohlf 1969:607). I follow Verbeek (1975) in defining feeding tactic diversity (FTD) by the formula $FTD = -\sum_i p_i \ln p_i$, where p_i is the proportion of feeding involving the i^{th} feeding tactic. Unless otherwise stated, Chi-square tests on contingency tables employ Yates correction for continuity with d.f. = 1.

RESULTS AND DISCUSSION

Description of foraging tactics.—*Dropping* is the principal feeding mode of the bluebird. The ground is searched from a conspicuous perch and after locating prey, the bird sallies onto the ground and seizes its prey with the bill. Rarely is more than one food item obtained on a single drop to the ground. The food may be swallowed on the ground or brought to a perch for preparation and ingestion, but it is never held with the feet during capture and preparation. Only 21.7% of 189 small (< 1 cm long) food items were taken to a perch before ingestion compared to 88.5% of 43 large (> 2 cm long) food items. These percentages differ significantly ($t = 10.3, P < 0.001$).

Hunting bluebirds normally search the ground while perched upright. During inclement weather and more intensive feeding the head is lowered and the tail elevated. If low perches are not available bluebirds may perch horizontally part way up tree trunks or weed stalks to view the ground. When close to the ground bluebirds often turn the head and use monocular vision to search the ground. Binocular vision is frequently employed at relatively great heights. By changing perches when no food source is found, the bird is able to encounter a large number of possible foraging situations.

Flycatching involves capturing aerial insects by short flights into the air from a perch (usually the "new perch-short flight" pattern; Leck 1971), by more extended flights ("new perch-long flight"), or by seizing aerial prey without taking flight. I found that more than one item may be obtained per flight, and several aerial insects were fed to nestlings after a single flight, but Marshall (1957) and Krieg (1971) reported that only one item was captured per flight. Flycatching may temporarily become the only foraging tactic, as on summer evenings when aerial insects are highly visible in the long-angled sunlight (Morton 1967), after a rain, or at other times when certain prey species (e.g., swarming carpenter ants, *Camponotus* sp.) are abundant.

Gleaning occurs when the bird lands on and removes prey from the foliage and branches of trees or shrubs, or the main trunks of trees. Verbeek (1975), working with tyrannid flycatchers, defined gleaning as "capture of an insect sitting on any kind of substrate"; here, "gleaning" excludes prey capture on the ground. In early summer bluebirds glean small caterpillars (e.g., geometrids and pierids) from the leaves of trees. Many hymenopterans, dipterans, coleopterans, and plecopterans (see Pinkowski 1976b) are obtained from tree trunks by gleaning.

Flight-gleaning is a modification of the dropping tactic and has been described for kingbirds (*Tyrannus* sp.) by Smith (1966:219). The bird descends toward the ground after locating prey, but remains in flight while plucking prey from vegetation. It may flutter briefly while inspecting the prey, but it never does so before locating an item; this sets flight-gleaning apart from *hovering*, a search method observed in Mountain Bluebirds (*S. currucoides*) by Criddle (1927), Power (1966), and Pinkowski (1975b) but not observed in Eastern Bluebirds during this study. Flight-gleaning is employed in areas of tall weeds and therefore becomes more common as the season advances and vegetation height increases.

Hopping is not a common feeding mode. Except for flycatching (new perch-long flight), it is the only foraging tactic wherein the prey is not located from a conspicuous perch. When feeding by this method a bluebird moves along the ground and feeds upon prey that is encountered after it lands on the ground. Hopping is limited to roadways, recently plowed farmlands, lawns, burnt areas, and other disturbed habitats that have few perches and sparse ground cover.

Of 2638 foraging sequences observed during March through June, 78.8% were accomplished by the dropping mode, a slightly lower percentage than that (87.4%) observed by Goldman (1975) for bluebirds feeding on lawns in Ohio. Flycatching and gleaning were more common foraging tactics (10.7% and 6.8%, respectively) than hopping (2.6%) and drop-gleaning (1.1%).

Feeding on fruit.—Beal (1915) found that up to 57.6% of the diet of *S. sialis* may consist of fruit during winter. I noted that bluebirds rely heavily on fruit sources in late summer and immediately after their arrival in early spring. Staghorn sumac (*Rhus typhina*) and multiflora rose (*Rosa multiflora*) are the common fruits eaten in spring. Honeysuckle (*Lonicera* sp.), cherry (*Prunus* sp.), and mulberry (*Morus* sp.) are eaten in summer.

Three distinct methods of obtaining fruit are employed; a bluebird may (1) hover in the air while ingesting berries (analogous to and employing the same motor patterns as flight-gleaning); (2) perch on a limb and pluck berries from an adjacent limb (similar to gleaning); or (3) perch on a fruit head (e.g., staghorn sumac) and pluck fruit from directly beneath its feet (not unlike securing animal prey on the ground after a drop).

Feeding tactics and season.—Although the relative frequencies of feeding tactics used by Eastern Bluebirds vary during the nesting period, dropping is the principal tactic employed in all seasons (Table 1). Frequency of the

TABLE 1

SEASONAL VARIATION IN FEEDING TACTICS OF EASTERN BLUEBIRDS IN SOUTHEASTERN MICHIGAN, 1972–1973[a]

	Percentage Occurrence			
	March (N=584)	April (N=595)	May (N=770)	June (N=689)
Dropping	99.5	86.6	88.6	43.8
Flycatching	0.4	9.4[b]	5.6	26.3
Gleaning	0.1	0.4	1.2	24.2
Hopping	0.0	3.7	3.9	2.4
Drop-gleaning	0.0	0.0	0.8	3.4

[a] Based on 12 birds.
[b] Most records (35 of 56) obtained during one observation.

dropping tactic decreases in summer as vegetation height increases. A sparse ground cover is required for effective feeding by bluebirds using the dropping mode. After the breeding period bluebirds regularly hunted on mowed lawns around residences adjacent to the study area and evidently preferred such places to undisturbed areas containing tall vegetation.

Feeding tactic diversity is lowest in March (FTD = 0.034), is higher in April and May (0.491 and 0.487, respectively), and increases markedly in June (1.261). The increase in diversity is the result of more aerial feeding late in the season as food resources are increasingly exploited in a third (vertical) dimension. Willson (1974) characterized the Eastern Bluebird as an insectivore that feeds by sallying in the low vegetation stratum (a member of the "insectivore, low, sally" guild; see Root 1967). In spring "insectivore, ground, ground glean" adequately describes the species, but by the end of summer much fruit is consumed and "omnivore, low, sally" is probably more accurate.

Feeding modes and weather.—Feeding tactics were found to vary in frequency according to weather conditions. Of 89 feedings recorded in May and June during exceptionally cold (0–10°C), cloudy, and rainy or damp weather, 64 (71.9%) were accomplished by the dropping mode. A nearly identical percentage of dropping mode sequences was observed for the same period during warm (15–25°C), sunny, favorable weather (72.2%, N = 251). Flycatching was more common during favorable weather (14.7%) than during inclement weather (1.2%, $t = 2.2$, $P < 0.05$) whereas the reverse was true for gleaning (20.2% and 7.9% for inclement and favorable weather, respectively; $t = 2.0$, $P < 0.05$).

Flycatching is not a common feeding mode during excessively windy conditions, probably because aerial insects are reduced in number at these

TABLE 2

SEASONAL VARIATION IN FORAGING MEASUREMENTS OF EASTERN BLUEBIRDS IN SOUTHEASTERN MICHIGAN, 1972–1973[a]

	Spring Mean ± SD	Summer Mean ± SD
Base (m)	3.22 ± 1.85	7.04 ± 5.71
Height (m)	2.02 ± 1.09	3.76 ± 2.43
Predator-prey Distance (m)	3.97 ± 1.88	8.26 ± 5.81

[a] Values obtained by triangulations on the dropping tactic based on 12 birds with $N = 100$ for each period. The means of each measurement are significantly different ($P < 0.001$, Mann-Whitney U-test).

times (Freeman 1945). In May and June flycatching accounted for only 2.0% ($N = 99$) of all foraging sequences during strong winds, a significantly smaller percentage ($t = 2.2$, $P < 0.05$) than that observed during moderate or light winds (13.6%, $N = 1360$). Thus seasonal changes in foraging tactics are similar to weather-mediated responses in that flycatching is employed more often during favorable (warm, sunny, and calm) weather and as the season advances. Presumably more aerial insects are available in favorable weather and later in the season.

Factors influencing foraging height.—Measurements were made on 100 bluebird drops randomly observed in the early spring (15 March to 15 April) and 100 in the early summer (15 May to 15 June) to examine factors influencing foraging height and predator-to-prey distances. Each sample was evenly divided between males and females.

Bluebirds forage closer to the ground and consume prey located nearer to their perches in spring than in summer (Table 2). Seasonal variation in foraging height may be attributable to smaller, fewer, or less active vernal insects that are more difficult to detect at greater heights. Also, as noted above, more aerial feeding occurs in summer and the birds may adjust their foraging heights accordingly. As a consequence of the greater foraging area that each perch affords in summer, fewer perches are required later in the season. Bluebirds inhabit more open habitats during summer than spring, perhaps because of a reduced dependence on perches as the season progresses.

Pooled data for the spring and summer periods show positive regression when drop base (B) is plotted on foraging height (H) according to the relationship $B = 1.17 + 1.20H$ (measurements in m). The slope of the regression differs significantly from 0 ($F = 76.2$, $P << 0.001$, $r^2 = 0.28$), indicating that bluebirds search areas more distant from the perch when foraging at greater heights. Evidently the area searched (the "perceptual field"; Holling 1966, Salt 1967) more closely approximates a narrow annulus rather than all of the area within a circle as might be expected, and increases in length (L) according to the relationship $L = 2\pi B = 7.4 + 7.5H$.

The significant relationship between foraging height and drop base also suggests that the search angle A, defined here as $A = \tan^{-1} B/H$, remains relatively constant. In spring and summer the search angle averages 58° ($\tan^{-1}$ 3.22/2.02; Table 2) and 62° ($\tan^{-1}$ 7.04/3.76), respectively. Over the normal range of foraging heights (1–10 m) the search angle varies from 67° ($\tan^{-1}$ 2.37/1) to 53° ($\tan^{-1}$ 13.17/10) and is surprisingly constant in view of the wide range of foraging heights and bases. Deviations from the mean search angle may occur because of the deviations from the upright posture normally assumed by perch-feeding bluebirds, different head positions relative to the body (particularly as related to monocular or binocular viewing of the ground), or different perch inclinations relative to the ground.

Positive correlations exist between foraging height and temperature ($r = 0.42$, $P < 0.01$) and between height and sunshine percentage ($r = 0.17$, $P < 0.05$). Lunk (1962:15) found that Rough-winged Swallows (*Stelgidopteryx ruficollis*) feed close to the ground in cool, cloudy weather, and attributed this to prey response to these weather conditions. Increased sunshine increases insect movement (Gangwere 1966), but also may enhance the visual ability of avian predators because of greater illumination. Low temperatures often occur on cloudy days, however, and it is difficult to separate the effects of sunshine and temperature on foraging behavior.

No relationship was found when mean foraging heights were compared for the various wind speed categories (single factor ANOVA test, $F = 1.1$, $d.f. = 2/197$, $P > 0.5$).

Males and females of the same species are known to partition the feeding niche by foraging at different heights (Jackson 1970). A *t*-test, however, revealed no significant differences in the foraging heights ($t = 0.8$, $P > 0.5$) and drop bases ($t = 0.4$, $P > 0.5$) of male and female bluebirds.

Predator-to-prey distances were great for both males and females. Among males the maximum height recorded was 14.6 m, the maximum base was 28.3 m, and the maximum predator-to-prey distance was 29.0 m (measurements from 2 drops). A female dropped from a height of 10.7 m onto a 48.8 m base to obtain prey 50.0 m away. The distances from which prey were sighted were remarkable considering the small size of many of the insects involved.

Perch use.—Early in the season prey are not always encountered when the ground is searched and uninterrupted bouts of continuous feeding are frequent. Observations during March and April 1972 indicated that "perch success" (the ratio of the number of perches from which a drop is executed to the total number of different perches used) was significantly lower during March (76 of 140 perches successful, 54.2%) than April (502 of 702 perches successful, 71.5%; $\chi^2 = 15.3$, $P < 0.01$). In only 3 of 28 observation periods was perch success lower than 50.0%; all occurred in March and the lowest figure observed was 31.9%. After early May bluebirds rarely failed to locate prey from a perch and alternated feeding with other activities except when feeding nestlings.

Bluebirds foraging during March and April returned to the same perch after a drop on 83 of 568 occasions (14.6%). After hunting from an unsuccessful perch, bluebirds moved to a higher perch (as opposed to one distinctly lower) 50.0% of the time during March ($N = 34$), 68.3% during early April ($N = 41$), and 76.9% of the time during late April ($N = 26$). The trend to move to a higher perch later in spring is significant according to a test for a linear trend in proportions (Snedecor and Cochran 1967:246, $z = 2.2$, $P < 0.05$) and may occur because of increased availability of aerial prey that are searched for if prey is not located on the ground. In late spring, however, insects are more active and prey movement is less critical in the birds' ability to locate prey. Also, by late April most bluebirds are nesting and may exhibit greater selectivity in prey consumed. Possibly a greater variety of insects can be searched for at greater heights.

Time between drops during bouts of continuous feeding averaged 46.7 sec during March and April ($N = 61$), with a maximum of 186 sec. Time spent on a successful perch before a drop was made averaged 23.3 sec ($N = 291$) and was less during inclement weather conditions ($\bar{x} = 20.0$ sec, $N = 103$) than during favorable conditions ($\bar{x} = 25.2$ sec, $N = 188$); the means differ significantly ($t = 2.2$, $P < 0.05$). Time spent on unsuccessful perches before the bird moved to a new perch averaged 27.2 sec but was significantly less during inclement weather (22.7 sec, $N = 162$) than during favorable weather (34.5 sec, $N = 102$; $t = 4.6$, $P < 0.01$). Thus inclement weather imposes greater energy demands on the bird by necessitating more frequent movements (more perch changes and more drop attempts). Fewer insects are active during inclement conditions and reduced prey availability and activity evidently cause the birds to forage closer to the ground, thereby reducing the perceptual field because of the relatively constant search angle. A smaller area can presumably be searched more rapidly than a larger area.

Distances traveled by birds moving from an unsuccessful perch to a new perch averaged 7.6 m ($SD = 7.9$ m, $N = 132$) and were significantly greater (Mann-Whitney U-test, $P < 0.001$) than the average distance of 4.1 m ($SD = 5.5$, $N = 211$) traveled by birds foraging from a successful perch, based on observations made during March and April. The mean distance traveled when moving from an unsuccessful perch is 18.0% greater than twice the average drop base observed in the spring period (Table 2), indicating that the birds move only slightly more than the minimum distance required to afford them a completely new perceptual field. By contrast, birds leaving successful perches move only 63.7% of twice the average drop base and thus search successive areas that overlap. The tendencies for bluebirds to move shorter distances and search successively overlapping areas after foraging from successful perches are similar to the findings of Smith and Sweatman (1974), who noted that Great and Blue tits (*Parus major* and *P. caerulus*) were more likely to return to previous capture sites when food was encountered.

No differences were found when distances traveled in leaving successful and unsuccessful perches were compared for males and females ($P > 0.3$ in each case).

I found that pairs of bluebirds exhibited great differences in the relative sizes of areas used for foraging during the nestling period. Ten foraging ranges were examined in spring 1972 to determine the effect of perch abundance on the size of the foraging area. Although the size range of an entire foraging area was surprisingly large (4.5–38.9 ha), the size of the area containing perches was relatively constant (3.9–8.4 ha). The variances of the 2 sets of measurements (91.4 and 2.2, respectively) are significantly different ($F = 41.5$, $P < 0.01$), suggesting that perch distribution may influence territory size.

Factors limiting bluebird abundance.—Although the absence of nest cavities may limit the number of Eastern Bluebirds (Pinkowski 1976a), the availability of perches may also be an important limiting factor in some ecological situations. Habitats having few or no perches are rarely used by Eastern Bluebirds; these areas elevate the energy demands imposed on foraging birds by necessitating more prolonged flights as the birds move from one foraging situation to another.

Several aspects of this study suggested that the feeding requirements of bluebirds are stricter in spring than summer. The bluebirds I observed experienced little difficulty in obtaining food in summer and used a greater variety of habitats at that season. Of 39 nest boxes used by bluebirds at one time or another, 23 were used in spring compared to 37 in summer. The difference in use frequency for the 2 seasons is significant ($\chi^2 = 12.2$, $P < 0.001$) and appears related to the fact that foraging heights are less in spring and more perches are required at that season. In Michigan temperatures below

5–8°C are common until late May and, when accompanied by overcast conditions, inhibit bluebirds from feeding on insects. Interestingly, most records of severe bluebird mortality in "winter" (Musselman 1941, Kenaga 1958) actually refer to extensive mortality in early spring (late February to early April).

Optimum conditions for bluebirds occur in areas containing an abundance of dead trees and limbs that are used as nest cavities and as foraging perches. Poor soil and a sparse ground cover help create ideal feeding conditions.

SUMMARY

Eastern Bluebird foraging behavior was studied in southeastern Michigan during 1972 and 1973. Bluebirds seize most prey after a short flight ("drop") to the ground from a conspicuous perch. Other foraging tactics that may be used are flycatching, gleaning, flight-gleaning, and hopping. Frequencies of various feeding modes depend on season and weather, although dropping comprised 78.8% of the foraging sequences observed under all conditions. The base of a feeding drop increases with foraging height, suggesting a relatively constant search angle.

Prey is usually located from a perch before it is pursued and habitats having a short, sparse ground cover are preferred by feeding bluebirds. Foraging height is greater in summer and during favorable, warm weather than in spring or cold, inclement weather. Bluebirds travel shorter distances to new perches if prey is sighted from the previous perch than if prey is not sighted. Males and females exhibit no differences in temporal and spatial use of perches. Perch abundance, however, influences the size of the area required by adults feeding nestlings and may be a factor limiting the distribution of bluebirds, especially in spring.

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COMPARATIVE FEEDING BEHAVIOR OF IMMATURE AND ADULT HERRING GULLS

Nicolaas A. M. Verbeek

Many birds do not breed until they are 2 or more years old. Such delayed breeding is generally found among large, long-lived, non-passerine species. Lack (1954) suggested that delayed breeding has probably evolved in species in which reproduction at an earlier age would not be likely to succeed or might be harmful to the parents. Ashmole (1963) and Amadon (1964) suggested that young birds might be unable to catch food as efficiently as adults do. Recently, a number of field studies have shown that the ability to obtain food improves with age (see Buckley and Buckley 1974 for references). Given the inefficiency, it might be expected that the young have to compensate somehow for their lack of success, e.g. by spending more time in feeding. The object of this study was first to establish feeding efficiency in young and adult Herring Gulls (*Larus argentatus*), which show delayed breeding, and then to see how the young make up for any inefficiencies.

The study was made on Walney Island, Cumbria, England, in 1973 and 1974. Herring Gulls and Lesser Black-backed Gulls (*L. fuscus*) breed on the southern end of the island. The colony is very dependent on nearby food sources such as the large intertidal areas of Morecambe Bay and a garbage dump on the island.

METHODS

At low water during spring tides extensive mussel (*Mytilus edulis*) beds are exposed in Morecambe Bay. Associated with the mussels is the common starfish (*Asterias rubens*). Large numbers of Herring Gulls of all age classes fed upon these starfishes. Because of the distance between my observation post and the nearest beds (ca. 400 m) I could only distinguish (I used a 20–45 × zoom scope) between adults and immature birds (all those showing brown feathers). The immatures included birds at least 1 year old and older. The exact number of birds under observation is unknown as birds arrived and left continuously. At any one time approximately 50 birds were present, mainly adults. The gulls fed on starfishes (not mussels) by plunge diving for them, sometimes disappearing completely under water. Both immatures and adults fed in the same water apparently under similar conditions and in similar places. When I saw a gull diving I recorded whether it was successful (emerging with a starfish) or unsuccessful, and what the subsequent fate of the starfish was. Because the period when starfishes were available was short (about 2 hours) and infrequent (only during spring tides), I recorded as many dives as possible (different birds) rather than watching individuals over a period of time. Under these circumstances I could not obtain information on diving rates. Neither was it feasible to obtain meaningful information on the size of the starfishes taken. The data were collected during 25 hours between 3 and 21 April 1973.

On 5 and 6 April 1974, Hans Kruuk and I watched Herring and Lesser Black-backed gulls feeding at low tide on the crab, *Hyas araneus.* Gulls that managed to get a crab were often pursued by others in aerial chases. On both days we counted all the gulls feeding in a small bay, and the proportion of the various age classes represented. For each chase we recorded the number, the species, and the age classes participating as pursuers as well as the age class and the species of the pursued bird. In addition we noted whether the pursued bird lost its prey, and if possible, which pursuer obtained it. We distinguished between first-year-birds (brown young of the previous year), subadults (those showing a mixture of first-year and adult coloration), and adults. Subadult Lesser Black-backed Gulls were not seen in the general area of the colony until 19 April. We therefore assumed that all first-year-birds and subadults in our sample were Herring Gulls. In the analysis, chases in which one or more Lesser Black-backed Gulls pursued another of their species were not included. I did include those Lesser Black-backed Gulls that were chased by Herring Gulls and those that chased jointly with Herring Gulls.

On 3 occasions at low water during spring tides an assistant and I counted all the gulls feeding in Morecambe Bay. The counts were made when the birds returned to the colony. We sat on the shore between the colony and the mussel beds and each of us counted the gulls that flew through his half of the sky. After 15 min I recorded our scores and the counting began anew. This was repeated until almost all gulls had returned to the colony.

RESULTS

Adult Herring Gulls were more successful in catching a starfish on the first dive (18 [64%] out of 28 dives) than immatures (3 [16%] out of 19 dives). These results are significantly different ($\chi^2 = 8.16$, d.f. 1, $P < 0.01$). This has been shown too for the Brown Pelican (*Pelicanus occidentalis*) (Orians 1969) and the Sandwich Tern (*Sterna sandvicensis*) (Dunn 1972), but not for the adult and juvenile Royal Tern (*S. maxima*) (Buckley and Buckley 1974).

Following a successful dive many starfishes were dropped in being brought up from the bottom, or in flight during transport from the water to the land. The gulls often did not attempt to retrieve these starfishes, perhaps because they fell in deep water. Many others were stolen when a diving gull surfaced or while it was being pursued in flight. In cases where they were not pursued in flight, adult Herring Gulls ($N = 28$) dropped 3 out of 28 starfishes, while immatures ($N = 6$) dropped 3 out of 6. These results are not significantly different ($P = 0.053$, Fisher exact probability test). Immature Royal Terns drop significantly more fish than adults do (Buckley and Buckley 1974), and Dunn (1972) suggests the same for Sandwich Terns.

On the mussel beds a gull could lose its starfish when supplanted, when occupied defending a starfish by long-calling (Tinbergen 1959), or when a third bird took it while the owner was busy chasing another gull. The proportion of starfishes eaten versus those not eaten (Table 1) by adult and immature birds is not significantly different ($\chi^2 = 1.65$, d.f. 1, $P > 0.05$). I

TABLE 1

DIFFERENCES BETWEEN ADULT AND IMMATURE HERRING GULLS IN THE FATE OF A STARFISH ONCE IT IS CAUGHT BY DIVING

Fate of starfish	Adult Herring Gull	Immature Herring Gull
Eaten	28 (36%)	1 (10%)
Dropped	26 (33%)	4 (40%)
Stolen	23 (30%)	4 (40%)
Abandoned	1 (1%)	1 (10%)

think that this is only because my sample for the immatures is small (Table 1). I gathered data only on those birds that were actually seen to dive. Many cases where birds were seen to be feeding on the beds without my knowing how they had obtained their starfish in the first place, went unrecorded. I gained the impression from these additional observations that young birds were more prone to have their starfish stolen than adults.

Many gulls feed in Morecambe Bay at low water during spring tides. For instance, on 20 April we counted 20,473 gulls returning to the colony. In Fig. 1A this count is plotted in relation to low tide. Similar counts were made on 3 May (19,142 gulls) and 4 July (20,304 gulls). Considering the short time that the mussel beds are exposed it is doubtful that any of these gulls had enough time to make more than 1 trip. Each of the 3 curves in Fig. 1A has a major and a minor peak. The medians of any 2 curves in Fig. 1A are not significantly different.

During preliminary counts prior to 20 April I had noticed that adult Lesser Black-backed Gulls and immatures tended to return to the colony later in relation to low tide than did adult Herring Gulls. To analyze this I counted the proportion of immatures in 500 gulls of both species that flew past me. Once 500 gulls had been counted I repeated the procedure until almost all gulls had returned to the colony. For each 500 gulls I recorded the period over which the count was obtained and the midpoint of the period was entered in Fig. 1B. The same procedure was used to obtain a curve (not shown) for the proportion of adult Lesser Black-backed Gulls among all gulls returning to the colony. I used this information to analyze the species and age composition of the returning birds. For instance, the curve of 20 April (Fig. 1A) is redrawn in Fig. 1C. Clearly, the minor peaks (Fig. 1A) referred to earlier are the result of the later return of Lesser Black-backed Gulls, and immatures of both species.

In an aerial chase a bird carrying a crab could be pursued by 1 to 9 other gulls. Although relatively few first-year-birds were present, they participated

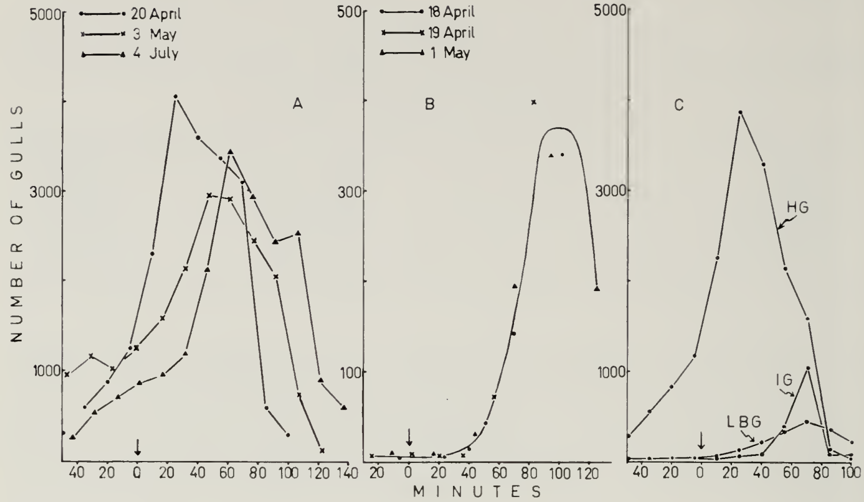

FIG. 1. Number of gulls returning from the mussel beds to the colony plotted in relation to low tide (↓). (A) Each point on the graph is placed in the middle of a 15-min period and indicates the number of all gulls returning during that time span. (B) The number of immature Herring and Lesser Black-backed gulls per 500 gulls of all ages counted for each point on the graph. (C) Adult Herring Gulls (HG), adult Lesser Black-backed Gulls (LBG), and immature gulls (IG) of both species. See text for further explanation.

in many more chases per bird than adult Herring Gulls (Table 2). Of the 82 recorded chases, 67 involved 1 or more of the 39 immatures present. Of the 111 adult Herring Gulls 1 or more participated in only 24 chases. Comparing the number of successful pursuers (i.e. those birds that managed to obtain the prey from the bird they were pursuing) with the number of birds involved as pursuers (Table 2), all 3 age classes of Herring Gulls scored equally well ($\chi^2 = 0.982$, d.f. 2, $P > 0.05$).

Per bird, adult Herring Gulls were pursued significantly less than immature birds ($\chi^2 = 25.31$, d.f. 1, $P < 0.001$). All 3 age classes of the Herring Gull were equally successful in keeping their catch while being pursued ($\chi^2 = 0.39$, d.f. 1, $P > 0.05$).

DISCUSSION

Herring Gulls feed on a variety of foods in diverse places, including the intertidal, harbors, fields, and garbage dumps. The kinds of food obtained there require different types and degrees of skill. Starfishes are an important source of food as judged by the many birds that catch them and by the

TABLE 2

AERIAL CHASES IN A KNOWN NUMBER OF HERRING GULLS AND THE FREQUENCY WITH WHICH EACH AGE CLASS IS PURSUED AND TAKES PART AS PURSUER

		Pursuing birds			Pursued birds		
Age class	No. of birds present	No. of times pursued	No. of times pursued/ birds present	Successful pursued bird[1]	No. of times involved as pursuer	No. of pursuits/ birds present	No. of successful pursuers[2]
First year	10	15	1.5	11	31	3.1	5
Subadult	29	21	.7	14	70	2.4	8
Adult	111	19	.2	10	30	.3	6

[1] Those birds that managed to keep their prey.
[2] Those birds that managed to obtain the food from the bird they were pursuing.

large amounts of calcarious remains found in the colony (Shaffer 1971, pers. obs.). Young birds should thus learn to catch them and this study shows that they do. To make up for their lack of success, several alternatives are possible. For instance, the young may try harder by spending more time diving, by diving more frequently, by being more persistent in diving repeatedly for the same starfish until successful, or by feeding on other types of food as well (i.e. by being generalists). These important aspects could not be studied under the circumstances. One other way of making up for their shortfall in obtaining food is to resort to stealing, either on the ground or in the air.

In this study the immatures participated in a greater number of pursuits than one would have expected from the number of immatures present (Table 2). Adult Herring Gulls do not chase others as much as do immatures (Table 2). Apparently as the young mature, chasing becomes less important as a way of obtaining food. There may be several reasons for this. Adults may be less successful as chasers than younger birds, but this was not the case. Secondly, adults may give up sooner than immatures and very short chases involving adults may thus go unrecorded. Some evidence from aerial chases over the garbage dump in Oxford, England, in winter shows that young birds were as tenacious as adults. Apparently, the propensity of immature Herring Gulls to steal is real (Drury and Smith 1968). Moyle (1966) reports similar observations for immatures of *Larus glaucescens*.

Because of their general inefficiency, it seems reasonable to assume that the immatures require more time than the adults to satisfy their food requirements. This is indirectly supported by the fact that most of the immatures returned to the colony later than most of the adult Herring Gulls, the bulk of which returned 45 min earlier than the immatures (Fig. 1C).

The data suggest that at any given age a Herring Gull employs mostly those feeding skills that produce the best results. As the birds mature they learn new skills, improve on them, and discard or de-emphasize others. For an immature Herring Gull stealing on the ground and in aerial chases is apparently important. However, the young spend some time learning the feeding skills used by adults. Older birds do not chase as much as younger ones and I assume that for them other forms of feeding are more efficient in terms of time and energy expenditure.

SUMMARY

Immature Herring Gulls are less efficient in capturing starfishes by diving and possibly also in transporting them in flight than are adults. In contrast to the adults, the immatures steal much of their food from other gulls on the ground and in aerial pursuits. As the birds mature, stealing gives way to independent methods of finding food.

ACKNOWLEDGMENTS

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REQUEST FOR ASSISTANCE

WANTED: Data on the Seasonal Distribution of North American Gulls.—We are developing a procedure whereby the U.S. Air Force can predict the potential seasonal hazard to aircraft represented by gulls in parts of North America. This knowledge will be used to schedule missions around high risk areas thereby reducing the likelihood of bird-aircraft collisions. Supplemental data on local gull populations are needed from all parts of the continent. The assistance of field workers is solicited to aid us in this task.

For each observation, please provide the following information: list of species present, approximate number of each species, precise locality description, dates observed, any information about causes for concentrations (e.g. sanitary landfill operation), and any details about the frequency of such concentrations in the respective areas. Information is sought from inland as well as coastal localities.

Please submit reports of your gull observations to Dr. William E. Southern, Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115. Data will be gathered for a 2-year period beginning 1 September 1977.

COMPARATIVE MORTALITY OF BIRDS AT TELEVISION TOWERS IN CENTRAL ILLINOIS

James W. Seets and H. David Bohlen

There have been a number of studies of mortality of migrating birds at television towers in the U.S., including some in Illinois (Brewer and Ellis 1958, Cochran and Graber 1958, Parmalee and Parmalee 1959, Parmalee and Thompson 1963, Graber 1968). Most of these considered mortality at a single tower. Kills of birds at television towers offer one means of learning the timing and geographic patterns of migration and the physiological and population traits of the migrants. The great potential of tower-kill data to provide information on migration has not been fully realized, however, because the coverage of towers has been too limited.

In Illinois in 1973 there were 33 TV transmitting towers and 29 cable TV towers 152.4 m or higher. Fourteen of these were located more or less in an east-west line across central Illinois.

From August to December 1972, we attempted to check 7 of the large (182.9 m or more in height) television towers in central Illinois (Fig. 1) for bird kills. We had 2 primary goals: (1) to acquire research specimens for the Illinois Natural History Survey and the Illinois State Museum, and (2) to acquire comparative data on migration patterns across the state.

METHODS

The towers were checked on all mornings that followed nights with reduced visibility from fog or other precipitation, or with low cloud cover, or both. Seets and his associates at the Natural History Survey checked towers from Macon County (Argenta tower) eastward, and Bohlen and his associates checked the Springfield and Bluffs towers. All intact specimens were collected, weighed, and frozen to be processed later. Crippled birds were counted but not collected. Visible evidence, such as a few feathers or other remnants of carcasses, suggested that several birds in each kill had been eaten by predators. These remnants were also counted but not collected. Great Horned Owls (*Bubo virginianus*), soldier beetles (Cantharidae), and sexton beetles (Silphidae: *Nicrophorus*) appeared to be the principal predators and scavengers involved. Ants were seen on many of the dead birds.

An effort was made to determine the precise timing of each kill, using data from weather stations at Springfield Capitol Airport, Chanute Air Force Base (Fig. 1), and from the U.S. Department of Commerce Daily Weather Maps Weekly Series. The dates of kills referred to in this paper (Table 1) are the dates the birds were collected—the mornings after the kills.

The 2 towers at Springfield are only 3.2 km apart and we have considered them as one location. The central Illinois towers are in generally flat terrain. Vegetation surrounding the towers was either closely mowed grass or standing soybeans and corn, making

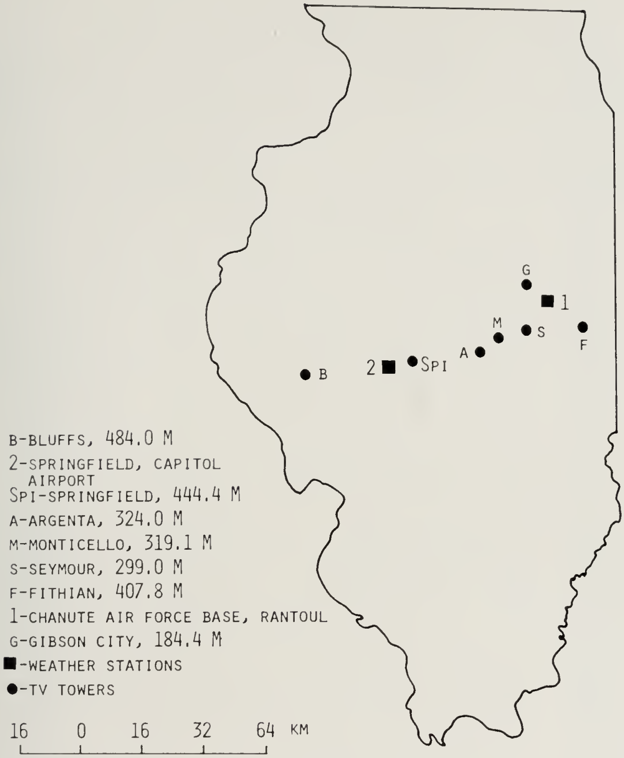

FIG. 1. Location of television towers checked for bird kills.

it difficult to obtain exactly comparable collections from the different towers. However, we believe that collections were at least 70% complete for each tower, based on checks made by several observers both on the mornings after the kills and on subsequent mornings.

All of the towers studied were similarly constructed, being triangular in cross section with at least 6 sets of cable guys at each corner. The towers ranged in height from 184.4 m to 484.0 m (Fig. 1).

RESULTS AND DISCUSSION

On 13 dates between 2 September and 12 November 1972, 5465 birds were collected at the 7 television towers in central Illinois. Most of the birds (93.4%) were killed on 4 nights: 1–2 September, 26–27 September, 28–29 September, and 30–31 October; more than half (59.8%) were killed on the night of 26–27 September.

TABLE 1

SPECIES RECORDED IN THE 4 LARGEST KILLS AT CENTRAL ILLINOIS TELEVISION TOWERS IN THE FALL OF 1972[1]

	2 Sept.					27 Sept.							29 Sept.	31 Oct.		
Species	F[2]	S	A	SPI	B	F	S	G	M	A	SPI	B	SPI	F	M	A
Pied-billed Grebe (*Podilymbus podiceps*)					2						1		1			
Virginia Rail (*Rallus limicola*)									1							
Sora (*Porzana carolina*)	2			3	2	2			2	5	8		2			
Yellow Rail (*Coturnicops noveboracensis*)									1		1		1			
Common Flicker (*Colaptes auratus*)											1	3	2			
Red-bellied Woodpecker (*Melanerpes carolinus*)												1				
Red-headed Woodpecker (*Melanerpes erythrocephalus*)									1			1	1			
Yellow-bellied Sapsucker (*Sphyrapicus varius*)						2			14	4	5	2	3			
Great Crested Flycatcher (*Myiarchus crinitus*)				1	1											
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	1			1					1	1	3					
Alder Flycatcher (*Empidonax alnorum*)				6												
Least Flycatcher (*Empidonax minimus*)								1		1	1		1			
Red-breasted Nuthatch (*Sitta canadensis*)	1					1				1		1	1			
Brown Creeper (*Certhia familiaris*)								1			3	2				
House Wren (*Troglodytes aedon*)										1			1			
Winter Wren (*Troglodytes troglodytes*)													1			
Long-billed Marsh Wren (*Telmatodytes palustris*)						1				1	1	2	1		1	
Short-billed Marsh Wren (*Cistothorus platensis*)									2		2	1			1	
Gray Catbird (*Dumetella carolinensis*)						10		1	28	15	25	5	1			
Brown Thrasher (*Toxostoma rufum*)												1				

TABLE 1—*Continued*

Species	2 Sept.					27 Sept.							29 Sept.	31 Oct.		
	F[2]	S	A	SPI	B	F	S	G	M	A	SPI	B	SPI	F	M	A
Wood Thrush (*Catharus mustelina*)				1		1	3		8	10	1	1				
Hermit Thrush (*Catharus guttata*)								1		2				1	2	
Swainson's Thrush (*Catharus ustulata*)	27		11	39		11			16	5	2		1			
Gray-cheeked Thrush (*Catharus minima*)	3		1	1		28		3	25	19	3		2			
Veery (*Catharus fuscescens*)	23		21	59	26	1			3	2						
Golden-crowned Kinglet (*Regulus satrapa*)												1		5	14	
Ruby-crowned Kinglet (*Regulus calendula*)						1		3	9	8	3	4	2		3	
Yellow-throated Vireo (*Vireo flavifrons*)						1		1	1	2	1					
Solitary Vireo (*Vireo solitarius*)						1		1	4	1	1	1				
Red-eyed Vireo (*Vireo olivaceus*)	31		29	153	42	4	4	6	11	18	9	1	4			
Philadelphia Vireo (*Vireo philadelphicus*)	2		2	3		11	1	1	8	14	5	2	3			
Black and White Warbler (*Mniotilta varia*)	2		1	10	4	16	5	3	31	30	17	5	7			
Prothonotary Warbler (*Protonotaria citrea*)				1												
Golden-winged Warbler (*Vermivora chrysoptera*)	1		1	5					2	1	1		1			
Tennessee Warbler (*Vermivora peregrina*)	54		20	177	46	73	9	14	98	80	52	6	27			
Orange-crowned Warbler (*Vermivora celata*)									3	2	3	1	2	2		
Nashville Warbler (*Vermivora ruficapilla*)				2	1	12	8	24	48	30	14	1	5	1		
Northern Parula (*Parula americana*)				1		4		4	8	3			1			
Yellow Warbler (*Dendroica petechia*)				10	6						1					
Magnolia Warbler (*Dendroica magnolia*)	17		1	14		74	17	24	133	96	15	3	44			
Cape May Warbler (*Dendroica tigrina*)						2		1	3	2						

TABLE 1—*Continued*

Species	2 Sept.					27 Sept.							29 Sept.	31 Oct.		
	F[2]	S	A	SPI	B	F	S	G	M	A	SPI	B	SPI	F	M	A
Black-throated Blue Warbler (*Dendroica caerulescens*)						3		4	5	5	2	1	2			
Yellow-rumped Warbler (*Dendroica coronata*)						11	1	6	27	11	4		14	6	111	3
Black-throated Green Warbler (*Dendroica virens*)	2			4	2	42	14	17	65	81	13	7	13	1		
Blackburnian Warbler (*Dendroica fusca*)	12		1	21	5	7	2	1	8	4	3	1				
Chestnut-sided Warbler (*Dendroica pensylvanica*)	7		1	14	5	11	3	7	39	39	14	5	9			
Bay-breasted Warbler (*Dendroica castanea*)			1	5	2	79	13	13	61	51	14	6	29			
Blackpoll Warbler (*Dendroica striata*)	7					26		7	18	3	5		1			
Pine Warbler (*Dendroica pinus*)									1	1			1			
Palm Warbler (*Dendroica palmarum*)	1					20	3	5	12	6	7	1	14			
Ovenbird (*Seiurus aurocapillus*)	19	1	9	71	33	91	30	41	143	142	51	26	53			
Northern Waterthrush (*Seiurus noveboracensis*)	11		2	52	17	1	3		14	18	7	1	9			
Connecticut Warbler (*Oporornis agilis*)	1		1	3		3	1			1						
Mourning Warbler (*Oporornis philadelphia*)				1		2				1	1					
Common Yellowthroat (*Geothlypis trichas*)	1			2	2	8		4	23	20	41	6	17			
Wilson's Warbler (*Wilsonia pusilla*)						1	1		2	4	2		1			
Canada Warbler (*Wilsonia canadensis*)	1			7	7		1		1	1						
American Redstart (*Setophaga ruticilla*)	23		5	22	7	48	5	12	60	33	13		23			
Bobolink (*Dolichonyx oryzivorus*)	17		2	34	5	2			2	2	4		3			
Northern Oriole (*Icterus galbula*)		1	1	5	4											
Scarlet Tanager (*Piranga olivacea*)						1	1		1	2		1				
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)				4	2	16	2		36	18	23	4	10			

Table 1—*Continued*

	2 Sept.					27 Sept.							29 Sept.	31 Oct.		
Species	F[2]	S	A	SPI	B	F	S	G	M	A	SPI	B	SPI	F	M	A
Indigo Bunting (*Passerina cyanea*)				1					3	2	5	1	1			
Dickcissel (*Spiza americana*)				1						1			1			
Savannah Sparrow (*Passerculus sandwichensis*)				1		1				2	1		1	4	7	2
Grasshopper Sparrow (*Ammodramus savannarum*)									1						1	
Sharp-tailed Sparrow (*Ammospiza caudacuta*)						1			1							
Dark-eyed Junco (*Junco hyemalis*)														1	9	
Chipping Sparrow (*Spizella passerina*)									1					1	1	
Field Sparrow (*Spizella pusilla*)														1	5	1
White-crowned Sparrow (*Zonotrichia leucophrys*)															1	
White-throated Sparrow (*Zonotrichia albicollis*)									3	3			1	1	11	
Lincoln's Sparrow (*Melospiza lincolnii*)						1			2	2	2		1	2	2	
Swamp Sparrow (*Melospiza georgiana*)						3			2			2		2	11	1
Song Sparrow (*Melospiza melodia*)														3	2	1
TOTAL 5,138	266	2	110	735	221	634	127	206	992	807	391	107	319	29	184	8

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[1] Eight additional mortalities included a Brown Creeper and a Black-throated Blue Warbler on 10 October at SPI, a Short-billed Marsh Wren, a Grasshopper Sparrow and a Henslow's Sparrow at A, and Virginia Rail, a Red-winged Blackbird, and a Fox Sparrow on 12 November at SPI.

[2] For identification of localities, see Fig. 1.

TABLE 2

A COMPARISON OF THE RATIOS OF BIRDS KILLED AT TOWERS IN WESTERN ILLINOIS AS COMPARED TO KILLS AT TOWERS IN EASTERN ILLINOIS DURING SEPTEMBER FOR THE YEARS 1958, 1962, AND 1972[1]

	1958		1962		1972	
Species	16–17 Sept. West[2]	15–17 Sept. East[3]	24–25 Sept. West[3]	24–25 Sept. East[3]	2–27 Sept. West	2–27 Sept. East
Swainson's Thrush	1.0	3.1	1.0	4.5	1.3	1.0
Gray-cheeked Thrush	1.0	1.3	1.0	5.2	1.0	1.6
Veery	1.3	1.0			3.8	1.0
Red-eyed Vireo	1.1	1.0	2.8	1.0	4.3	1.0
Tennessee Warbler	3.8	1.0	2.1	1.0	1.8	1.0
Magnolia Warbler	2.8	1.0	1.0	1.4	1.0	5.2
Bay-breasted Warbler	4.3	1.0	1.9	1.0	1.0	3.7
Northern Waterthrush	5.3		2.8	1.0	3.4	1.0
Common Yellowthroat	2.8		2.8	1.0	2.0	1.0
Bobolink	1.0	6.0	1.1	1.0	3.7	1.0
Chestnut-sided Warbler	11.9	1.0	2.1	1.0	1.0	1.9
Ovenbird	3.9	1.0	1.7	1.0	1.0	5.7
American Redstart	3.7		1.0	1.2	1.0	2.0
Total Birds	827	147	213	296	1,454	3,144

[1] In comparing the ratios, data were adjusted to correct differences in total birds killed between eastern and western towers during the given dates for each year.

[2] Data for 1958 West are from Parmalee and Parmalee, 1959.

[3] Data for 1958 East, 1962 East, West are from Graber, 1968.

Inspection of our data shows no consistent relationship between tower height, terrain, or tower location and number of birds killed for the kills we studied. Kills were neither consistently high nor low at any particular tower. We believe that the number of birds killed at a given tower on a given night is related primarily to local weather conditions and to the number of birds flying.

Kills in relation to weather factors.—The kills occurred following the passage of cold fronts, usually when conditions of low overcast (550 m or less) and reduced visibility (< 8 km) prevailed; however, 4 of the kills occurred when the lowest overcast was 1220 m to 1830 m and the visibility was 11.3 km or more. On the 4 nights when 93% of the birds were killed, ceilings were 550 m or less. All kills occurred within 32 h (usually within 6 h) after the passage of cold fronts, when the winds were from the north. We do not know exactly when during the night the kills occurred. It may be important to know the precise timing of the kills when comparing bird losses at the different towers (Table 2), because the time factor may have a bearing on the species killed.

TABLE 3

SPECIES RECORDED IN THE SMALL KILLS AT CENTRAL ILLINOIS TELEVISION TOWERS IN THE FALL OF 1972[1]

Species	SPI[1] 4 Sept.	SPI 14 Sept.	S 14 Sept.	F 14 Sept.	SPI 21 Sept.	SPI 28 Sept.	SPI 10 Oct.	SPI 12 Oct.	SPI 18 Oct.	A 28–29 Oct.	SPI 10–12 Nov.
Virginia Rail											1
Sora Rail		1									
Yellow-billed Cuckoo	1										
Brown Creeper							1				
House Wren											1
Winter Wren											1
Long-billed Marsh Wren						3	1				
Short-billed Marsh Wren										1	
Catbird						2	1				
Wood Thrush	1					1					
Hermit Thrush							2			1	
Swainson's Thrush	3	7	1	9							
Gray-cheeked Thrush				1		1	1				
Veery	10	1		1							
Golden-crowned Kinglet							2		1	2	1
Ruby-crowned Kinglet							2		1	1	1
Solitary Vireo						1			1		
Red-eyed Vireo	9	2				2					
Philadelphia Vireo	1					2					
Black-and-white Warbler	2	1					1				
Tennessee Warbler	11	1		2	3	8	3				
Orange-crowned Warbler							3		2		
Nashville Warbler					1	4	4		1		
Northern Parula							2				
Magnolia Warbler						2	2				
Black-throated Blue Warbler							1				

TABLE 3—*Continued*

Species	SPI[1] 4 Sept.	SPI 14 Sept.	S 14 Sept.	F 14 Sept.	SPI 21 Sept.	SPI 28 Sept.	SPI 10 Oct.	SPI 12 Oct.	SPI 18 Oct.	A 28–29 Oct.	SPI 10–12 Nov.
Yellow-rumped Warbler						1	23			28	8
Black-throated Green Warbler						6	3	1			
Blackburnian Warbler	1	2									
Chestnut-sided Warbler	1	1				2					
Bay-breasted Warbler	1	1			2	1	2				
Blackpoll Warbler							1				
Palm Warbler		1					7				
Ovenbird	8				1	11	2				
Northern Waterthrush	4	2				1					
Common Yellowthroat	1				1	8	5		1		
Canada Warbler	2										
American Redstart	3	1			2						
Red-winged Blackbird											1
Northern Oriole	1										
Scarlet Tanager		1			1						
Rose-breasted Grosbeak						1	1				
Indigo Bunting							2	1			
Savannah Sparrow										4	5
Grasshopper Sparrow										1	
Henslow's Sparrow										1	
Dark-eyed Junco										2	2
Field Sparrow										1	2
White-throated Sparrow								1			1
Fox Sparrow											1
Lincoln's Sparrow						1					
Swamp Sparrow							4	2		2	1
Song Sparrow							1				1

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[1] For identification of localities, see Fig. 1.

In analyzing the relationship of the kills to weather, we have emphasized the data for the large kills in order to have sufficient numbers for comparison. Comparative data for the large kills are presented in Table 1 and the small kills are summarized in Table 3.

Comparison of kills.—Graber's (1968) radar transect data on the migration in central Illinois in September show that the number of nocturnal migrants is fairly uniform at different locations across the state. Thus, if weather conditions were the same at all towers, we would expect the number of birds killed at each tower to be similar, but, in fact, there are great differences in the numbers of birds killed at different towers on the same night (Table 1). On 27 September, for example, kills ranged from 107 birds to 992 at different towers of comparable height. There were very different numbers of birds killed at towers as close (19.3 km) as Seymour and Monticello—127 versus 992. Such differences cannot be explained without more detailed weather records than are presently available.

Although the data from radar transects for central Illinois indicate a fairly uniform distribution of total night migrants across the state in September, this does not necessarily indicate a uniform statewide distribution of each species. Because large television towers are well distributed across central Illinois, the kills at those towers provide a means of comparing the species composition of the flights of migrants in the eastern and western segments of the state. In making such a comparison, we find that some species appear relatively more numerous in the kills on the western side of the state while other species are more prevalent on the eastern side. Chi-square analysis of the data for species involving 20 or more individuals indicated that the species composition did, in fact, differ significantly between the eastern and the western towers ($\chi^2 = 736$; $P < 0.001$). The analysis seems to indicate a difference in the relative numbers of birds of individual night migrating species between the east and west sides of Illinois.

In a few cases, species were not present in kills on one side of the state but were represented on the other side. These instances included the Common Flicker (6), Great Crested Flycatcher (2), Alder Flycatcher (6), and Yellow Warbler (17), all found at western towers but not at eastern towers. Only the Cape May Warbler (8) and Grasshopper Sparrow (1) were present at eastern towers but not at western towers on nights when kills occurred on both sides of the state.

Other species were present in kills on both sides of the state but differed significantly in numbers from one side to the other (Table 2). It is worthwhile to compare our 1972 data on the species killed at western versus eastern towers with Graber's (1968) and Parmalee's data for 1958 for the same region (Table 2). In several species (for example, see thrushes) the pattern was consistent in all years.

Rare and/or infrequent species.—A few species deserve special comment, either because of their rarity, or because of their infrequent occurrence in tower kills.

Yellow Rail: Single Yellow Rails were found among tower kills at Springfield on 27 and 29 September and at Monticello on 27 September, marking the first time that the Yellow Rail was found among tower kills on the eastern side of the state.

Red-bellied Woodpecker: The kill of night migrants on 27 September 1972 at the television tower at Bluffs included a Red-bellied Woodpecker, a supposedly non-migratory species.

Black-throated Blue Warbler: On 27 September 1972, 17 Black-throated Blue Warblers were killed on the eastern side of the state and 3 were killed on the western side. Three were killed on the western side on 29 September (2) and 10 October (1). These kills were high compared with the number of Black-throated Blue Warblers (1 or 2 a season) seen in the field in Illinois.

Henslow's Sparrow: One was found among tower kills on the eastern side of the state for the first time on 28–29 October 1972, at Argenta.

Sharp-tailed Sparrow: The Sharp-tailed Sparrow was found for the first time in kills at eastern towers on 27 September at Fithian (1) and Monticello (1).

Field Sparrow: On 31 October 1972 a Field Sparrow was found for the first time among eastern tower kills at Fithian (1), Monticello (5), and Argenta (1).

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ILLINOIS NATURAL HISTORY SURVEY, URBANA 61801 (JWS), AND ILLINOIS STATE MUSEUM, SPRINGFIELD 62706 (HDB). ACCEPTED 1 JUNE 1976.

EFFECT OF FLOCK SIZE ON FORAGING ACTIVITY IN WINTERING SANDERLINGS

James Silliman, G. Scott Mills, and Stephen Alden

Birds in flocks may increase the proportion of time spent feeding and thus food intake by dividing the time spent watching for predators among flock members. This advantage of foraging in flocks has been supported by mathematical analysis (Pulliam 1973) and by experimental work with aviary birds (Powell 1974). Field work with Wood Pigeons (*Columba palumbus*) (Murton et al. 1971) showed that single birds had lower feeding rates and spent more time looking around than flock birds, but Murton (1971) interpreted this as indicating that single birds were seeking to join flocks for reasons unrelated to predator protection. Page and Whitacre (1975) found that predation is substantial on wintering shorebirds and that they are less susceptible to predation when in flocks, but no evidence exists that flocking shorebirds increase their foraging activity. To test this possibility, we examined foraging activity in relation to flock size in wintering Sanderlings (*Calidris alba*). Because Barash (1974) found that chickadees in flocks have fewer aggressive encounters than single birds, we looked for similar behavior among Sanderlings.

METHODS

Data were collected by 9 investigators from 26 to 28 November 1974 at Punta Santa Rosa 37 km northwest of Kino, Sonora, Mexico. The beaches on the south side of the point are sandy while those on the north, at the mouth of a channel, are composed of algae-covered rocks approximately 4–6 cm in diameter. Sanderlings were the most common shorebirds present.

Investigators dispersed along the beaches in 4 groups. Each group consisted of 1 recorder and 1 or 2 observers; group members and roles were changed frequently. Each group was equipped with a spotting scope, stopwatch, mechanical counter, and binoculars. The first bird observed in a flock was selected by counting back from the lead bird using random numbers less than 10. Successive birds were picked by counting back a random number from the position of the last bird observed. When the count exceeded the number of remaining birds, counting continued with the lead bird. For purposes of analysis we decided to take approximately equal numbers of observations of birds in 3 classes on rocky and sandy beach: singles, flocks of 2–10 shorebirds, and flocks of greater than 10. Shorebirds other than Sanderlings were included in the total flock size, since all birds contribute to the possible reduction of predator alert time.

We recorded the total seconds out of 1 min that a Sanderling appeared to be foraging (hereafter called foraging time). The observer timed foraging activity with a stopwatch while the recorder monitored 1 min intervals. We also recorded the number of feeding movements in 1 min (hereafter called foraging rate) using a mechanical counter. To test for possible differences in foraging method due to substrate type or flock size, we

TABLE 1

FORAGING TIMES* OF SANDERLINGS IN DIFFERENT FLOCK SIZES ON DIFFERENT HABITATS

	Flock size								
	Singles			2–10			> 10		
Habitat	N	x̄	s²	N	x̄	s²	N	x̄	s²
Sandy	33	53.8	79.0	54	49.3	191.0	67	53.3	151.0
Rocky	34	49.9	67.6	45	51.1	157.3	55	53.2	90.7
Combined	67	51.8	75.8	99	50.1	174.7	122	53.3	122.9

* Total seconds in 1 min spent foraging.

classified foraging movements as probes if the bill penetrated the surface, or pecks if it did not. We estimated the number of movements on the few occasions that they were too rapid to be counted directly. Thirty-two of the total 475 min of foraging data include birds observed between 30 and 45 sec whose rates were prorated to 1 min. No sleeping birds or birds observed for less than 30 sec were included in the data analysis. Aggressive interactions were recorded only for those birds selected for foraging observations.

Due to large variances, we transformed the data as the square root of $(X + .5)$ to normalize them for statistical tests. Statistical analysis was done with the aid of the University of Arizona computer services using the SPSS statistics programs.

RESULTS

Sanderling flocks on sandy beaches tended to be small and move rapidly whereas those on rocky beaches were slower and sometimes large enough to include both sleeping and foraging birds. We collected no quantitative data on the relative frequency of flock sizes, but flocks of 2 to 10 birds seemed most common. Single birds were fairly common but usually did not remain single for long before being joined by others.

There was no appreciable change in mean time spent foraging due to par-

TABLE 2

FORAGING RATES* OF SANDERLINGS IN DIFFERENT FLOCK SIZES ON DIFFERENT HABITATS

	Flock size								
	Singles			2–10			> 10		
Habitat	N	x̄	s²	N	x̄	s²	N	x̄	s²
Sandy	28	26.9	401.4	40	51.0	1708.3	31	37.8	881.8
Rocky	22	43.7	627.8	41	57.0	889.9	25	61.9	1832.4
Combined	50	34.3	561.1	81	54.1	1287.0	56	48.6	1426.4

* Number of movements per minute.

TABLE 3

POLYNOMIAL ANALYSIS OF VARIANCE—FORAGING RATE WITH FLOCK SIZE ON SANDY BEACH

Source	Degrees of freedom	M. S.
Between	2	25.54*
Linear Term	1	10.33
Quadratic Term	1	42.05*
Within	96	5.32

* F probability $< .05$

ticipation in flocks by Sanderlings (Table 1). Analysis of variance showed no significant relationship between flock size and foraging time in either habitat (sandy $P = .22$, rocky $P = .54$) or in both combined ($P = .22$).

However, the foraging rate of Sanderlings in flocks ($\bar{X} = 51.8$) was considerably higher than that of single birds ($\bar{X} = 34.3$), and this difference was significant by a 1-tailed t-test ($t = 3.15$, $P = .001$). The increase in foraging rate was not associated with a change in foraging method. Of a sample of 504 movements by single birds, 92% were probes, while 90% of 7091 movements by birds in flocks were also probes.

Mean foraging rate tended to increase as flock size increased on rocky beach (Table 2), but this trend was not significant by analysis of variance ($P = .48$). There was a marked decline of foraging rate in flocks greater than 10 on sandy beach, shown to be significant by polynomial analysis of variance (Table 3). Mean foraging rates of birds on rocky beach were higher in all cases than on sandy beach (Table 2). This difference was significant by a 2-tailed t-test for single birds ($t = 2.93$, $P = .005$) and very nearly so for flocks ($t = 1.97$, $P = .051$). Ninety % of foraging movements were probes on both rocky and sandy beach ($N = 2111$ and 5484 respectively).

We found a positive correlation between aggressions per bird-minute and flock size ($r = .212$, significance of $r = .0001$). Increased aggressive in-

TABLE 4

AGGRESSIONS OF SANDERLINGS IN DIFFERENT FLOCK SIZES ON DIFFERENT HABITATS

	Flock size		
Habitat	Singles	2–10	> 10
Sandy	.076* (53)	.122 (90)	.376 (96)
Rocky	.019 (53)	.092 (76)	.100 (80)

* Aggressions per bird observed per minute. Number of bird-minutes in each category in parentheses.

teractions in larger flocks were due to increased aggressions per bird (Table 4) and increased numbers of birds participating. Aggressions were more frequent in all size classes on sandy beach.

DISCUSSION

The increased foraging rate of Sanderling in flocks is equivalent to increased food intake if the proportion of successful feeding movements remains relatively constant, as Goss-Custard (1970a) found for Redshank (*Tringa totanus*). We attribute the lack of a corresponding increase in foraging time to our inability to measure the brief pauses between foraging movements.

The increased foraging rate of Sanderlings in flocks could be attributed to causes other than less time spent looking for predators. Krebs (1974) suggested that herons in flocks fed at a faster rate than solitary individuals because flocks form at patches of abundant food. However, Sanderling flocks and single birds foraged in the same areas and flocks moved cohesively along the beach. Murton (1971) and Krebs (1974) have argued that single birds spend less time foraging because they are searching for flocks to join. This seems unlikely in the case of Sanderlings since flocks were seldom far from foraging single birds. Finally, Sanderlings in this study did not change their foraging method when in flocks to achieve the increase. We conclude that increased foraging rate may be related to less time spent searching for predators between feeding movements.

Our data indicate that Sanderlings do not join flocks to reduce aggressive encounters, as Barash (1974) found for chickadees. Recher and Recher (1969) found that Semipalmated Sandpipers (*Calidris pusilla*) likewise increase aggressive encounters in flocks.

The decreased foraging rate of birds in large flocks on sandy beach did not occur on rocky beach and may have been caused by limited food on sandy beach. Sanderlings on sandy beach had lower feeding rates, more aggressive encounters, and higher flock speed than those on rocky beach, suggesting that food was less abundant on sandy beach. Higher aggression among shorebirds has been associated with lower food availability (Recher and Recher 1969), as has higher flock speed of woodland passerines (Morse 1970). Large flocks on habitats with limited resources may deplete locally available prey thereby reducing the average feeding rate (Goss-Custard 1970b). Protection from predators does not diminish as flock size increases, but competition for food where resources are limited may determine an optimum flock size.

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ACTIVITY PATTERNS OF FEMALE RUFFED GROUSE DURING THE BREEDING SEASON

Stephen J. Maxson

Ruffed Grouse (*Bonasa umbellus*) are difficult to observe for extended periods in the wild. Consequently, despite the considerable research attention this bird has received (e.g. Bump et al. 1947, Gullion and Marshall 1968, and others), few precise data are available concerning its activity patterns. Recent radiotelemetry studies in Minnesota (Archibald 1973 and several studies cited therein) have increased our knowledge of this aspect of the Ruffed Grouse's behavior but activity patterns of female Ruffed Grouse during the breeding season remain poorly documented. This paper reports a radiotelemetry study of female Ruffed Grouse activity patterns from pre-incubation through post-incubation periods at the University of Minnesota's Cedar Creek Natural History Area located about 45 km north of Minneapolis, Minnesota.

METHODS

Field observations were made from 1 April–30 June 1971 and 1 April–7 July 1972. The Ruffed Grouse population was at a peak level during this investigation. Spring counts of drumming males totaled 30 and 28 on the square mile study area in 1971 and 1972 respectively.

Female Ruffed Grouse were captured by baited lily-pad traps (Gullion 1965), nest traps (Weller 1957), dip-netting on the nest (Robel et al. 1970), and by nightlighting (Huempfner et al. 1975). Hens captured on their nests were handled in the field to minimize the time they were kept off the eggs. All others were placed in burlap bags and transported to the Cedar Creek laboratory where they were weighed, sexed, aged, leg-banded, and equipped with a 24–26 g transmitter similar in harness design to one described by Brander (1968). Expected transmitter life ranged from 50–75 days but usually birds were recaptured and fitted with new transmitters before this time. All birds were released at the point of capture.

Radio-marked grouse were monitored with an automatic radio-tracking system (Cochran et al. 1965). Two towers 0.8 km apart support directional receiving antennas continually rotating at 1⅓ rpm. During each antenna revolution, radio signals emanating from the transmitter equipped grouse were received by the antennas. Signals were relayed to a centrally located laboratory and, after amplification and modification, were recorded on 16 mm film as degree bearings for each tower. These bearings were used to determine the location of the bird by triangulation. With the use of a microfilm reader, an activity designation (active, inactive, or unknown) was determined at 15 min intervals for each bird. Marshall and Kupa (1963) determined that the pitch of the radio signal changed as a grouse moved about. This change in signal pitch associated with activity is reflected as irregularities in signal peaks on the film record (Sargeant et al. 1965). During each 15 min period (except during incubation) a grouse was considered active if 4 or more signals exhibited these irregularities, or if a change in bearing of 1 or more degrees

Table 1
Percentage of Time Female Grouse Were Active

						Post-incubation			
		Pre-incubation		Incubation		With Brood		Without Brood	
Bird No.	Age	No. Days	% Time Active	No. Days	% Time Active	No. Days	% Time Active	No. Days	% Time Active
1657	J	28	44.5	27	4.5	20	52.7	—	—
1690	J	36	51.2	25	4.8	—	—	—	—
1691	A	35	47.3	26	3.5	26	51.5	—	—
1695	J	36	48.7	25	3.9	9	58.4	—	—
1698	J	—	—	—	—	—	—	29	67.5
1699	J	—	—	—	—	8	56.9	—	—
2200	A	—	—	—	—	30	58.5	—	—
2201	J	—	—	—	—	—	—	29	60.5
2202	—	—	—	—	—	—	—	18	51.0
2210	J	45	47.9	10	4.9	—	—	—	—
2219	J	—	—	21	4.1	—	—	—	—
2235	A	—	—	25	3.1	—	—	—	—
2238	J	46	37.3	26	4.4	—	—	—	—
2239	J	43	55.6	26	5.8	30	54.4	—	—
2241	J	37	41.7	17	4.1	—	—	43	59.0
2246	A	36	48.4	26	3.4	18	47.1	—	—
2248	J	—	—	25	4.7	—	—	—	—
Mean		38	46.9	23	4.3	20	54.2	30	59.5

occurred for either tower. During the incubation period activity changes were determined to the nearest minute.

Data for each bird were divided into pre-incubation, incubation, and post-incubation periods and were analyzed in 2 ways using the University of Minnesota's Control Data 6600 computer system. First, the sampled activity for each day was plotted giving every 15 min interval an activity symbol (active, inactive, or unknown). This illustrated day-to-day periods of activity. Second, the percentage of time a bird was active during each 15 min interval over a given time period (pre-incubation, incubation, or post-incubation) was plotted, giving a composite 24-h day comprised of data for all days during a time period. This illustrated activity trends throughout the specified period.

All times given are C.S.T.

RESULTS

Activity data were obtained from 17 female Ruffed Grouse during the study. Table 1 summarizes the percentage of time the birds were determined to be active during the pre-incubation, incubation, and post-incubation periods. Percent activity tended to be greater during the post-incubation period than the pre-incubation period, perhaps due to increased daylength. Hens with

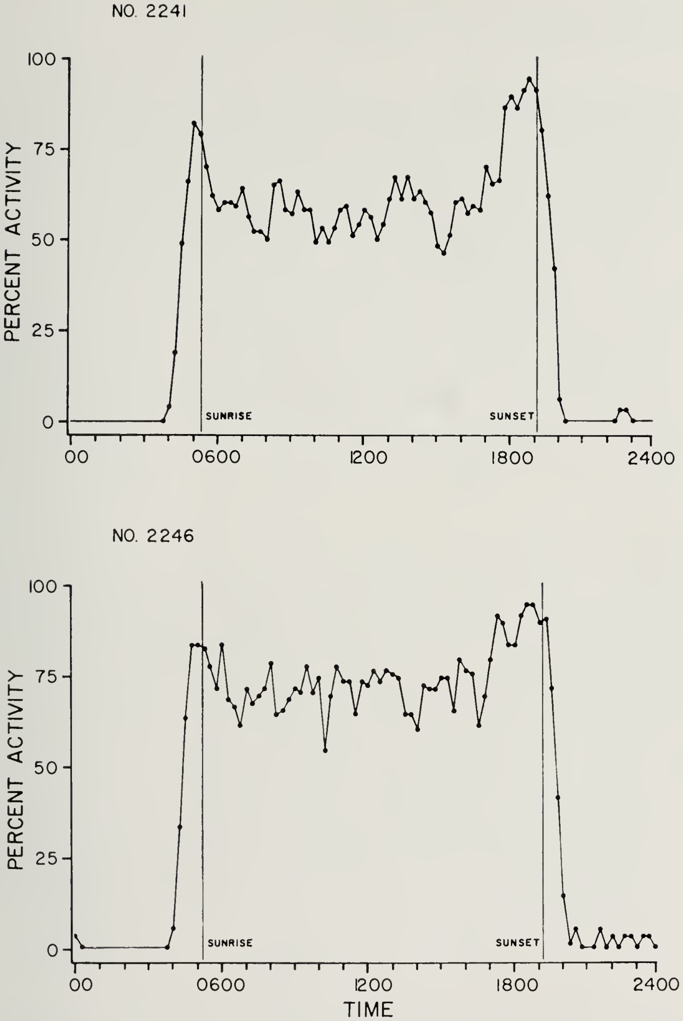


Fig. 1. Temporal distribution of percentage of 15-min intervals active during the pre-incubation period for Hens 2241 and 2246.

broods tended to have a lower percent activity than those without broods. During incubation, activity was greatly reduced and limited to a few short feeding periods each day.

No relationship between age (juvenile 10–12 months old, adult 22 months or older) and activity levels was evident except during incubation when the 3 adult hens monitored exhibited the 3 lowest activity levels. There was no apparent relationship between color phase of the birds and activity levels.

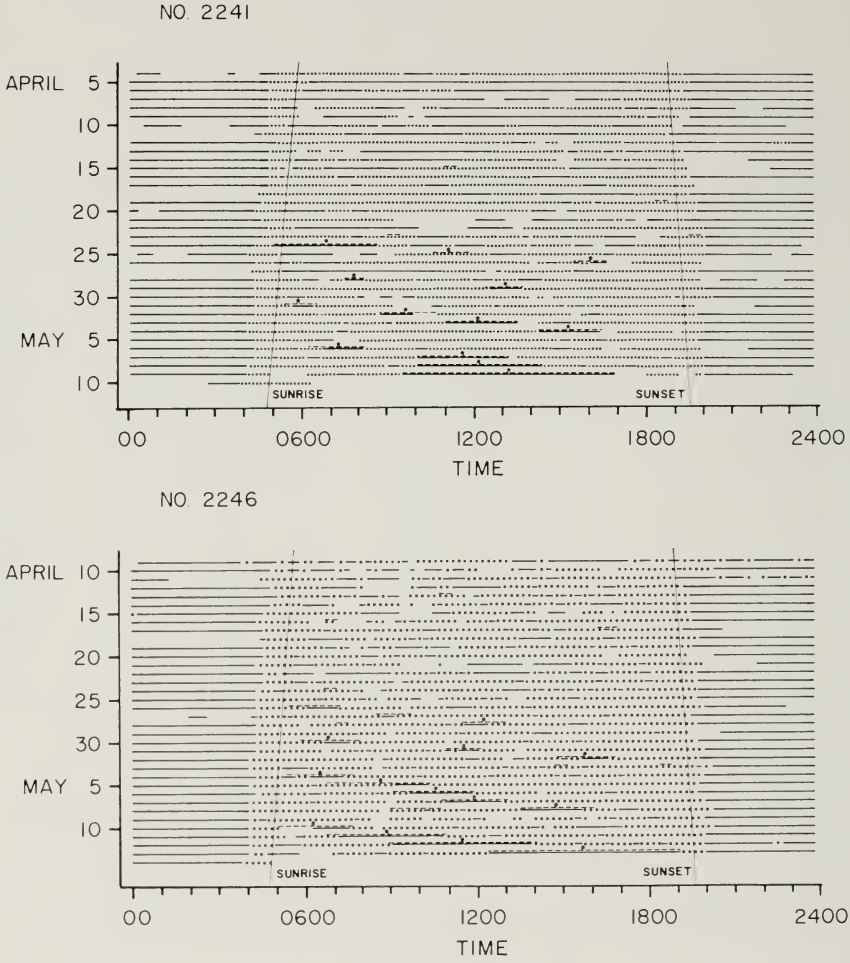


FIG. 2. Daily periods of activity, visits to the nest site, and probable egg laying periods for Hens 2241 and 2246 during the pre-incubation period (—— = inactive, · · · = active, – – – = hen at or near nest site, * = nest visits during which egg laying probably occurred, blank = no data).

Pre-incubation.—The temporal distribution of percentage of 15 min intervals active during the pre-incubation period was determined for 9 hens (Maxson 1974). Fig. 1 gives 2 examples of these data. Activity seldom occurred at night. Peaks of activity were closely associated with sunrise and sunset. The evening peak was greater than the morning peak for all hens.

Activity levels during the day fluctuated and were variable among birds. Daytime activity seldom fell below the 50% level and sometimes exceeded the dawn-dusk peaks for short periods.

Fig. 2 illustrates daily activity for 2 hens. Daytime activity, for all hens combined, began prior to sunrise on 302 of 306 (98.7%) grouse-days and ceased after sunset on 296 of 310 (95.5%) grouse-days. Activity usually began 30–60 min before sunrise and in most cases ceased 15–45 min after sunset. The exact timing of activity onset and cessation varied slightly from day to day and was likely influenced by weather changes.

Egg laying.—By coordinating activity and location data for 8 hens from which nearly continuous telemetry records were obtained, it was possible to determine when they had visited their nest sites prior to the beginning of incubation. I assumed that eggs were laid during some of these visits, although I could not determine exactly when egg laying occurred during a nest visit. Fig. 2 indicates all occasions whan Hens 2241 and 2246 were known to be at or near their nest sites as well as probable egg-laying visits. Both hens had 13-egg clutches.

Visits to the nest followed a definite pattern. Hens seldom visited the nest site prior to the onset of egg laying, suggesting that nest construction was not very time-consuming. Once egg laying began, hens were rarely near the nest site except during presumed laying visits. During laying visits they normally remained inactive on the nest from 1 to several hours. As the clutch approached completion, hens tended to remain on the nest for longer periods. Egg-laying visits occurred 1–5 days in succession at intervals ranging from 25–30 h. Eggs were laid slightly later during each day of a laying sequence. When the next egg of a sequence appeared to be due sometime after the end of evening activity, the egg was not laid until the following morning thus beginning another sequence with the usual 25–30 h interval between eggs. The number of days in a laying sequence varied both among birds and for the same individual as well. As examples, the laying sequences for several hens were the following: Hen 2210, 1-2-2-3-4; Hen 2239, 2-3-3-3; Hen 2241, 3-2-4-4; Hen 2246, 1-3-5-4 (numbers indicate the number of consecutive days during which an egg was laid while hyphens indicate the skipping of a day between eggs). Similar overall patterns of egg laying were observed for all hens monitored.

Since renesting by Ruffed Grouse in the wild has been proven on only 1 occasion (Barrett 1970:79–81), evidence is presented here that Hen 1695, which had only 8 eggs and did not begin incubating until 20 May (several days later than the other hens), successfully renested. Fig. 3 illustrates the activity of this hen during the pre-incubation period. Although some gaps occur in these data, the probable laying times of 7 eggs were determined.

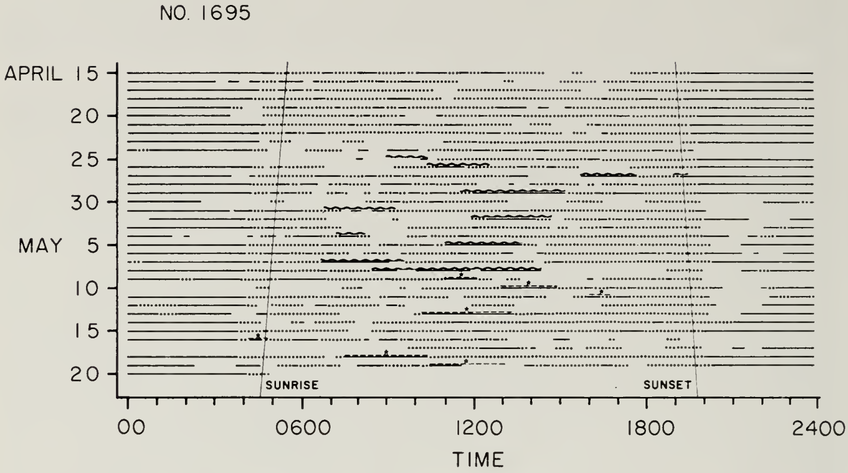


FIG. 3. Daily periods of activity, visits to the nest site, probable egg laying periods, and probable visits to a previous nest site for Hen 1695 during the pre-incubation period (—— = inactive, · · · = active, - - - = hen at or near nest site, * = nest visits during which egg laying probably occurred, ~ = hen at or near probable first nest site, blank = no data).

The remaining egg may have been laid during the data gap on the morning of 17 May. The first egg of the clutch was apparently laid on 9 May. Prior to this date a pattern of activity similar to that occurring during egg laying was evident. Inactive periods possibly associated with egg laying are indicated in the figure. The telemetry record indicates that these were all at a single location approximately 160 m from the nest. This suggests that an earlier nest had been established on 25 April (about the same time other hens were beginning to lay) and that up to 10 eggs had been laid. On 8 May, prior to the onset of incubation, they were likely destroyed by a predator. The second nest was apparently established the following day on 9 May.

Examination of the nest visit pattern suggests that the original clutch size would have been 14 (assuming that the first egg was laid on 25 April and the 14th was laid on 13 May). No nest visits occurred on 14 and 15 May. This was the only hen which skipped more than 1 day between laying sequences. Probably this time lag was required for formation of additional eggs. Remating may have been necessary as well.

Incubation.—Activity patterns during the incubation period were determined for 12 hens. Field observations and the telemetry record indicated that hens normally left the nest only to feed. The number of nest absences per day varied from 1–5 but was most often 2 or 3 (Table 2). While no hen

TABLE 2

NUMBER OF DAYS HENS HAD FROM 1 TO 5 NEST ABSENCES[1]

Bird No.	Total No. Nest Absences Per Day				
	1	2	3	4	5
1657	—	5	11	—	—
1690	—	4	8	7	—
1691	1	6	9	4	—
1695	1	11	5	2	2
2210	—	6	1	—	—
2219	—	1	6	—	—
2235	—	11	2	—	—
2238	—	2	8	2	—
2239	1	11	4	2	—
2241	—	5	7	—	—
2246	—	11	7	—	—
2248	—	—	7	6	2
TOTAL	3	73	75	23	4

[1] Includes only days on which nearly constant telemetry records were obtained.

had the same number of absences per day throughout the incubation period, some (e.g. Hen 2235) were fairly consistent in making 2 feeding trips per day whereas others (e.g. Hen 2238) usually made 3 trips.

The length of 590 nest absences was determined to the nearest minute and the total minutes off the nest per day was calculated for 177 grouse-days. Table 3 summarizes these data and indicates intra- and inter-bird variability. Eight birds had mean absence lengths of 18–24 min. Hen 2239 had 1 unusually long absence of 197 min. This was more than twice the length of the longest absence recorded for any of the other birds. Possibly this hen was disturbed by a predator while feeding and failed to return to the nest in the usual amount of time. Excluding the 197 min absence, Hen 2239 had absences ranging from 14–65 min (mean 37 min). On days hens were absent only twice, the last absence tended to be longer than the first (44 of 73 grouse-days (60%)). In contrast, of 102 days when hens were absent more than twice, the last absence of the day was the longest on only 42 (41%) occasions.

The total number of minutes off the nest varied from day to day for individual hens. Overall, juvenile hens spent more time off the nest than adults (juvenile mean 66 min, adult mean 46 min) suggesting that adults are more efficient incubators. Among birds, there was no consistent relationship between mean absence length and mean total minutes off the nest per day. Also, hens did not consistently increase or decrease nest attentiveness as incubation progressed except during the last day or 2 when eggs were in the process

TABLE 3

SUMMARY OF NEST ABSENCES DURING THE INCUBATION PERIOD

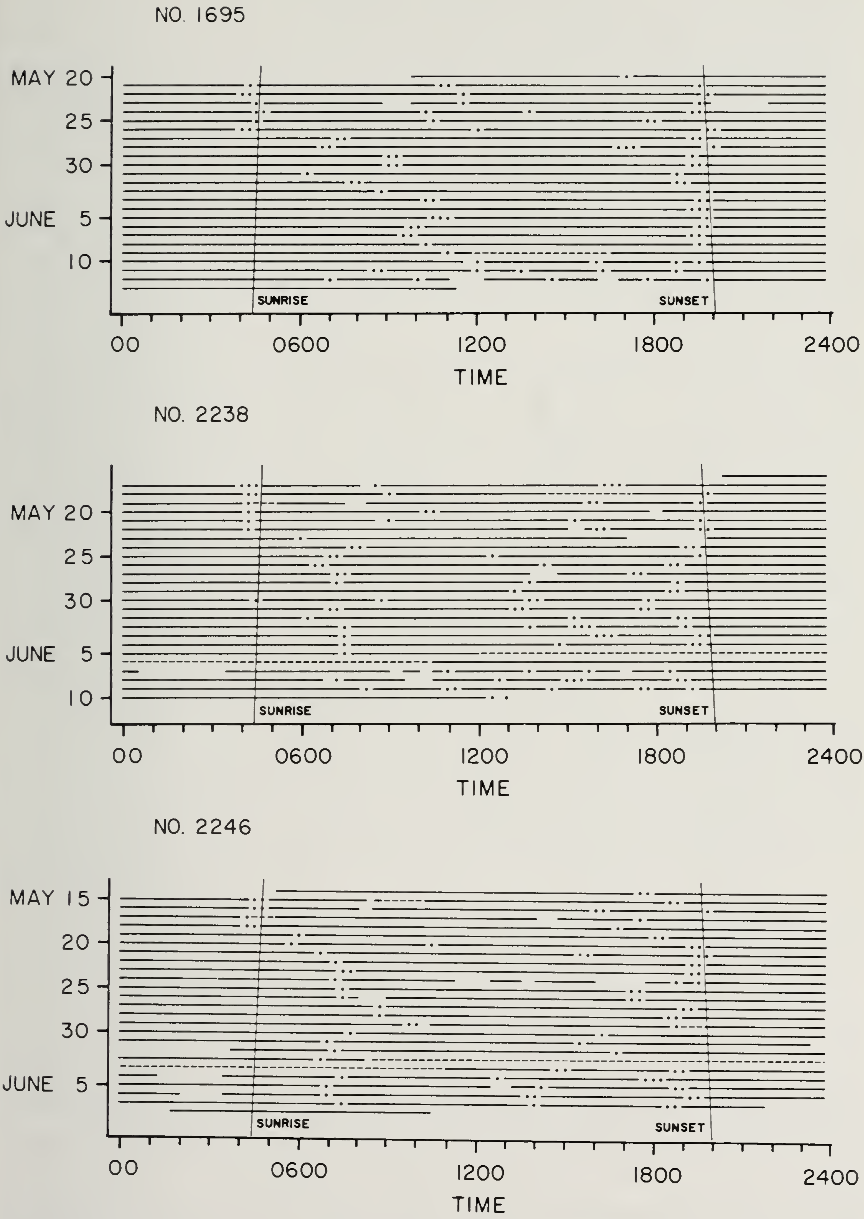
Bird No.	No. of Recorded Absences[1]	Absence Length (min)		Total Time Off Nest Per Day (min)[2]	
		Mean	Range	Mean	Range
1657	49	28	17– 77	70	47– 93
1690	65	19	8– 56	57	40– 77
1691	59	15	7– 32	41	18– 58
1695	64	21	6– 42	58	41– 96
2210	19	34	20– 82	65	46– 81
2219	32	24	11– 37	62	46– 76
2235	38	24	12– 59	46	34– 76
2238	50	22	13– 41	66	45– 93
2239	47	40	14–197	90	28–242
2241	37	23	5– 32	60	43– 81
2246	57	21	8– 37	52	33– 77
2248	73	19	7– 33	70	53–100

[1] Includes only absences where departure and return were determined to the nearest minute.
[2] Includes only those days on which nearly constant telemetry data were obtained.

of hatching. At that time the birds seemed restless and were frequently active at the nest site for short periods.

Daily activity of 3 hens is illustrated in Fig. 4. All hens demonstrated a shift in the temporal distribution of the first activity period of the day as incubation progressed. Activity usually began prior to sunrise during the early stages of incubation but later the start of activity was delayed as much as 4–5 h after sunrise. The beginning of this shift in activity ranged from 20–30 May in 1971 and from 16–25 May in 1972. Synchrony among hens was evident in 1972 when 5 of 7 began this shift during 22–25 May. The shift began during different stages of the incubation period (from the 4th to 19th day) for different hens. No relationship was evident between the onset of the activity shift and any trend in average hourly temperature, wind velocity and direction, or amount and time of occurrence of precipitation.

A possible relationship between plant phenology and the activity shift was noted in 1972 when phenologic events were studied in detail. During the week of 18–25 May the leaves of most trees and shrubs reached full size. The rapid leafing out resulted in a "closing in" of the forest canopy. During this period the ferns which made up much of the understory grew rapidly and nearly attained full size (approx. 1 m). The net effect was a marked reduction in the amount of light reaching the forest floor. Synchronization of circadian activity rhythms has been shown to be strongly affected by the day-



NO. 1695

NO. 2238

NO. 2246

Fig. 4. Daily periods of activity during the incubation period for Hens 1695, 2238, and 2246 (—— = inactive, · · · = active, – – – = known disturbances by humans, blank = no data).

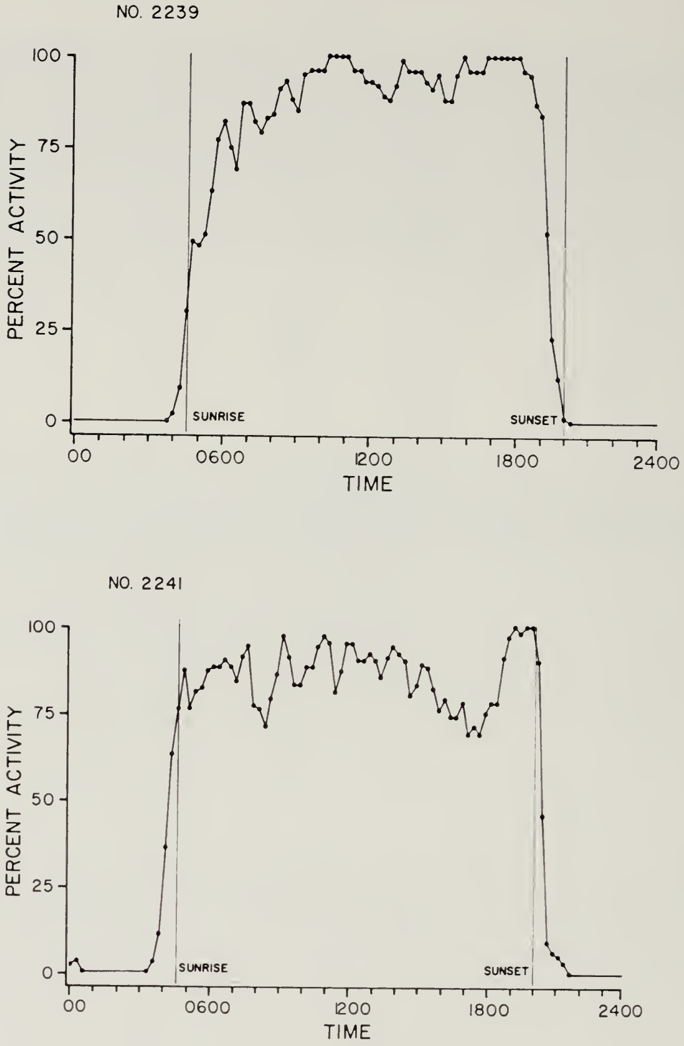


Fig. 5. Temporal distribution of percentage of 15-min intervals active during the post-incubation period for Hen 2239 (with brood) and Hen 2241 (no brood).

night cycle of illumination (Aschoff 1966). If the onset of morning activity during incubation is associated with light intensity at the nest, activity would likely start increasingly later as the tree canopy leafed over and herbaceous vegetation grew up around the nest.

On several occasions precipitation noticeably affected normal activity patterns. On 19 May 1971 a snow-rain storm from about 04:15–10:30 left a temporary accumulation of snow on the ground. Of 3 hens incubating at that time 2 did not leave the nest to feed until 14:00–14:15. The third remained on the nest until 17:30. Rain occurred during most of the morning hours on 29 May 1972. Several hens including 2238 and 2246 (Fig. 4) delayed or omitted the normal morning feeding period. On another occasion, at the onset of a hard rain shower, several hens which had been feeding returned to their nests almost immediately. This behavior is adaptive since egg temperatures are maintained during periods when rapid chilling would probably occur if the hen was absent.

Post-incubation.—Temporal distribution of percentage of 15 min intervals active during the post-incubation period was determined for 7 hens with broods and 4 broodless hens which had lost clutches to predators (Maxson 1974). As examples of these data Fig. 5 illustrates the activity patterns of Hen 2239 (with brood) and Hen 2241 (no brood). With but a single exception (Hen 2202), once activity peaked in the morning the birds maintained a high percentage of activity throughout most of the daylight hours until activity ceased in the evening. These daytime levels of activity were often higher than those observed during the pre-incubation period. Evening activity peaks tended to be greater than early morning peaks, but the pattern was not so consistent as during pre-incubation.

A difference in timing of the dawn-dusk peaks between hens with broods and those without broods was readily apparent. Brood hens did not attain the morning activity peak until 1–2¾ h after sunrise. The evening peak occurred 15 min–2 h prior to sunset. Broodless hens reached morning activity peaks 15–30 min after sunrise and evening peaks from 15 min before to 15 min after sunset.

Daily activity during the post-incubation period is illustrated for Hens 2239 and 2241 in Fig. 6. Hen 2239 began activity 2–3 h after sunrise during the first few days following hatching of the chicks. Thereafter, the onset of activity became progressively earlier until it approached sunrise on the 13th day. An almost identical pattern was exhibited by all brood hens. For the post-incubation period as a whole, brood hens began activity after sunrise on 101 of 114 (88.6%) grouse-days. Activity ceased prior to sunset on 104 of 115 (90.4%) grouse-days. In contrast, broodless hens initiated daytime activity prior to sunrise on 74 of 105 (70.5%) grouse-days and ceased activity after sunset on 55 of 83 (66.3%) grouse-days.

No doubt the delaying of morning activity onset and early evening activity cessation by brood hens is related to brooding of the chicks during cooler

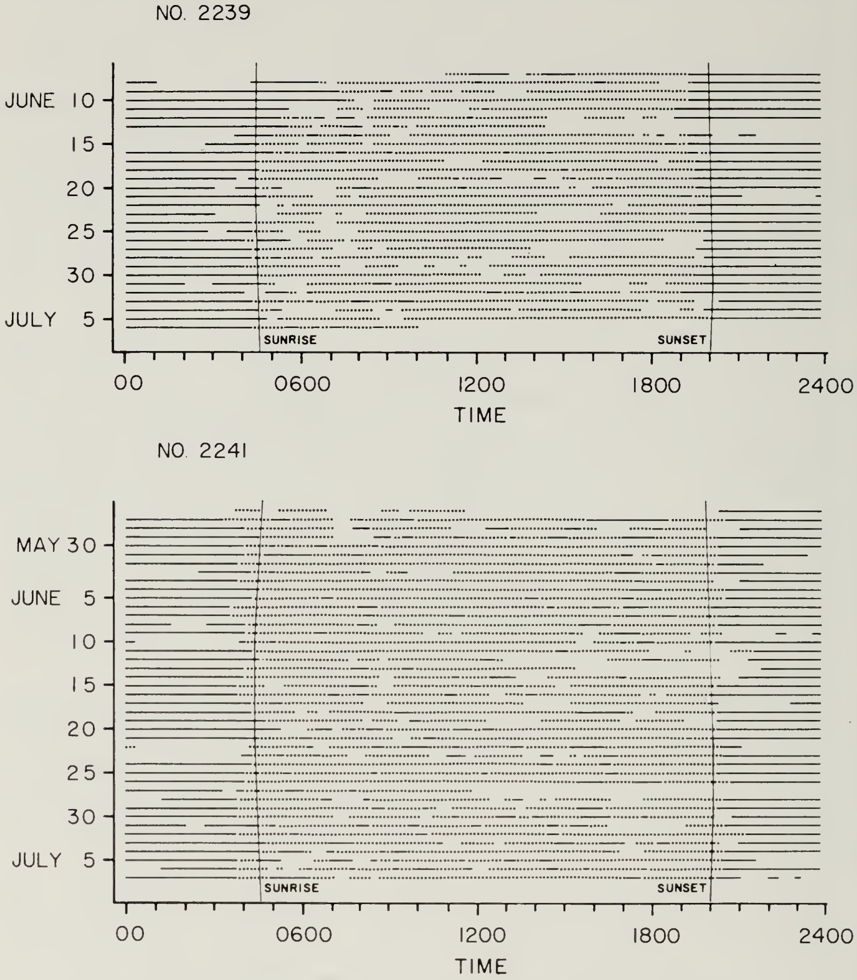


FIG. 6. Daily periods of activity during the post-incubation period for Hen 2239 (with brood) and Hen 2241 (no brood) (—— = inactive, · · · = active, blank = no data).

periods of the day. Brooding at these times was most pronounced during the first few days when chicks were least able to maintain body temperatures. Young chicks moving about during early morning hours would be exposed to wetting and rapid chilling due to heavy dew normally present. As the chicks grew older and more independent of the brooding hen, activity patterns of these hens gradually began to resemble those of broodless hens.

DISCUSSION

A major concern of telemetry studies is that the transmitter may cause behavioral changes in the study animals. Since many telemetry studies are conducted on animals difficult to observe in the wild, effects of the transmitter on behavior are difficult to determine. Boag (1972) stated that activity levels as well as food intake by captive female Red Grouse (*Lagopus l. scoticus*) were lower among radio-marked birds than controls, especially during the first week after transmitter attachment. At Cedar Creek properly fitted transmitter harnesses had no noticeable effects on behavior of Ruffed Grouse. The harnesses fitted so well that within a short time after release only the whip antenna on the bird's back was visible. During field observations it was not possible to distinguish marked from unmarked birds unless the whip antenna could be seen. Observations of captive grouse at Cedar Creek by Huempfner and Maxson (unpubl. data) also failed to reveal behavioral differences between marked and unmarked birds.

Data concerning Ruffed Grouse activity are available from several telemetry studies. Huempfner (unpubl. data) found that mid-day activity during the winter months (especially when birds were able to snow-burrow roost) was substantially lower than mid-day activity levels recorded during the present study. Brander (1965) reported that radio-marked Ruffed Grouse, in the absence of sufficient snow for burrowing, roosted at sunset and left the roost about 30 min before sunrise during March and April. His birds were inactive from mid-morning until mid-afternoon especially during March. The inactive periods probably reflect the need to conserve energy during the winter months. Schladweiler (1965) stated that Ruffed Grouse generally began activity 30–60 min before sunrise and ceased activity 30–60 min after sunset during the breeding season. Once activity began his birds tended to remain active most of the day without any prolonged inactive periods. Weather disturbed them little except when chicks were small. Probably a transition from prolonged mid-day inactive periods (Brander 1965, Huempfner unpubl. data) to few inactive periods during daylight hours (Schladweiler 1965, the present study) occurs during spring as temperatures increase and snow cover disappears.

The pattern of activity found in the present study (Figs. 1 and 5) is similar to the 2-peak activity pattern reported for several species of day-active birds by Aschoff (1966). The pattern of dawn peaks usually being lower than the dusk peaks was also evident in the data of other Cedar Creek researchers, e.g. Archibald (1973) for male grouse during spring and Pierson and Tester (unpubl. data) for several grouse of both sexes during November. This may prove to be the normal pattern throughout the year in this species. These morning and evening activity peaks are probably associated with feeding periods. Archibald (1973) observed male grouse feeding in trembling aspen (*Populus tremuloides*) clones during these times. On several occasions in the present study, I observed female grouse feeding in male aspen clones during the morning and evening activity peaks.

Egg laying.—Egg laying patterns similar to those of the present study (Figs. 2 and 3) have been found in domestic chickens (*Gallus gallus*) (Warren and Scott 1935, Scott and Warren, 1936), and pheasants (*Phasianus colchicus*) (Labisky and Jackson 1966). Warren and Scott (1935) stated that differences in time intervals between eggs in a sequence were probably due to differences in the time an egg spends in the uterus. Scott and Warren (1936) determined that skipping of one or more days between laying sequences was caused by a delay in ovulation of the first egg of a sequence rather than by overnight retention of a fully developed egg in the uterus. Probably the Ruffed Grouse follows a similar pattern of delaying ovulation between laying sequences.

The tendency for hens to remain inactive on the nest during laying visits for longer periods as the clutch neared completion was also noted in Spruce Grouse (*Canachites canadensis franklinii*) (McCourt et al. 1973).

Incubation.—Bump et al. (1947:288–289), Kupa (1966), and Schladweiler (1968) reported that incubating Ruffed Grouse usually left the nest for short periods, only a few times per day, as I found in the present study (Table 2, Fig. 4).

Skutch (1962) stated that, with the exception of certain nidifugous species, most birds which incubate alone cover their eggs 60–80% of the daytime. Tetraonids of at least several species exhibit nest attentiveness greater than 80%. In the present study, hens averaged 95.7% of the incubation period on the eggs. Kupa (1966) stated that Ruffed Grouse hens spent an average of 23 h and 12 min (96.7%) on the nests each day. Lennerstedt (1966) reported that a Capercaillie (*Tetrao urogallus*) hen, during 12 days of its incubation period, was off the nest only 4.9% of the time. McCourt et al. (1973) stated that 2 incubating Spruce Grouse spent 93% of daylight hours on the nest.

The shift in timing of the first activity period of the day exhibited by all hens in the present study (Fig. 4) has not been noted by other researchers. Lennerstedt (1966) reported that activity periods of an incubating Capercaillie were fairly evenly distributed throughout the day except from 18:00–23:00 when no absences occurred. Although his study was conducted under conditions of continuous daylight the data indicate that onset of activity periods between 03:00–06:00 gradually shifted from slightly after 03:00 to about 05:20 over the period of study. This shift is similar to that observed during my study but more data are needed to determine if the pattern is consistent among birds.

SUMMARY

Seventeen female Ruffed Grouse were equipped with radio transmitters and monitored with an automatic radio tracking system. Activity data were divided into pre-incubation, incubation, and post-incubation periods for each hen.

During the pre-incubation period peaks of activity were closely associated with sunrise and sunset. The evening peak was greater than the morning peak for all hens. Activity normally began 30–60 min prior to sunrise and ceased 15–45 min after sunset. Daytime activity seldom fell below the 50% level.

Egg laying patterns were determined for 8 hens. Hens seldom visited the nest site prior to the onset of egg laying and, once laying began, were rarely near the nest except during presumed laying visits. During laying visits hens typically remained inactive on the nest from 1 to several hours. Laying visits occurred 1–5 days in succession at 25–30 h intervals. When the next egg of a sequence appeared to be due sometime after the end of evening activity the egg was not laid until the following morning.

Evidence is presented that one hen successfully renested.

During incubation hens most often left the nest 2 or 3 times per day to feed. Most birds averaged 18–24 min per absence and 57–70 min off the nest per day. All hens exhibited a change in timing of the first activity period of the day as incubation progressed. This activity change may be related to plant phenology.

During post-incubation, once activity began in the morning, birds usually maintained a high percentage of activity throughout most of the daylight hours until activity ceased in the evening. Evening activity peaks tended to be higher than morning peaks. Brood hens did not attain the morning peak until 1–2¾ h after sunrise. The evening peak occurred 15 min–2 h prior to sunset. In contrast, broodless hens reached morning peaks 15–30 min after sunrise and evening peaks from 15 min before to 15 min after sunset. This difference between hens with and without broods is related to brooding of the chicks during the cooler portions of the day by the brood hens.

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WEIGHTS AND FAT CONDITION OF SOME MIGRANT WARBLERS IN JAMAICA

A. W. Diamond, P. Lack, and R. W. Smith

In the Old World, deposition of fat before migrating has been described in both summer and winter quarters of many Palaearctic bird species (references in Pearson 1971), but in the New World there has been only one study outside continental North America (Rogers and Odum 1966). During a study of the annual cycles of forest birds in Jamaica (Diamond 1974), we caught over 400 parulid warblers of 19 species (see also Diamond and Smith 1973, Lack and Lack 1973). This paper describes the variation in weight and visible fat condition of 302 of the 7 most commonly caught species; mean weights of all the migrant warblers caught are given in an Appendix. Warblers were caught between October 1970 and May 1971 by A. W. D. and P. L., in August and September 1971 by A. W. D. and from September 1971 to April 1972 by R. W. S. and S. Gowen. Nomenclature follows Bond (1971) for birds, and Adams (1972) for plants.

TRAPPING SITES AND METHODS

The 4 main trapping sites (Fig. 1a) were as follows:

Port Henderson Hill.—Altitude 155 m. Low xeric scrub ("dry limestone scrub forest" of Asprey and Robbins 1953), much disturbed by cutting for charcoal, rarely exceeding 3 m high, and dominated by red birch ("Gumbo Limbo") (*Bursera simaruba*) and the tall cactus *Stenocereus hystrix*;

Mona Woods.—Altitude 185 m. A small patch of secondary riverine forest, with a canopy 15 to 18 m high and a dense undergrowth of shrubs and creepers. Most birds were caught beside a stream leading out of the Mona Reservoir;

Irish Town.—Altitude 770 m. A small garden on the crest of a ridge, with thick scrub on the slopes and secondary forest, mostly of native trees, in the valley on one side;

Green Hills.—Altitude 1080 m. The garden of the Institute of Jamaica Field Station, surrounded by montane forest, on the northern (windward) side of the western end of the Blue Mountain range.

All the birds were caught in mist nets, mostly between dawn and noon but some, especially at Irish Town, in the evening. All birds were weighed to the nearest 0.25 g on a "Pesola" spring balance with a range of 0–50 g.

Subcutaneous fat was estimated as follows (Diamond 1974): each of 4 areas of the body (furculum, axilla, abdomen, and rump) was scored independently, on a scale from 0 (no fat) to 3 (fat mounded), giving a summed possible range of scores of 0–12. Fat score and weight were correlated (Spearman's rho $= 0.3$, $p < .01$), but the relationship is weak enough that weight and fat score did not always vary in parallel.

Insufficient data were obtained for a detailed analysis of diurnal changes in weight or fat in any one species. However when all 7 species were treated together, weights taken before 10:00 were significantly less (by about 5%) than those taken after 10:00

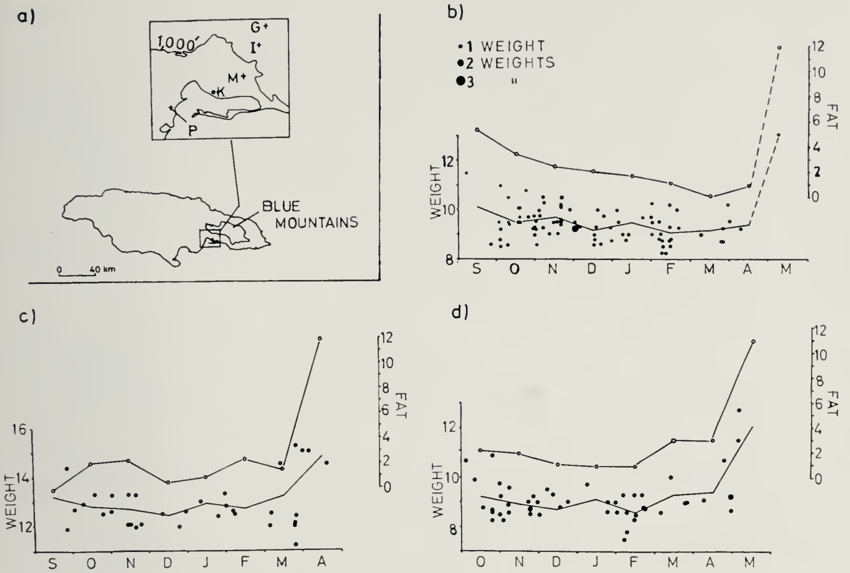

FIG. 1. (a) Sketch map of Jamaica. Inset: location of netting sites described in text. (b)–(d) Changes in weight and visible subcutaneous fat through the winter for (b) Black-and-white Warbler, (c) Worm-eating Warbler, and (d) Black-throated Blue Warbler. Individual weights are shown as solid circles; a solid line connects monthly means. Open circles show monthly median fat scores. Weight and fat are corrected for diurnal variation (see text).

($p < .001$, 2-tailed t-test). Fat scores before 10:00 also averaged 60% lower than those after 10:00 ($p < .001$, 2-tailed median test). Unless noted otherwise, all weights and fat scores in this paper are "morning" ones, those after 10:00 having been corrected by subtracting 5% (weight) or 60% (fat score). Weight loss of birds kept overnight was greater than 5%, averaging 8.9% (12 birds) ; 5% represents the average weight difference over a time period varying from 0 to 12 h, and so is less than the weight lost overnight, i.e. over 12 h.

In 4 species it has been possible to compare the weights from Jamaica with weights from a North American breeding area, the Powdermill banding station in Pennsylvania (referred to below simply as "Pennsylvania") ; Powdermill weights from June and July only have been used, since birds caught then are likely to be local breeders rather than migrant birds. The other 3 species were not caught regularly in the summer at Powdermill so for comparison we have used weights given by Baldwin and Kendeigh (1938) and Wetherbee (1934) although these, like our Jamaican weights, may include some migrant birds.

SPECIES ACCOUNTS

Black-and-white Warbler (*Mniotilta varia*).—These were common throughout the island, and were seen from early September through May. This was one of 2 species caught regularly at all 4 trapping sites. Fat score declined gradually through the winter (Fig. 1 b); weight remained steady, but weights of retrapped birds (Table 1) appeared to decrease slightly through the winter. The few birds caught in April were slightly heavier than those trapped in March, and the single bird caught in May had the maximum possible fat score and was about 25% heavier than any bird caught during the winter. Winter weights were significantly lower than the mean weight (10.9 g) of 15 birds caught in Pennsylvania in June and July (2-tailed t-test, $p < .001$), and several February weights were below the lowest weight (8.5 g) recorded by Drury and Keith (1962) in migrant birds.

Worm-eating Warbler (*Helmitheros vermivorus*).—Widespread from late September to April. This rather skulking species fed mainly in undergrowth and was caught at all the trapping sites except Port Henderson. The few birds caught in September were lean; fat scores rose thereafter, except in December, but weights remained steady through the winter until March, when both weight and fat score rose sharply (Fig. 1 c). One individual retrapped in late March was 21% heavier than in early February.

Black-throated Blue Warbler (*Dendroica caerulescens*).—This species arrived later than most others, none being caught before October; it was caught in all the trapping sites except Port Henderson. Weight and fat declined slightly from October through February, rising thereafter to a maximum in May (Fig. 1 d). The weights of the 2 birds retrapped in May were 46% and 62% higher than their respective winter weights (Table 1). Several birds caught in October and November were considerably heavier than most caught during the winter. Two birds weighed in February were close to the fat-free weight of 7.6 g given by Connell et al. (1960).

Prairie Warbler (*Dendroica discolor*).—Found mainly in the lowlands, Prairie Warblers were caught between late August and April, most commonly at Port Henderson but also at Mona Woods and Irish Town. Weight and fat were high in autumn and spring, low from October through March (Fig. 2 a). The average weight of 3 immatures in summer, 7.2 g (Wetherbee 1934), is higher than most winter weights.

Ovenbird (*Seiurus aurocapillus*).—This and the Black-and-white Warbler were the only species caught regularly at all trapping sites. Most birds were lean in September and October (Fig. 2 b), and weights increased from September through November, then remained steady until March. The few individuals caught in April were the fattest and heaviest Ovenbirds caught during the study, and one bird caught twice in April increased in weight by 41% in 20 days. Most winter weights were below the mean weight of 19.7 g given by Wetherbee (1934) and Baldwin and Kendeigh (1938) for 15 birds between May and August, but were not significantly different from those of 16

TABLE 1
WEIGHT CHANGES IN RETRAPPED INDIVIDUAL WARBLERS

Black-and-white Warbler					
A*	18 Oct—9.75**	F	17 Nov—9.5	K	30 Nov—9.5
	8 Jan—9.0		16 Dec—9.0		21 Feb—9.25
			12 Jan—9.0		25 Mar—9.25
B	31 Oct—9.25		8 Mar—9.0		
	1 Nov—8.5			L	24 Jan—9.75
	6 Nov—9.25	G	20 Nov—10.25		30 Jan—9.75
			11 Dec—9.5		6 Feb—9.5
C	31 Oct—9.0				
	4 Dec—9.25	H	1 Dec—9.25	M	20 Feb—10.0
	14 Feb—9.25		16 Dec—8.5		25 Mar—8.75
			8 Feb—8.25		
D	3 Nov—10.0			N	18 Oct—9.5
	29 Mar—10.25	I	16 Dec—9.0		28 Nov—9.0
			15 Feb—8.75		
E	6 Nov—10.5			O	7 Nov—10.25
	31 Jan—10.25	J	1 Feb—9.0		4 Dec—9.5
			9 Feb—8.5		
Worm-eating Warbler					
A	1 Nov—12.5	C	18 Oct—13.25	E	6 Feb—12.5
	23 Jan—12.5		16 Nov—13.75		25 Mar—15.25
B	14 Nov—12.0	D	14 Nov—11.5	F	17 Oct—12.75
	5 Mar—12.0		29 Dec—12.5		27 Nov—12.5
			24 Mar—12.0		
Black-throated Blue Warbler					
A	31 Oct—9.75	D	14 Feb—8.25	H	3 Nov—8.25
	24 Jan—9.0		20 Feb—8.75		16 Nov—9.25
	30 Jan—9.0				24 Nov—8.75
	14 Feb—9.25	E	24 Nov—8.75		8 Jan—9.75
			5 May—12.75		
B	24 Nov—8.5			I	17 Dec—8.75
	7 Feb—7.5	F	13 Mar—10.0		23 Dec—9.0
			25 Apr—10.75		
C	7 Dec—9.5			J	24 Dec—7.0
	6 Feb—9.25	G	24 Oct—11.0		5 May—11.5
			30 Apr—10.0		

TABLE 1 (Continued)

Ovenbird					
A	31 Oct—16.5	C	12 Jan—19.5	F	29 Oct—20.0
	30 Nov—17.5		15 Feb—19.5		12 Nov—20.25
	29 Dec—17.0				
	20 Jan—17.0	D	24 Mar—19.5	G	11 Dec—19.0
	31 Jan—15.25		31 Mar—20.25		23 Dec—19.5
B	23 Oct—19.0	E	28 Nov—18.25	H	23 Jan—19.0
	8 Apr—17.5		12 Dec—18.5		30 Jan—19.25
	28 Apr—24.5				
				I	24 Nov—19.25
					24 Dec—20.25
Common Yellowthroat					
A	23 Dec—9.5	D	19 Nov—9.0	G	2 Oct—11.25
	11 Jan—9.75		9 Feb—9.25		11 Dec—10.25
			16 Feb—9.25		
B	1 Feb—10.25			H	11 Dec—10.5
	9 Feb—9.75	E	29 Dec—9.0		28 Apr—10.0
			30 Jan—9.0		
C	16 Feb—10.5			I	11 Dec—10.5
	24 Mar—9.75	F	8 Nov—9.75		8 Apr—8.75
			25 Apr—11.5		
Prairie Warbler					
A	17 Nov—6.5	B	17 Nov—6.25		
	12 Jan—6.5		8 Mar—6.5		
	15 Feb—6.5				
American Redstart					
A	1 Nov—7.0	B	14 Feb—7.0		
	29 Dec—6.5		5 Mar—7.0		
	24 Jan—6.5				

* Dates and weights for each lettered group indicate successive captures of one individual.
** Weight in grams.

birds caught in Pennsylvania in June and July and were well above the mean fat-free weight of 16.0 g given by Rogers and Odum (1966).

One bird, retrapped 5 times at Irish Town, dropped in weight suddenly in January and was not caught again (Table 1); its last recorded weight was about 20% below the average winter weight.

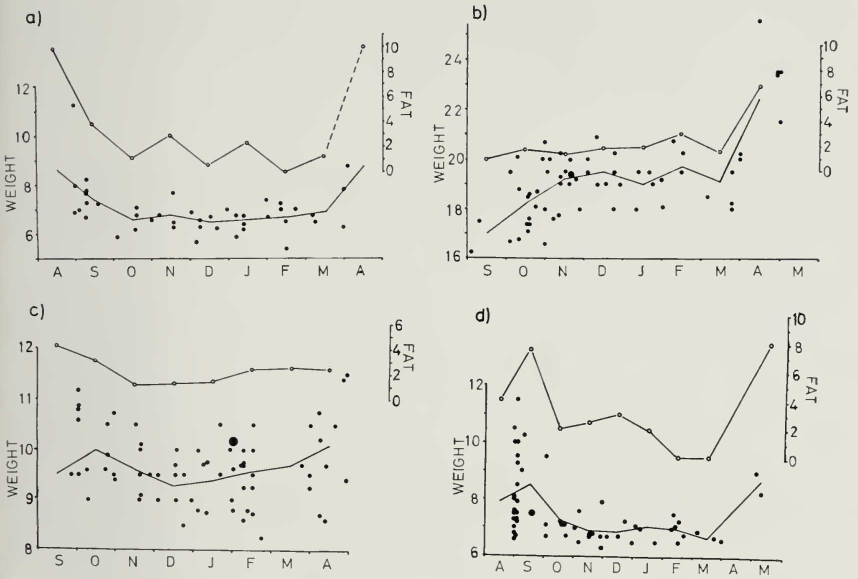

FIG. 2. As Fig. 1 (b)–(d). (a) Prairie Warbler. (b) Ovenbird. (c) Common Yellowthroat. (d) American Redstart.

Common Yellowthroat (*Geothlypis trichas*).—Present from September through April, Yellowthroats favored dense undergrowth and long grass; most were caught in Mona Woods, where both these habitats abound, but a few were trapped at Irish Town and Green Hills. Weight and fat were as high in autumn as in spring (Fig. 2 c). Most winter weights were below the 10.4 g mean of 24 summer weights given by Wetherbee (1934) and Baldwin and Kendeigh (1938), but did not differ significantly from those of 60 birds weighed in Pennsylvania in June and July.

American Redstart (*Setophaga ruticilla*).—We caught this species between late August and mid-May (although according to Bond (1971) it is found throughout the year in the Greater Antilles) in all habitats but most commonly at Port Henderson. Autumn weights were very variable, and many were higher than the few spring weights obtained (Fig. 2 d). Both fat score and weight declined from September through November; fat apparently declined again from January through March, while weight remained constant, but this apparent difference may be due to the small number of birds scored for fat during this period. Most winter weights were within the range of fat-free weights (6.6 to 7.1 g) given by Rogers and Odum (1964), and most were below the lowest weight (7.1 g) recorded by Drury and Keith (1962) in migrant birds; the mean weight of birds caught in Jamaica was significantly lower than the mean (8.6 g) of 25 birds caught in June and July in Pennsylvania (2-tailed t-test, $p < .001$).

DISCUSSION

All the species described here increased in both weight and fat score prior to the spring migration. As has been found in North American migrants leaving Central America (Rogers and Odum 1966) and in Palaearctic migrants leaving Africa (Pearson 1971), very few fat individuals were caught in spring, and populations disappeared very soon after the first fat birds were recorded; this could be due either to birds laying down fat very quickly, or to their departing while still lean, or to a change in feeding behavior which makes the birds more difficult to catch. That some Palaearctic migrants in Africa do lay down fat very quickly is well known, but Pearson (1971) thought that some leave their wintering areas, particularly those well to the south of the Sahara, in a relatively lean condition. The same may be true in Jamaica, since Cuba would make a convenient stepping-stone for birds making for Florida, a further 300 km to the north, but we caught too few birds in spring to be able to decide among these possibilities.

Rogers and Odum (1966) found that many migrants arriving in Central America in autumn were extremely lean and may have begun to use non-fat tissue as fuel. Some species were very lean on arrival in Jamaica (*Helmitheros vermivorus*, *Seiurus aurocapillus*), but most were quite heavy on arrival and some (*Dendroica discolor*, *Geothlypis trichas*, *Setophaga ruticilla*) were as fat then as in the spring. Pearson (1971) interpreted the presence of heavy, fat birds in autumn as evidence of migration through the area. He pointed out that this could be confirmed only by retrapping birds which arrive with very little fat, put on weight quickly and then leave, but only very intensive trapping could reveal this pattern. It is also possible that winter residents may lose weight after arrival in autumn, having put on more fat than was used to reach the winter quarters. This seems to happen more often in spring than in autumn, at least in the New World (Rogers and Odum 1966); among Palaearctic species there is less evidence, but Reed and Sedge warblers (*Acrocephalus scirpaceus* and *A. schoenobaenus*) frequently lose weight after arriving in their summer quarters in Britain (G. Hirons, pers. comm.). Presumably it is advantageous for a migrant to put on as much fat as possible before a long flight, even if some of it is not needed if flying conditions prove favorable.

Most birds which winter in the Antilles arrive there from the north (Drury and Keith 1962). Some of these species winter in northern South America as well as the West Indies, but others, such as Prairie and Black-throated Blue warblers, winter almost exclusively on Caribbean islands. Most Prairie and Black-throated Blue warblers which arrive in Jamaica are probably winter residents. It is possible, however, that some Prairie Warblers pass through Jamaica on their way to winter quarters further east in the Caribbean, since Jamaica lies only a little to the south of the direct line between the western end of the Prairie Warbler's breeding range and islands in the eastern Caribbean. American Redstarts, Yellowthroats and Black-and-white Warblers all winter in northern South America as well as in the Antilles, and the heavy individuals of these species which were caught in autumn may have included some migrating birds. Few heavy Worm-eating Warblers were caught in autumn; this species does not winter in South America (Bond 1971) so most of the birds caught in Jamaica are probably winter residents, though a few may be on migration to Central America. The Ovenbird was the only species in which there was evidence that any birds arrived in a depleted condition; no particularly heavy birds were caught in autumn, although the species does winter in northern South America and some migration through Jamaica might have been expected.

A notable feature in most species was the low level of fat carried through the winter; median fat scores for the months November through February were between 1 and 4. Leck (1972) suggested that migrants in Panama were under greater feeding pressure than residents, particularly in bad weather, and if this were also true in Jamaica, it might explain the low fat levels carried by migrants during the winter. However, in Jamaica at least, there is little if any competition between migrants and residents (Lack and Lack 1973), and most resident species are fatter during the winter than during the breeding season (Diamond 1974). Residents do not show any spring fattening comparable to that of migrants. Most begin to breed at the same time as the migrants lay down fat, presumably in response to the increase in insect numbers which begins in February and March.

In addition to the small fat deposits carried by most species in winter, 2 species, the Black-and-white Warbler and American Redstart, were also lighter than birds weighed in summer on their breeding grounds. Comparisons between Jamaican and North American weights must be treated with caution, since the origin of the Jamaican wintering birds is not known. It is worth pointing out that warblers may well be leaner and lighter in winter than in summer; a similar suggestion was made by Moreau (1944) in comparing the weights of Palaearctic migrants in Europe with those in Africa. In both cases the comparison is difficult because there are so few published weights of breeding birds.

SUMMARY

Weights and fat scores are described for 7 species of migrant parulids mist-netted in Jamaica in 1970–72.

Weights were variable in autumn in most species, some of which may have been on migration; most autumn arrivals were probably winter residents. Fat levels and weights were low during the winter and 2 species (Black-and-white Warbler and American Redstart) were significantly lighter than birds caught in June and July in Pennsylvania.

Mean weights of all species increased in spring, though few birds were trapped then and it is possible that some individuals left Jamaica with low fat levels.

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APPENDIX

MEAN WEIGHTS (G) OF MIGRANT PARULID WARBLERS IN JAMAICA

		n	$\bar{x}$	s^2	max
Black-and-white Warbler	♂	14	9.25	0.2	10.0
Mniotilta varia	♀	30	9.5	0.2	13.0
Swainson's Warbler		18	15.0	1.1	17.5
Limnothlypis swainsonii					
Worm-eating Warbler		37	13.0	0.8	15.25
Helmitheros vermivora					
Tennessee Warbler		3	8.5	0.1	–
Vermivora peregrina					
Northern Parula	♂	7	7.0	0.7	–
Parula americana	♀	10	7.0	0.3	–
Magnolia Warbler		6	7.75	0.9	–
Dendroica magnolia					
Cape May Warbler		13	9.25	0.3	10.0
Dendroica tigrina					
Black-throated Blue Warbler	♂	7	9.0	0.2	–
Dendroica caerulescens	♀	19	8.75	0.4	12.75
Black-throated Green		9	7.5	0.4	–
Warbler *Dendroica virens*					
Blackburnian Warbler		1	8.75	–	–
Dendroica fusca					
Yellow-throated Warbler		2	8.5	–	–
Dendroica dominica					
Pine Warbler		1	10.5	–	–
Dendroica pinus					
Blackpoll Warbler		1	13.5	–	–
Dendroica striata					
Prairie Warbler	♂	17	7.5	1.3	11.25
Dendroica discolor	♀	18	6.75	0.3	8.0
Palm Warbler		3	9.5	0.2	–
Dendroica palmarum					
Ovenbird		63	19.25	3.2	25.5
Seiurus aurocapillus					
Northern Waterthrush		10	15.75	0.6	20.75
Seiurus noveboracensis					
Common Yellowthroat	♂	30	9.75	0.3	11.25
Geothlypis trichas	♀	18	9.25	0.5*	11.5
American Redstart	♂	21	7.5	0.8	11.5
Setophaga ruticilla	♀	28	7.5	1.3	10.25

* Differences between sexes significant different at .01 level.

** Differences significant at .001 level (2-tailed t-test).

GENERAL NOTES

Wing molt of the Kittlitz's Murrelet.—Knowledge of the relation between timing of molt and other annual cycle events in birds is important to an understanding of breeding seasons. Although no study of the natural history of the Kittlitz's Murrelet (*Brachyramphus brevirostris*) has been conducted, published field observations and information on molt obtained from museum specimens presented here permit the timing of molt in relation to breeding to be outlined.

I examined 213 specimens from the collections of the Denver Natural History Museum (DNHM), Museum of Comparative Zoology at Harvard Univ. (MCZ), Univ. of British Columbia (UBC), Univ. of California Museum of Vertebrate Zoology (MVZ), Univ. of Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), the American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Chicago Natural History Museum (CNHM), Carnegie Museum (CM), Peabody Museum of Natural History (PMNH), Univ. of Alaska (UA), and the Univ. of Kansas Museum of Natural History (KU).

The status of each primary of the 14 specimens in molt was recorded by assigning to each growing feather a score, according to its growth stage, of 1 (empty or pin feather) 2, 3, or 4. Full-grown new feathers score 5, so that in newly molted birds, each feather is scored 5. A completed molt score is 50 since I quantified feather replacement only on the left wing (Table 1).

Bent (U.S. Natl. Mus. Bull. 107, 1919) and Demente'ev and Gladkov (Birds of the Soviet Union, Vol. 2. IPST, Jerusalem, 1968) stated that adult Kittlitz's Murrelets undergo 2 seasonal molts, a partial prealternate molt in spring and a complete prebasic molt in late fall or early winter. Kozlova (Fauna of the USSR: Birds 2:1–140, IPST, Jerusalem, 1961) noted that although the dates of the complete prebasic molt are not known, the partial prealternate molt is completed by late May. The prealternate molt occurs apparently rapidly between mid-April and mid-May. Laing (Victoria Mem. Mus. Bull. 40, 1925) took a male in basic plumage on 22 March 1924 in Chignik Bay, Alaska. A male (MCZ 250797) taken on 9 April 1916 near Bethel, Alaska, is in its basic plumage with no wing or body molt and little wear of the remiges. A female (Bailey, Colorado Mus. Nat. Hist., Pap. Ser. 8, 1948) taken on 28 April 1922 near Wales and a female (USNM 92184) collected near Cape Etolin, Alaska, on 3 April 1883 are in their basic plumages as are 2 males (KU 40294, 40295) taken on 15 April 1960 near Point Hope. Four males (AMNH 757401, CNHM 456901, MCZ 320031, MVZ 14534) and 2 females (AMNH 753398, 753399) taken in Glacier Bay on 16 May 1913 are in their alternate plumages.

The simultaneous wing molt does not begin until late August (see Table 1); the birds are rendered flightless. A female (DNHM 19287) taken by A. M. Bailey near Barrow on 26 July 1936 is of interest. Its primaries were molted and being replaced by new ones and the bird was flightless. It had failed possibly at breeding and had initiated a rapid and early wing molt. Premature body molting due to apparent breeding failure has been reported in auklets (*Aethia* spp.) by Bédard (Can. J. Zool. 47:1025–1050, 1969) and in the Marbled Murrelet (*B. marmoratus*) by Sealy (Bird-Banding 46: 141–154, 1975).

The breeding season (egg-laying to fledging of young) of the Kittlitz's Murrelet in Alaska spans the period from early June to mid-August (Thayer, Condor 16:117–118, 1914; Bailey, Auk 44:1–23, 1927; Ford, Auk 53:214, 1936; Thompson et al., Auk 83: 349–351, 1966; Bailey, Condor 75:457, 1973; J. Bédard, pers. comm.).

TABLE 1

MOLT OF THE LEFT PRIMARIES OF THE KITTLITZ'S MURRELET[a]

Specimen	Date, sex, locality, molt status	Primary number									
		1	2	3	4	5	6	7	8	9	10
CNHM 159075	26 Sept. 1929, ♂ Barrow: score 25	2	2	3	3	3	3	2	3	2	2
CNHM 159076	17 Sept. 1941, ♂ Barrow: score 21	1	1	2	2	3	3	3	2	2	2
CNHM 159077	26 Sept. 1929, ♀ Barrow: score 29	1	2	2	3	3	4	4	4	3	3
CNHM 159078	26 Sept. 1929, ? Barrow: score 30	1	2	2	3	4	4	4	4	3	3
DNHM 19287	26 July, 1936, ♀ ? ? score 22	2	2	2	2	3	3	2	2	2	2
LACM 78605	fall, 1962, ♀ Barrow: score 26	1	1	1	2	3	3	4	4	4	3
PMNH 1460	17 Sept. 1941, ♂ Barrow: score 18	2	2	2	2	2	2	1	2	2	1
PMNH 9278	25 Aug. 1936, ? Barrow: score 8	1	1	1	1	1	1	1	1	0	0
PMNH 9279	25 Aug. 1936, ? Barrow: score 14	1	1	2	2	2	2	2	2	0	0
PMNH 9285	17 Sept. 1941, ♀ Barrow: score 0	0	0	0	0	0	0	0	0	0	0
UMMZ 125204	25 Aug. 1936, ♀ Barrow: score 16	2	2	2	2	2	2	2	2	0	0
UMMZ 125205	25 Aug. 1936, ♂ Barrow: score 7	1	1	1	1	1	1	1	0	0	0
UMMZ 125206	17 Sept. 1941, ♂ Barrow: score 18	2	2	2	2	2	2	2	2	1	1
UMMZ 125207	17 Sept. 1941, ♂ Barrow:score 21	2	2	2	2	2	2	2	2	3	2

[a] Explanation of symbols: 0, feather that is old; 1, empty socket or pin feather; 2, growing feather with vane up to one-third grown; 3, growing feather with vane between one-third and two-thirds grown; 4, growing feather with vane more than two-thirds grown but not full length; 5, feather full length, but still with blood in calamus.

Thus, the prebasic molt does not overlap breeding; the young have fledged by the time this molt begins in late August. The separation of breeding and prebasic molt has been recorded also in the Marbled Murrelet and Ancient Murrelet (*Synthliboramphus antiquus*) by Sealy (Bird-Banding 46:141–154, 1975; Condor 78:294–306, 1976).

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Memorial Fund of the American Museum of Natural History and the National Research Council of Canada.—Spencer G. Sealy, *Dept. of Zoology, Univ. of Manitoba, Winnipeg, Canada. Accepted 9 Apr. 1976.*

Incidence of runt eggs in the Canada Goose and Semipalmated Sandpiper.—There are few published reports of runt (dwarf) eggs in nature (Rothstein, Wilson Bull. 85:340–342, 1973) and little is known about the rate at which they occur in a given population. In 1973, while working under contract for the Canadian Wildlife Service on North Twin Island in James Bay, we examined about 950 eggs of various species. These included about 500 eggs (122 nests) of the Canada Goose (*Branta canadensis*) and 29 eggs (8 nests) of the Semipalmated Sandpiper (*Calidris pusilla*). In one Canada Goose nest, found on 19 May, there were 3 normal eggs ($\bar{x}$ 82.9 × 56.5 mm, 148 g) and a runt (46.4 × 35.8 mm, 39 g). The runt was only 26% of normal weight and unusually spherical. After boiling it was opened and found to contain a rather fibrous yolk, 5 mm in diameter. We did not disturb the normal eggs and their number had not changed by 25 May. Another Canada Goose nest, found on 16 June, contained 2 runt eggs (61.1 × 35.2 mm, 39.8 g; 56.0 × 34.3 mm, 35.0 g), but no normal eggs. These runts had no yolks and were, in Palmer's terminology (Handbook of North American Birds, Yale Univ. Press, New Haven, Conn., 1:13, 1962), "long elliptical." The female goose was apparently incubating the eggs in a normal manner and, unless it was a replacement clutch, had probably been so doing for nearly the full term—as other clutches were already hatching. One Semipalmated Sandpiper's nest contained 3 normal eggs ($\bar{x}$ 29.8 × 21.5 mm, approx. vol. 70.5 cc) and a runt egg (22.2 × 16.1 mm, approx. vol. 29.5 cc) of normal shape and color, but a volume only 42% normal. The normal eggs hatched 3 July but the fate of the runt is unknown.

Based on the above figures, the rate of occurence of runt eggs is 0.6% for the Canada Goose or 0.4% if the 2 runts found in one nest are considered a single instance, 3.4% for the Semipalmated Sandpiper and 0.4% for all eggs examined by us in 1973. Unfortunately the samples are not random, because if no runts had been found there would have been no report. Museum samples are also liable to be biased upwards, because of a tendency for the unusual to be collected. If, therefore, we are to obtain reliable estimates of the rate of incidence of runt eggs in general and perhaps to make comparisons between species and populations it will be necessary for those handling large numbers of eggs to keep, at least approximate, records of the number of eggs they examine, even if no abnormality is found. Barth (Zool. Mus. Univ. Oslo, Contrib. 81, 1967) found only 1 runt among 4560 eggs (0.02%) in 4 species of gulls (*Larus*) and Ricklefs (Bird-Banding, 46:169) one runt in about 2000 eggs (0.05%) of the Starling (*Sturnus vulgaris*). We cannot recall previously finding a runt in the many eggs examined.—T. H. Manning and Brenda Carter, *RR 4 Merrickville, Ontario, Canada, KOG INO. Accepted 22 Apr. 1976.*

Late fledging date for Harris' Hawk.—On 29 November 1975, as part of an Arizona Raptor Study Committee project, we banded two nestling Harris' Hawks (*Parabuteo unicinctus*) approximately 40 km north of Phoenix, Maricopa County, Arizona. These 2 birds subsequently fledged sometime between 2 and 4 December 1975. This is the latest recorded fledging date for the species.

Previously recorded late dates are: a nest with fledged young in October and

November (LeSassier and Williams, Wilson Bull. 71:386–387, 1959); nests with young fledged in September (Pache, Wilson Bull. 86:72–74, 1974); and nest with recently fledged young 26 October 1975 (Mader, Auk in press).

The Arizona nest was located in excellent Harris' Hawk habitat. Additionally, 1975 was a year of high desert cottontail (*Sylvilagus auduboni*) numbers, and the caretaker of the nearby golf course was systematically shooting these mammals and not retrieving them. Coyotes (*Canis latrans*) were observed carrying off the carcasses, and the Harris' Hawks may also have been using this source of food; cottontail skulls, tails, and legs were found in the nest and around the base of the nest site. A few feathers of Gambel's Quail (*Lophortyx gambelii*), and the tail of a Harris' antelope ground squirrel (*Ammospermophilus harrisii harisii*) were also collected from the nest.

The nest was built in a Saguaro (*Carnegiea gigantea*), about 7 to 8 m from the ground. Because of the large size and lack of cup in the nest, we believe it to have been rebuilt or added to several times. Klimosewski first saw it in the winter of 1974–75, and in the spring of 1975 he saw an adult female sitting on the nest; however, no young were fledged from this presumed nesting attempt. The next indication of use was on 22 November 1975, when 2 large young were seen in the nest.

Two males and a female (sex determined by comparative size), all in adult plumage, were in attendance at this nest both in the spring and in November/December and would support the conclusion that this late nesting was at least the second attempt by the same group. A nest-helping system has been recorded for Harris' Hawks by Mader (Living Bird, 14:59–85, 1975).—ELEANOR L. RADKE, *P.O. Box 446, Cave Creek, AZ 85331* and JOHN KLIMOSEWSKI, *1810 N. 16th Ave., Phoenix, AZ 85007.* *Accepted 15 March 1976.*

The spatial distribution of wintering Black-bellied Plovers.—The Black-bellied Plover (*Pluvialis squatarola*) is a common winter resident along much of the coastal United States. Individuals in foraging flocks of wintering Black-bellied Plovers are generally quite scattered. This is in contrast to most other winter shorebirds (e.g., Sanderlings, *Crocethia alba*; Semipalmated Plovers, *Charadrius semipalmatus*; Knots, *Calidris canutus*; and Ruddy Turnstones, *Arenaria interpres*) which frequent the same beaches in fairly compact flocks. This note discusses the spatial distribution of wintering Black-bellied Plovers along the Gulf coast beaches of Sanibel Island, Florida. From 25 through 30 December 1975, I made 13 surveys of Black-bellied Plovers on Sanibel Island, each time pacing off the distance between adjacent plovers. I measured 201 inter-plover distances, sampling only sections of beach bordered by vegetation. I avoided stretches of beach with many people and all areas where there were dogs, for the plovers seemed to avoid both situations. To avoid sampling regions where recent disturbance (e.g., a dog running along the beach) may have caused all the plovers to leave the area temporarily, I did not record any inter-plover distances which were greater than 270 m. The groups of inter-plover distances were homogeneous (Kruskal-Wallis test, $P > .975$), so all samples were combined.

The null hypothesis that thc 201 observed distances are indistinguishable from a random distribution of plovers along the beach was tested against the alternative hypothesis that observed distances were more evenly spaced than a random distribution of plovers would produce; the plovers were obviously not clumped. The random distances were generated from the equation,

$$N_m = \frac{1}{S} \sum_{I=1}^{m} \frac{1}{S - I + 1} .$$

where N_m is the proportional length of the *m*th segment of a line divided into S random lengths (MacArthur, Proc. Natl. Acad. Sci. U.S. 43:293–295, 1957). To account for the fact that I sampled only inter-plover distances which were less than 270 m, I used $S = 239$ to produce 201 random distances which were less than the proportional equivalent of 270 m, and 18 random distances which would not have been recorded because they were greater than the proportional equivalent of 270 m. ($S = 238$ or 240 also produces 201 appropriate random distances, and the ensuing statistics are similar to those presented here.) The 2 frequency distributions are presented in Table 1; the null hypothesis, that Black-bellied Provers are randomly distributed within the scattered foraging flocks, is strongly rejected (G-test, $P < .001$). The plovers are somewhat evenly dispersed within the foraging flocks.

TABLE 1

OBSERVED INTER-PLOVER DISTANCES COMPARED WITH EXPECTED RANDOM DISTANCES

Distance (m)	Observed	Expected
0–29	22	43
30–59	36	37
60–89	43	29
90–119	36	24
120–149	31	20
150–179	18	16
180–209	7	13
210–239	4	10
240–269	4	9
	201	201

In an attempt to investigate how such spacing was maintained, I paid close attention to 4 sets of 2 Black-bellied Plovers which were less than 3 m apart. Additionally, on 3 occasions, I was successful in "herding" together 2 plovers which had originally been separated by more than 30 m. In 30 min of observation on each of the 7 pairs, I never observed any behavior (aggressive or otherwise) which seemed responsible for the spacing. In all cases, the plovers which were close together would simply slowly move apart. Apparently, the birds space themselves by mutual avoidance rather than by aggressive actions. The fairly large standard deviation (57.4 m) around the mean inter-plover distance (95.9 m) also suggests a low-key spacing behavior. In contrast to the subtlety of the intra-specific behaviors which produced the spacing, it was not at all uncommon to see a plover peck at and chase away other species of shorebirds which wandered by. This is in contrast to the finding of Recher and Recher (Wilson Bull. 81:140–154, 1969) that intra-specific aggression was much more common than inter-specific aggression in foraging flocks of migrant shorebirds.

Goss-Custard (pp 3–35 *in* Social Behavior in Birds and Mammals, J. H. Crook, ed., Academic Press, London, 1970) described 2 main types of shorebird foraging flocks: compact and widely scattered. He suggested that flocking while foraging facilitates detection of predators (e.g., Page and Whitacre, Condor 77:73–83, 1975), and that compactness of the flock is dependent on whether or not feeding efficiency is decreased by compact flocking. The observation that Black-bellied Plovers are somewhat evenly spaced within these foraging flocks is consistent with the idea that such scattered flocking is an attempt to avoid intra-specific interference.

Mitchell A. Byrd, Bruce S. Grant, Stewart A. Ware, Barbara S. Warren, and two anonymous reviewers made very helpful comments on an earlier draft of this note. H. Wade and Barbara R. Stinson provided room and board on Sanibel Island. My sincere thanks to all of the above.—CHRISTOPHER H. STINSON, *Dept. of Biology, College of William and Mary, Williamsburg, VA 23185.* *Accepted 13 Apr. 1976.*

Predation and dispersion of Herring Gull nests.—Tinbergen (1960, The Herring Gull's World, Harper and Row, New York) reported that Herring Gulls (*Larus argentatus*) deserted most nests from which red fox (*Vulpes vulpes*) took eggs. The adults so affected reportedly renested at the borders of the colony, and their deserted territories were incorporated into territories of adjacent pairs. This "spreading out phenomenon," as it was termed, was believed to function as a passive defense by dispersing the nests making their location by predators more difficult.

We noted a different response in the reactions of Herring Gulls to red fox (*Vulpes fulva*) predation on South Manitou Island in northern Lake Michigan (Leelanau Co., Mich.). During studies of productivity at this colony in 1974, Shugart marked and mapped the location of 51 nests in a strip transect (10 m × 215 m) encompassing about 15% of the central nesting area. Eggs in the 51 nests were marked. Hatching began 18 May and newly hatched chicks were banded within 1–2 days of their hatching date. Shugart made the following observations. In 23 of the 51 nests during the first week of hatching, 18 chicks were killed by fox, 16 other chicks disappeared and were probably taken by fox, and 9 small chicks apparently died from exposure during nightly fox visits to the colony. Evidences for the fox predation were the presence of fox tracks on the perimeter of the colony and canine tooth punctures in the chick carcasses following the nights in question. Seven unhatched eggs that remained in the predated nests were found broken and addled outside of nests several days after the chicks were killed, disappeared, or died. The latter indicated that incubation of the original remaining eggs did not continue after the nests were predated.

Within 2–8 days after the death of the first Herring Gull chicks, Shugart observed that grass and twigs were being added to the predated nests or that new nests were being constructed near the original nests. Eight (34%) of the original predated nests had additional eggs laid in the same nest cup. Of the remaining pairs, 14 (61%) apparently laid in newly constructed nests 1 to 9 m ($\bar{x} = 2.05$ m, SD $= 1.21$ m) from the originally predated nests. The distance between initial nests in the sample area averaged 4.88 m (SD $= 2.15$ m) which is significantly more ($t = 4.580$, $P < 0.001$) than the distance between the predated nests and the newly constructed nests. Because new clutches of eggs appeared in the original nests or in new nests constructed near the original nests, we consider it likely that the same pairs of adults were renesting on the same territories.

Renesting after hatching and death of chicks from the original clutch has previously been reported for the Herring Gull (Paludan, Vidinsk. Medd. fra Dansk naturh. Foren., 144:1–128, 1951), the Glaucous-winged Gull (*Larus glaucescens*) (Vermeer, Occas. Paper, B. C. Prov. Mus. No. 13, 1963) and the Black-headed Gull (*Larus ridibundus*) (Ytreberg, Nytt. Mag. Zool. 9:5–15, 1960, cited *in* Vermeer, Can. Wildl. Serv. Rep. 12, 1968). These papers cite only a few instances of renesting after chicks from the original clutch died. To our knowledge extensive renesting after predation has not been previously reported. Renesting in the same place after predation probably indicates a lack of plasticity in breeding responses of Herring Gulls and was maladaptive in the instance reported here since all eggs produced in the renesting were destroyed by foxes.

The response of South Manitou Herring Gulls to fox predation was different from that reported by Tinbergen (op. cit.). Renesting did not occur at the borders of the colony although apparently adequate space was available. Spreading out or even desertion of the original territory may not be assumed to be a singular response to predation because in this instance Herring Gulls renested in the same territory after hatching and predation upon the first clutch. The response of the Herring Gull to predation upon eggs or chicks may be related to the stage of the breeding cycle or the length of time spent on 1 territory, or both.—GARY W. SHUGART, *Dept. of Biological Sciences, Northern Illinois Univ., DeKalb 60115* and WILLIAM C. SCHARF, *Dept. of Biology, Northwestern Michigan College, Traverse City 49684.* *Accepted 5 May 1976.*

Egg quality in relation to nest location in Ring-billed Gulls.—A number of studies of colonial nesting birds have shown that pairs which nest in the center of a colony have a higher reproductive success than pairs nesting near the outside or periphery of the colony. This phenomenon has been recorded for the Black-headed Gull (*Larus ridibundus*) (Patterson, Ibis 107:433–459, 1965), Adelie Penguin (*Pygoscelis adeliae*) (Tenaza, Condor 73:81–91, 1971; Spurr, Ibis 117:324–338, 1975) and Black-legged Kittiwake (*Rissa tridactyla*) (Coulson, Nature 217:478–479, 1968). Coulson et al. (Auk 86:232–245, 1969) found that eggs in centrally located nests of Black-legged Kittiwakes were significantly larger than eggs in nests on the periphery and postulated that part of the early mortality of peripheral Black-legged Kittiwake and Shag (*Phalacrocorax aristotelis*) nestlings may be due to the smaller size and quality of the eggs, particularly the yolk.

From our studies of Ring-billed Gulls (*L. delawarensis*) on Granite Island, northern Lake Superior, Ontario (48°43′N, 88°29′W), we have found proportionately more eggs hatched in the center than in the periphery of the colony (see Ryder, Wilson Bull. 87:534–542, 1975). We define central and peripheral nests respectively as those in the geometric center of the colony and those forming the outside border (see Dexheimer and Southern, Wilson Bull. 86:288–290, 1974). Stimulated by the suggestion of Coulson et al. (Auk 86:232–245, 1969) that egg yolk quality might be related to nestling mortality, we tested eggs from both areas for relative amounts of nutrient and energy content in the yolk assuming that differences in these parameters might provide a clue to help explain the low hatching success of peripherally located eggs. Romanoff (Pathogenesis of the Avian Embryo, Wiley, N.Y., 1972) stated that deficiencies of various compounds in the egg may seriously disturb embryonic development and lead to premature death.

We collected one freshly-laid egg from each of 24 3-egg clutches in the center and 28 3-egg clutches on the periphery of the Granite Island colony on 17 and 21 May 1975. The length and maximum breadth of each egg was measured to 0.001 cm with vernier calipers. Egg volume was calculated using the formula $V = 0.489 \cdot B^2(\text{max}) \cdot L$, where B is the maximum breadth and L the length of each egg (see Ryder, Wilson Bull. 87:534–542, 1975). Eggs were weighed to the closest 0.1 g on a triple beam balance in the field. Within 6 h after collection, whole yolks were separated from the albumen and stored frozen until chemical analyses were made.

TABLE 1

THE MEAN LENGTH, BREADTH, VOLUME, AND WEIGHT OF RING-BILLED GULL EGGS, GRANITE ISLAND, 1975[1]

	Location in Colony	
	Center	Periphery
length (mm)	58.34 ± 0.23[2]	57.80 ± 0.32
breadth (mm)	41.81 ± 0.12	41.88 ± 0.13
volume (cc)	49.71 ± 4.02	49.64 ± 4.63
weight (g)	53.93 ± 3.74	53.42 ± 4.06

[1] N = 24 eggs from center and 28 eggs from periphery of colony.
[2] 1 S.D.

In the laboratory each yolk was weighed wet to the closest 0.001 g on an analytical balance. Yolks were dried individually in a vacuum desiccator over sulphuric acid until constant weight and then analyzed for total protein, carbohydrate, and lipid content. Protein quantities were determined according to the procedure in Kolthoff and Sandell (Textbook of Quantitative Inorganic Analysis, MacMillan, N.Y., 1956). Lipid analyses followed Freeman et al. (J. Biol. Chem. 227:449–464, 1957) and carbohydrate determinations followed Dubois et al. (Anal. Chem. 28:350–356, 1956). The following constants given by Brody (Bioenergetics and Growth, Hafner, N.Y., 1945) were used to convert g organic material into caloric units: 9.45 Kcal/g lipid; 5.65 Kcal/g protein; 4.10 Kcal/g carbohydrate. These conversions were used for Brown Pelican (*Pelecanus occidentalis*) eggs by Lawrence and Schreiber (Comp. Biochem. Physiol. 47A:435–440, 1974) and Laughing Gull (*L. atricilla*) eggs by Schreiber and Lawrence (Auk 93:46–52, 1976).

Table 1 presents data on the length, breadth, volume, and total weight of central and peripheral eggs. In all parameters but breadth, eggs from central nests were slightly but

TABLE 2

NUTRIENT COMPOSITION OF RING-BILLED GULL EGG YOLKS, GRANITE ISLAND, 1975[1]

	Location in Colony		
Nutrient	Center	Periphery	Combined
protein	1.81 ± 0.33[2]	1.86 ± 0.26	1.84 ± 0.29
	10.20 ± 1.86[3]	10.54 ± 1.48	10.39 ± 1.65
carbohydrate	0.05 ± 0.02	0.06 ± 0.02	0.05 ± 0.02
	0.19 ± 0.08	0.24 ± 0.10	0.22 ± 0.09
lipid	4.44 ± 0.69	4.59 ± 0.48	4.53 ± 0.58
	41.99 ± 6.48	43.42 ± 4.56	42.80 ± 5.47

[1] N = 21 for center, 27 for periphery and 48 for combined sample.
[2] Weight (g).
[3] Energy (Kcal).

not significantly larger, $P > 0.05$) than eggs from peripheral nests. Protein, carbohydrate, and lipid weights and their energy values from both locations were equal (Table 2).

These results support the finding that embryos of equivalent age from the center and periphery of the Granite Island colony (Ryder and Somppi, Wilson Bull. 89:243–252, 1977) showed no significant differences in developmental characteristics and size. It appears that the differences in hatching success in relation to nest location in our colony may not be due solely to differential quantities of proteins, carbohydrates, and lipids in the yolks. The results do not preclude the possibility that differences exist in the types and quantities of essential amino acids and/or other compounds which may be important in determining egg hatchability. Additionally, low egg success in peripheral areas may reflect lower parental attentiveness than in central regions.

We thank L. Somppi, C. Ryder and T. Carroll for assistance in collecting and measuring eggs in the field. Financial support for this and related research on gull ecology was provided by the National Research Council of Canada and a Lakehead University President's Research Grant. We appreciate the cooperation and interest of R. Trowbridge for allowing us to base field operations at Bonavista.—JOHN P. RYDER, *Dept. of Biology, Lakehead Univ., Thunder Bay, Ontario, P7B 5E1*, DONALD E. ORR AND GHOMI H. SAEDI, *Dept. of Chemistry, Lakehead Univ., Thunder Bay, Ontario, P7B 5E1.* *Accepted 25 Mar. 1976.*

Roof-nesting by Common Terns.—During the summer of 1975 a pair of Common Terns (*Sterna hirundo*) nested on the flat roof of a building on Great Gull Island, New York (at the eastern end of Long Island Sound). Gill (Auk 70:89, 1953) reported Common Terns nesting on a boat on Long Island. I find no reference in the literature to Common Terns nesting on buildings. Least Terns (*S. albifrons*) have been reported nesting on roofs in Florida (Fisk, Am. Birds, 29:15–16, 1975).

On 12 July 1975 I first noticed a Common Tern sitting on the roof of 1 of the old army buildings, now used as sleeping quarters on Great Gull Island. On 13 July I climbed onto the roof and found 2 warm eggs in a shallow depression where I had seen the adult tern sitting. A loose layer of pebbles on the flat surface of the roof covered most of the tar and roofing paper. The nest depression was shielded on 1 side by a piece of roofing paper and was partly lined with small pieces from a rotting board lying on the roof about 1 m from the nest. While I was on the roof one of the adult terns dove at me. A tern was last seen incubating on 25 July during a storm. On 26 July and on following days no birds were seen on the nest. On 18 August 1 egg was left in the nest. I opened it and found an embryo which I judged to be 11 to 12 days old using the criteria of Hays and LeCroy (Wilson Bull. 84:187–192, 1971).

On Great Gull Island Common Terns often nest on the crumbling concrete of the old fort which covers most of the island (Cooper et al., Proc. Linn. Soc. 71:108–118, 1970). Most of the concrete surfaces are effectively at ground level. At times terns have nested on concrete lookout platforms at least 2 m above the ground. This roof nest was about 4 m above the ground. The roof's pebble surface gave the nest a substrate similar to the island's pebble beaches. During the period when the roof-nest terns probably chose their nest site, many of the traditional nesting areas were overgrown or still being defended. A resulting shortage of nesting habitat may have caused the selection of the roof as a nest site. I do not think that the desertion of the eggs on the roof was due to any particular disadvantage in the nest site, rather, it may have been caused by factors which influenced the desertion of many nests on the night of the storm of 25–26 July.

Roof-nesting, like the use of other man-made structures on Great Gull Island, demonstrates the adaptability of Common Terns in their choice of nest sites. It will be interesting to see whether the use of roofs for nesting continues and increases in future seasons.

I am grateful to Helen Hays and to Kenneth C. Parkes for their comments on the manuscript.

This note is contribution No. 42 from the Great Gull Island Project.—Anne E. MacFarlane, *325 E. 72nd St., New York 10021. Accepted 20 April 1976.*

Rapid chick separation in Whip-poor-wills.—This note describes a poorly known aspect of Whip-poor-will (*Caprimulgus vociferus*) behavior and emphasizes the possible importance of nestling behavior to survival.

While hiking through second-growth deciduous forest in Jasper County, Illinois, on 5 May 1972, I flushed a female adult Whip-poor-will from 2 eggs resting in a shallow leafy depression. The nest site, "nest," and eggs were typical of published descriptions for the species. During the next 13 days I visited the site 5 times and always found the female incubating at precisely the same location with the eggs slightly rearranged within the nest. On 22 May (4 days from the last visit) the female allowed me to approach to 1 m before flushing. As she flushed, 2 chicks simultaneously separated in opposite directions to a distance of about 15 cm from each other. Their separation occurred so rapidly and unexpectedly to me that I am uncertain whether the chicks were flipped apart by the female with her feet as she flushed, or whether they separated under their own power. I noted no discrete hops. That one chick rather forcefully tumbled forward to rest, left me with the immediate impression that it had been propelled. The chicks remained perfectly motionless, and their eyes remained closed during several minutes of observation.

Two days later, as the female flushed, the chicks separated about 40 cm from each other by a series of rapid but perceptible hops. They moved in exactly opposite directions as before. I was impressed again by the rapidity of their separation, by their motionlessness after a simultaneous and quick stop, and by the effectiveness of their camouflage. The chicks' eyes were first noted to be open on 27 May when the chicks hopped apart about 65 cm along perpendicular paths as the female flushed.

On 31 May only 1 chick hopped from the nest (to about 60 cm). The second chick "froze" within the nest. On this visit I saw the male adult and droppings around the nest for the first time. The male appeared at the moment of typical distraction behavior by the female (sharp "thurp" calls; posturing with dropped wings, fanned tail and erect head; injury-feigning skirmishes through the leaves).

The original nest site was abandoned on 2 June and was littered with droppings. I unexpectedly flushed the brooding *male* about 8 m away, but was looking in the wrong direction to observe the chicks directly as he flushed. They rested about 1 m apart and faced in opposite directions. The male exhibited distraction behavior similar to that of the female. The male was brooding at this same site on 4 June, but neither chick moved when he flushed.

On 6 June the male was brooding the chicks about 15 m from the original nest site. All 3 flushed together. The chicks each flew in straight lines about 45° from one another to a distance of about 12 m. One chick landed in a branch 2 m up, and the other landed on the forest floor. The male immediately placed himself between me and the chick on the branch and exhibited distraction behavior. The female did not appear. Neither adult nor chicks could be found in the vicinity the following day.

There are 4 references to possible rapid chick separation in Whip-poor-wills in the literature (Bent, U.S. Natl. Mus. Bull, 176, 1940; Fowle and Fowle, Can. Field-Nat. 68:37, 1954; Raynor, Bird-Banding 12:98–104, 1941; Tuttle, Bird-Lore 13:235–238, 1911), but the behavior is described nowhere in detail nor interpreted. The adaptive advantage of rapid chick separation is undoubtedly the increased probability that at least 1 of the chicks will survive nest disruption by a predator. I believe rapid chick separation is one more element of an anti-predator repertoire of adaptations in Whip-poor-wills which includes, in addition, cryptic coloration, brood site movement, and adult distraction behavior.—ERIC L. DYER, *Station 17, Vanderbilt Univ. Hospital, Nashville, TN 37232. Accepted 30 July 1976.*

An intraspecific mortal attack.—On the morning of January 6, 1976, I was looking out my window as 2 female House Sparrows (*Passer domesticus*) dove (hurtled) into the grass nearby. One held the other by the neck and after a few seconds the struggling victim lay still. The attacking sparrow, still on top of the nearly lifeless one, began to strike hammering blows with its bill on the head of the victim. Several sparrows flew near, and all flew off leaving the motionless body on the ground. Minutes later a House Sparrow returned, jumped on the dead sparrow and again struck it on the head several times, then flew away.

On 8 January I observed a similar incident involving female House Sparrows. The attacking sparrow held the neck of the struggling one, which eventually got loose. Both flew off, one pursuing the other.—VERA LEE GRUBBS, *3816 Elmer Lane, Shreveport, LA. 71109 Accepted 1 Mar. 1976.*

Rufous-sided Towhees mimicking Carolina Wren and Field Sparrow.—Eastern populations of the Rufous-sided Towhee (*Pipilo erythrophthalmus*) do not exhibit any marked local dialects, and the high percentage of unique song patterns in the songs of a local population suggests that what a bird hears when it is developing its song does not play an important role in determining the song patterns developed (Borror, Condor 77:183–195, 1975). It is thus of considerable interest to encounter eastern towhees whose songs (or song parts) are excellent mimics of other species. This paper is a report on the songs of 2 towhees (of several hundred I have recorded), one using an introduction consisting of Carolina Wren song phrases, and the other singing Field Sparrow songs. Both birds were seen when recorded.

Mimicry of Carolina Wren.—On 27 July 1975 I recorded a towhee near Murray, Kentucky (OSU recording No. 13679, with 67 songs), some of whose songs had an introduction consisting of (or containing) from 1 to 3 song phrases of a Carolina Wren (*Thryothorus ludovicianus*). The recording contained 5 different song patterns, 4 of which are shown in Fig. 1 (*A*, *B*, *E*, *F*); 2 (*A* and *E*) were normal songs for this population (a 2-note introduction followed by a trill) but 2 of the other 3 had Carolina Wren phrases in the introduction (*B* and *F* in Fig. 1), and a 5th contained only 2 Carolina Wren phrases (of the type in *F*, without the buzzy note and final trill). Most of the songs of the *B* pattern were sung in alternation with songs of the *A* pattern, while most songs of the *F* pattern were sung consecutively, only occasionally alternating with songs of the *E* pattern. There was only 1 song of the 5th pattern, which was in a series of *F* pattern songs. Two Carolina Wrens were heard near where this towhee was recorded, but neither sang songs of the patterns sung by the towhee.

The wren phrases in pattern *B* of this towhee are of a pattern that is fairly common in the wren; I have found it in the songs of 27 birds (of over 380 recorded, from 16 states)—20 in central Ohio, 4 in southern Ohio, 2 in southwestern Kentucky (one about 50 km from the Murray towhee), and 1 near Chincoteague, Va. The towhee songs of pattern *B* all contained 3 Carolina Wren phrases, uttered at the rate of 3.64 per sec; the wren songs of this pattern contained from 1 to 8 phrases (average of 345 songs, 5.10), uttered at rates of 3.23 to 4.61 (average 3.72) per sec. Sonagrams of the final phrases of 2 of these Carolina Wren songs are shown in Fig. 1 (*C* and *D*).

Carolina Wren phrases of the type in *F* (Fig. 1) are less common than those in *B*; I have found such phrases in only 9 birds—6 in central Ohio, 1 in West Virginia, 1 in southwestern Kentucky (about 25 km from the Murray towhee), and 1 near Tallahassee, Florida. The towhee songs contained only 1 or 2 (average, 1.6) of the wren phrases, uttered at the rate of 2.27 per sec; the wren songs of this type contained from 2 to 5 phrases (average of 88 songs, 3.50), uttered at rates of 2.15 to 2.40 (average, 2.28) per

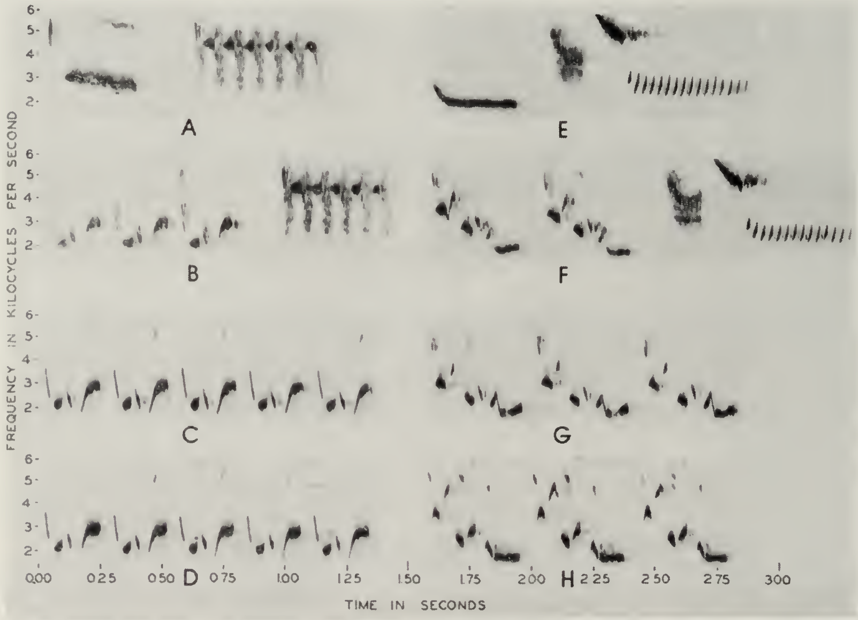

FIG. 1. Sonagrams of songs of a Rufous-sided Towhee (#13679, Murray, Ky., 27 July 1975), and final phrases of Carolina Wren songs. A, towhee, 13679–29; B, towhee, 13679–28; C, Carolina Wren, 12733–19, Blendon Woods, Franklin Co., Ohio, 19 March 1974; D, Carolina Wren, 12785–2, Georgesville, Ohio, 18 April 1974; E, towhee, 13679–58; F, towhee, 13679–55; G, Carolina Wren, 13651–20, Murray, Ky. (about 25 km from 13679), 8 July 1975; H, Carolina Wren, 3863–9, Blendon Woods, Franklin Co., Ohio, 18 April 1959.

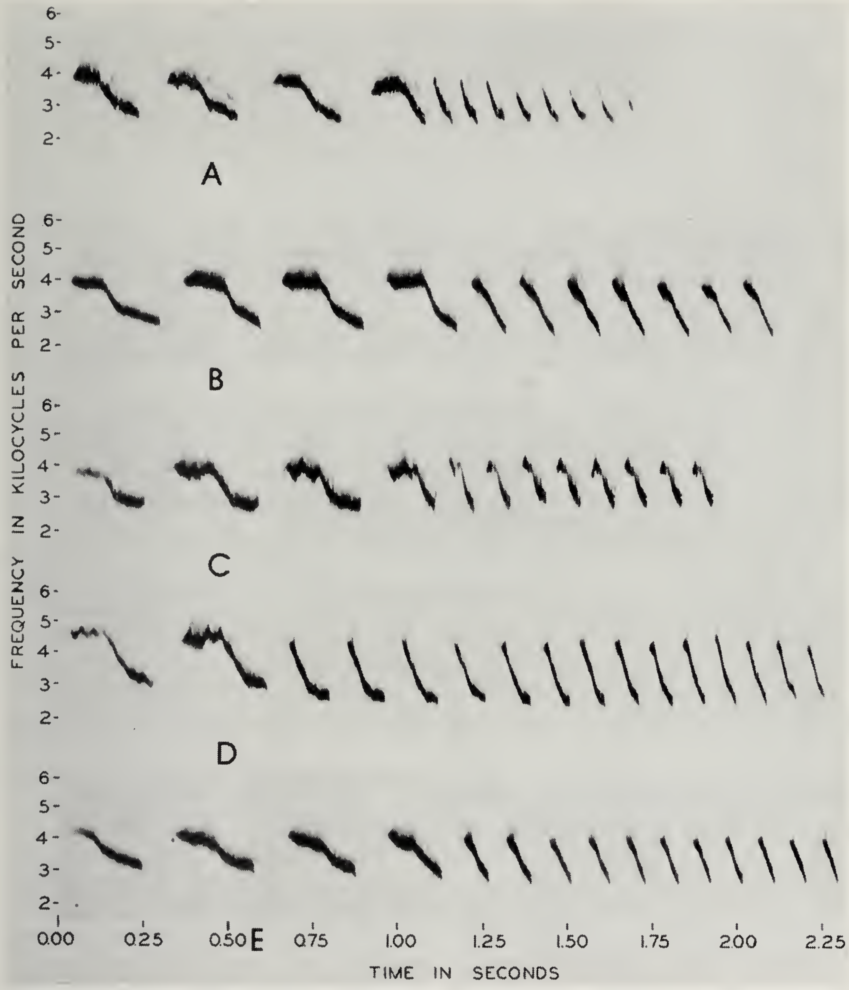

FIG. 2. Sonagrams of Rufous-sided Towhee (A) and Field Sparrow (B–E) songs. A, towhee, 3146–10, Blendon Woods, Franklin Co., Ohio, 2 April 1958; B, Field Sparrow, 9840–4, Blendon Woods, 6 April 1969; C, Field Sparrow, 3897–1, Blendon Woods, 24 April 1959; D, Field Sparrow, 3830–1, Blendon Woods, 1 April 1959; E, Field Sparrow, 9271–1, Blacklick Woods, Franklin Co., Ohio, 29 March 1968.

sec. Sonagrams of the final phrases of 2 of these Carolina Wren songs are shown in Fig. 1 (*G* and *H*).

Mimicry of Field Sparrow.—On 2 April 1958 I recorded a towhee in Blendon Woods, Franklin Co., Ohio (OSU recording No. 3146, with 13 songs), singing Field Sparrow (*Spizella pusilla*) songs. When I first heard this bird I thought it was a Field Sparrow, and it was not until I saw the bird and watched it sing that I realized that these songs were being sung by a towhee. All the songs in the recording were of the same type or pattern; the songs were distinctly 2-parted and the notes were down-slurred, with the 3 or 4 notes in the first part uttered at the rate of 3.54 per sec, and the 4 to 8 in the second part uttered at the rate of 12.90 per sec. Individual songs contained 8–12 notes (average, 10.7), and averaged 1.46 sec in length (Fig. 2, *A*). Field Sparrows are common in the area where this towhee was recorded.

Field Sparrow songs are subject to considerable variation, and while one rarely finds 2 birds singing identical songs, the various song patterns may be classified in a number of major groups. Goldman (Ph.D. Thesis, Ohio State Univ., 1972), in a study of 197 Field Sparrows, mostly from central Ohio, recognized 40 major song pattern types; the songs of this towhee were of a type he found in 8 of the birds he studied. Other people might recognize a different number of major song pattern types in Field Sparrows; in my studies I have recognized 15 major types, and the songs of this towhee were of a type that I found in about 9% of the birds I studied; 4 songs of this type are shown in Fig. 2(*B–E*).

The songs of this towhee are shorter and contain fewer notes than most Field Sparrow songs; the songs Goldman studied averaged 2.64 sec in length, with an average of 23.20 notes. The final notes in the towhee songs are uttered more slowly than those in most Field Sparrow songs; Goldman found the note rate in the last part of the song to range from 5.9 to 35.7 notes per sec, and averaged 16.97 per sec.

Discussion.—Except for the Mockingbird (*Mimus polyglottos*), mimicry of 1 species by another in wild North American passerines appears to be quite rare. It has been reported in several species, but in only a few cases has the report been supported by audio-spectrographic analyses (e.g., in the House Finch, *Carpodacus mexicanus*, by Baptista, Z. Tierpsychol. 30:266–270, 1972). Most reports of mimicry in passerines (e.g., Snow, Wilson Bull. 86:179–180, 1974; Immelman, *in* Bird Vocalizations, R. A. Hinde, ed., Cambridge Univ. Press, London pp. 61–74, 1974; Nottebohm, Am. Nat. 106: 116–141, 1972; and others) involve species occurring outside this country. In passerines exhibiting local dialects it is generally assumed (and has been demonstrated in several species) that an individual's songs are learned from other birds, but in species that do not exhibit local dialects there is less evidence of the bird's ability to mimic.

The excellent mimicry by these 2 towhees of the songs of another species indicate that this species is at least capable of mimicking other birds, even though data from other sources (e.g., Borror, Condor 77:183–195, 1975) suggest that the song patterns a towhee develops are not greatly affected by what it hears. Both of the areas where these 2 mimicking towhees were recorded contained other towhees, yet their songs were unique; even the "normal" introductions and trills of the Murray bird were unlike those of 4 other towhees I recorded the same day within 1 km of this bird. These mimicking towhees must have had unusual exposure to the species they mimicked, and copied them in developing their own songs.—DONALD J. BORROR, *Dept. of Entomology, Ohio State Univ., Columbus 43210.* *Accepted 21 May 1976.*

Heat loss from the nest of the Hawaiian honeycreeper, "Amakihi."—The Amakihi, *Loxops v. virens*, is the most adaptable of the endemic Hawaiian honeycreepers, in many instances nesting successfully under conditions which are surprisingly cold for islands within the tropics (Berger, Hawaiian Birdlife. Univ. Press of Hawaii, Honolulu, 1972). One of the factors that might enable them to accomplish this is the construction

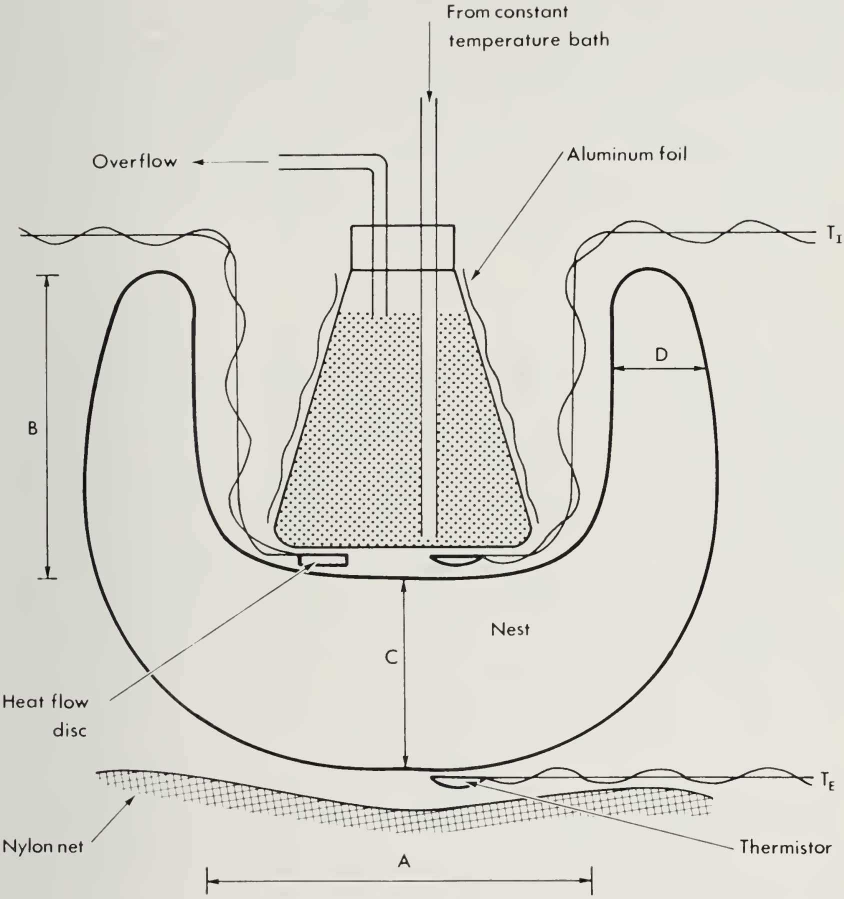

FIG. 1. Experimental arrangement for measuring the thermal conductance of the nest. Letters A–D indicate measured dimensions of nests; T_I and T_E are thermistors for measurements of the temperature difference across the nest wall.

of a well-insulated nest. The purpose of the study reported here was to measure the heat loss from the nest of the Amakihi under carefully controlled conditions.

Four nests were mounted on a wide-mesh nylon net, in an air-conditioned room. The air temperature varied from 23.8°C to 26.1°C on different days, but it did not change more than 0.3°C during any experiment. A 25 ml glass conical flask was inserted into the bowl of the nest, so that the bottom of the flask rested lightly on the floor of the nest (Fig. 1). The area of the flask in contact with the nest (12.5 cm^2) was greater than the area of eggs normally in contact with the nest, but it approximated the combined contact area of the eggs and parent bird, or of the nestlings. Interposed between the bottom of the flask and the floor of the nest was a Hatfield heat-flow disc

(J. Physiol. III, 10–11P, 1950), and a Yellow Springs Instrument Company (YSI) thermistor (No. 427). A similar thermistor was used to measure the temperature of the outer surface of the nest (Fig. 1). The sides of the flask were wrapped in aluminum foil to minimize radiant heat exchange between the flask and the nest. Water was circulated through the flask from a thermostatically controlled water bath. The thermistors were connected to a YSI Telethermometer (Model 46 TUC), and the heat-flow was recorded with a Turner microvoltmeter. Measurements of temperature and heat flow were made at intervals of 15 min until consecutive readings of heat flow agreed within 1 μV (approximately 1 W/m^2 or 0.86 kcal/m^2.hr). This occurred after 60–75 min. The dimensions of the nest were also recorded.

The results are summarized in Table 1. The temperature inside the nest was approximately equal to the temperature of the interface between the incubated eggs and the nest (Drent, Breeding Biology of Birds, Natl. Acad. Sci., Washington, D.C., 1973), although it varied in the different nests from 35.5°C to 38.3°C depending, in part, upon the thermal insulation of the nest. Heat flow through the nest wall was determined by, inter alia, the temperature difference across the nest wall (T_I-T_E, Fig. 1). The values for heat flow were divided by this difference to provide the figures given in Table 1. These figures have the dimensions of thermal conductance (J. Appl. Physiol. 35:941–961, 1973), and they are the inverse of thermal insulation. The thermal conductance of the nest was clearly influenced by the thickness of the nest wall; the lowest heat flows were recorded from the nests with the thickest walls. However, the relationship is not a simple one because heat is lost circumferentially through the nest as well as by direct radial transfer. The values for thermal conductance are probably rather higher than those that might be obtained from the nest *in situ*, because of the inevitable loss of nest materials during the removal and transport of the nest. It should also be borne in mind that the thermal conductance of the nest will vary with the air movement in the vicinity of the nest. In our study, the air movement was less than 3 m/min. It is interesting that the nest with the lowest thermal conductance (No. 2) was collected at an elevation of approximately 1140 m in the wet Alakai Swamp on the Island of Kauai. The mean annual temperature in this area is 15.7°C.

Unfortunately, there are few data in the literature with which to compare these values; the thermal properties of nests have been little studied (Drent, 1973; Kendeigh, Breeding Biology of Birds, Natl. Acad. Sci., Washington, D.C. 1973; Ricklefs, Avian Energetics, Publ. Nuttall Ornithol. Club, 1974). The most valid comparison that we can make is between the thermal conductance of the nest of the Amakihi, and that of the tissues

TABLE 1

DIMENSIONS AND THERMAL CONDUCTANCE OF 4 NESTS OF THE AMAKIHI

	Dimensions* (mm)				Thermal Conductance	
Nest No.	A	B	C	D	(W/m^2·°C)	(kcal/m^2·h°C)
1	60	32	20	20	5.716	4.915
2	55	44	54	30	2.783	2.393
3	45	36	15	15	4.555	3.917
4	53	28	50	20	3.486	2.998

* See Fig. 1.

and plumage of the adult bird. This comparison revealed that the thermal conductance of the 4 nests varied from 100 to 207% of the minimal conductance of the adult bird in a cold environment (MacMillen, 1974, Condor 76:62–69). As the thermal conductance of birds may very threefold, under different environmental conditions (Dawson and Hudson, Comparative Physiology of Thermoregulation, Vol. 1., Academic Press, New York, 1970), the thermal conductance of the nest and of the bird are of the same order of magnitude. We hope to obtain data on the thermal conductance of nests of other endemic Hawaiian birds, using the same technique, and to relate this information to the distribution and nesting habits of the birds.—G. C. WHITTOW AND A. J. BERGER, *Depts. of Physiology and Zoology, Univ. of Hawaii, Honolulu, 96822. Accepted 16 Apr. 1976.*

Spread of the Great-tailed Grackle in southwestern Louisiana.—The range extension of the Great-tailed Grackle (*Quiscalus mexicanus*) to the north and east was documented by Selander and Giller (Condor 63:29–86, 1961) and updated by Selander et al. (Condor 71:435–436, 1969). They indicated that the species occurred as far east in Louisiana as the Gibbstown-Bell City area of Calcasieu Parish. As recently as 1974, no further expansion eastward had been reported (Lowery, Louisiana Birds, 3rd ed. p. 548, La. State Univ. Press, Baton Rouge, 1974). We present evidence that a disjunct population of Great-tailed Grackles has existed unreported in the rice-growing region of south-central Louisiana for almost 2 decades. This area is more than 100 km ENE of the nearest known nesting sites in Calcasieu Parish (Fig. 1).

From 1960 to 1966, Ortego observed a small colony of Great-tailed Grackles in 2 live oaks (*Quercus virginiana*) near Ville Platte, Evangeline Parish. Local residents considered the noisy and conspicuous grackles to be fairly common summer birds, an indication that the colony had existed for some years. At about the same time, Guillory found a large colony of this species in a grove of live oaks at Mamou, also in Evangeline Parish. That colony existed until 1964.

When the Evangeline Parish colonies were discovered, *Q. mexicanus* was considered conspecific with *Q. major*, the boat-tailed Grackle, and as young birders both Ortego and Guillory identified the birds as Boat-tails. Some might question a retrospective identification of the birds as Great-tails. But no suitable Boat-tail habitat exists in the area, and in Louisiana, the Boat-tails breed only in or near coastal marshes (Lowery 1974). Ortego and Guillory observed the longer-tailed black males displaying on tall structures, and the smaller brown females feeding in nearby fallow rice fields. They both distinctly remembered that the males commonly used a call with "a clear ascending whistle." This provides conclusive evidence that the birds were indeed Great-tailed Grackles, for such a whistle is perhaps the most distinctive call of *Q. mexicanus* (Pratt, Birding 6:217–223, 1974).

Great-tailed Grackles were not reported again in the Louisiana rice country until 6 April 1972 when Pratt found 5 males near Ridge, Lafayette Parish and another male 1 km west of Maurice, Vermilion Parish. James A. Rodgers and Robert S. Kennedy (pers. comm.) sighted a flock of males and females near Kaplan, Vermilion Parish, on 13 May. In May 1973, Philip L. Bruner (pers. comm.) heard the distinctive whistle of a Great-tailed Grackle at Rayne, Acadia Parish. No nests were found in any of these areas.

In 1974, Great-tailed Grackles were again noted in Evangeline Parish. Guillory, Dennis H. Fontenot, and Dwight J. LeBlanc found the birds at LaHaye's Lake near

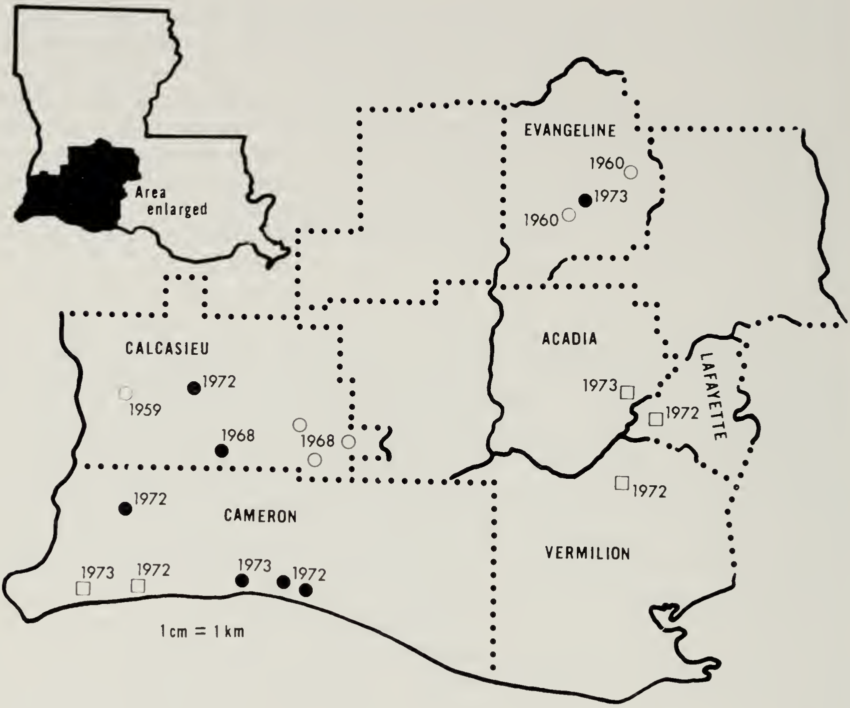

FIG. 1. Great-tailed Grackle distribution in southwestern Louisiana. Dates are for first observations. ● active breeding colonies 1975; ○ colonies abandoned 1975; ☐ breeding unconfirmed.

Redell, and 3 km SSW of Mamou. An unidentified local resident later reported that the LaHaye's Lake colony was present during 1973. At this colony on 6 September 1975, Ortego, Guillory, and Dennis Fontenot found 88 nests, a few of which appeared to be from the previous year. Seventy-five nests were built on 3 duck blinds. Such man-made structures are seldom used by Great-tailed Grackles at other localities in the state.

During the course of these and other observations, we have noted that Great-tailed Grackle colonies in Louisiana are extremely sensitive to harassment by man. Such a finding is surprising in light of the species' close association with human activities in other parts of its range (Skutch, pp. 334–350 *in* Bent, U.S. Natl. Mus. Bull. 211, 1958). Alvarez del Toro (Las aves de Chiapas, Gobierno del Estado de Chiapas, Tuxtla Gutierrez, 1971) points out that the birds maintain themselves in populated areas despite constant persecution, but such is not the case here.

Ortego reports that abandonment of the Ville Platte colony in 1966 followed the taking of some birds for food by local residents. At Mamou, residents considered the grackle colony, which increased in size annually, a nuisance and shot many of the birds. The colony site was subsequently forsaken.

Selander and Giller (1961) reported on a large mixed "*Cassidix*" colony near Vinton, Calcasieu Parish. They studied the colony during 2 successive years. Pratt established in 1972 that the birds had left the Vinton site, and could not be found within 14 km of the area. No apparent habitat changes have occurred since the earlier study. In the second year of their study, Selander and Giller collected a large series of specimens at this colony. In another colony at Sabine, Texas, these investigators collected all resident males. That colony was no longer extant in 1972. Selander et al. (1969) gave specific localities of several grackle colonies in 3 areas: north of Gibbstown, west of Bell City, and near Grand Lake, Louisiana. The colony near Grand Lake, situated in a residential area where collecting would be unwise, was still active in 1972. The colonies at the other sites were far from homes in easily accessible areas and were probably the source of the 134 specimens that Selander et al. (1969) collected. Neither of these colonies were active in 1972 or 1973, nor were there any grackle colonies nearby.

In June 1972, Pratt collected a series of 11 specimens from a mixed colony of "*Cassidix*" grackles in a pine grove 1 km south of the Lake Charles Airport in Calcasieu Parish. In March 1973, a few grackles were using the trees as temporary resting places, but they did not nest there again.

We believe that Great-tailed Grackles may be equally sensitive to disturbance in other parts of their range, but simply have no alternative nesting sites in areas where the population is at the carrying capacity of the local habitat. In southwestern Louisiana, where much suitable habitat is available, the conspicuous Great-tailed Grackles are still uncommon birds.

We thank Aubrey and Elvin LaHaye for allowing us to visit their lake, and Robert J. Newman for reviewing the rough draft of this paper.—H. DOUGLAS PRATT, *Museum of Zoology*, and BRENT ORTEGO, *School of Forestry and Wildlife Management, Louisiana State Univ., Baton Rouge 70893*; and HARLAND D. GUILLORY, *Louisiana State Univ., Eunice 70535. Accepted 27 Sept. 1976.*

Poplar leaf-stem gall insects as food for warblers and woodpeckers.—In November 1975, as leaves began to fall from the native cottonwood trees (*Populus fremonti*) at our ranch in the Chiricahua Mountains of southeastern Arizona, we noted that most of them had a gall attached to the petiole. Each gall was 10–15 mm across and had a slight split in one side. We had already noted that we had unusual numbers of Audubon's Warblers (*Dendroica coronata*) and Ruby-crowned Kinglets (*Regulus calendula*) in those cottonwoods and began paying more attention to their activity. By mid-November, we realized that the warblers were feeding on the ground in a small area under the cottonwoods, apparently on some small insect. At the same time we noted that both the Ladder-backed Woodpeckers (*Picoides scalaris*) and Arizona Woodpeckers (*P. arizonae*) spent most of the day in the cottonwoods, hanging on tiny twigs and feeding among the leaves, rather than on the trunk and limbs as usual. It was obvious that the galls, both while on the tree and after falling to the ground, were providing an abundant source of food for warblers, kinglets, and woodpeckers.

On 28 November, I collected some of the gall-infested leaves and sent them to the Cooperative Extension Service of Cornell University, State University of New York. They were identified as being caused by 1 or 2 species of aphids, *Pemphigus populitransversus* or *P. populicaulis*, or both. I do not recall any published account of the value of these insect galls as a source of food for migrating and/or wintering warblers and woodpeckers. I am indebted to Dr. Bernard Travis and Carolyn Klass for identification of the galls.—SALLY HOYT SPOFFORD, *Aguila-Rancho, Portal, AZ 85632. Accepted 2 May 1977.*

Perch height selection of grassland birds.—Zimmerman (Auk 88:591–612, 1971) and Wiens (Ecology 54:877–884, 1973) have suggested that most grassland bird species will usually select the highest perch available from which to sing. I observed this generalization to hold true for only 1 of 6 grassland-associated bird species in a study conducted from May 1973 to August 1974 in Kalamazoo County, Michigan.

The land used for the study consisted of a 56.7 ha alfalfa (*Medicago sativa*) field. A 30.7 ha study area was situated within the field so as to have a border of at least 55 m of alfalfa on all sides. It was then equally divided into three 10.24 ha subplots. Separating the 3 subplots from each other were buffer strips of 30 m. Each subplot was subsequently divided into a grid composed of 16 sections 80 m on a side. Grid intersections were marked with bricks painted white and countersunk into the ground.

During late June 1973 I added artificial perches to one subplot and, in December, I added identical perches to a second. The perches consisted of 2.5 × 2.5 cm pine stakes, 1.5 and 2.0 m tall and topped by a horizontal perch of 2.5 × 2.5 cm pine 30 cm long. The third subplot was not staked. No vegetation was as tall as the stakes. The greatest height reached by the alfalfa was approximately 0.5 m. In each case, 25 stakes (13 large and 12 small) were established in a pattern of alternating heights at grid intersections. Perch height selection was determined by recording each observed use of the perches during spot map censuses (Williams, Ecol. Monogr. 6:317–408, 1936).

Based on all species use (720 observations), no preference ($P > 0.05$) was indicated for either the high (2.0 m, 369 observations) or the low (1.5 m, 351 observations) perch structure (Table 1). Of 6 species for which there were sufficient data to conduct a chi-

Table 1

Perch Height Selection by Birds in an Alfalfa Field

Species	Perch use (Number of observations)				Chi square value[b]
	1.5 M		2.0 M		
	Observed	Expected[a]	Observed	Expected[a]	
American Kestrel (*Falco sparverius*)	8	9.6	12	10.4	0.51
Eastern Meadowlark (*Sturnella magna*)	6	20.4	34	19.6	20.73*
Red-winged Blackbird (*Agelaius phoeniceus*)	154	157.0	180	177.0	0.11
Savannah Sparrow (*Passerculus sandwichensis*)	132	120.5	114	125.5	2.15
Grasshopper Sparrow (*Ammodramus savannarum*)	23	13.0	3	13.0	15.38*
Vesper Sparrow (*Pooecetes gramineus*)	28	27.0	26	27.0	0.07
Preference by all species	351	345.6	369	374.4	0.16

[a] Expected ratios based on the frequency of high and low perches within territories of the individual species.

[b] Chi-square analysis, testing the hypothesis ($\alpha = 0.05$) that there exists no preference for a specific perch height; tested with one degree of freedom.

* Significant, ($P < 0.05$).

square test (expected ratios based on the frequency of high and low perches within the territories of the individual species), only 2 species, the Grasshopper Sparrow and the Eastern Meadowlark, showed a specific preference for 1 of the 2 sizes.

The Grasshopper Sparrow, according to Smith (U.S. Natl. Mus. Bull. 237, Part 2, 1968) and Wiens (Ecology 54:877–884, 1973) will normally select the highest perch available. The Grasshopper Sparrow, in this study, used ($P < 0.05$) the lower perches. Furthermore, in every territory established by this species, both large and small structures were present and therefore available for use.

Only the Eastern Meadowlark exemplified the generalization that higher perches will be used instead of lower ones. Of a total of 40 observations, the higher perches were selected ($P < 0.05$) 34 times.

Also using the perches but recorded 4 or fewer times were Mourning Dove (*Zenaida macroura*), Short-eared Owl (*Asio flammeus*), Eastern Kingbird (*Tyrannus tyrannus*), Barn Swallow (*Hirundo rustica*), American Robin (*Turdus migratorius*), Starling (*Sturnus vulgaris*), Bobolink (*Dolichonyx oryzivorus*), and Brown-headed Cowbird (*Molothrus ater*).

The general conclusion to be drawn appears to be that the above grassland-associated birds will use any elevated perch structure, at least up to 2 m tall. Some species may exhibit more specific tendencies, possibly preferring the highest available perch or preferring perches of a certain height range above the vegetation.

This note represents a part of a larger study completed as partial fulfillment for the Master of Arts degree at Western Michigan University. I am indebted to Dr. Richard Brewer for his critical review of this note. Thanks goes to Mr. Ray Vliek, without whose land and cooperation this study would not have been possible. Support for this research was provided by fellowships from the Upjohn grant for graduate studies in Biology and a Western Michigan University Graduate Student Research Grant.—KEITH G. HARRISON, *Dept. of Biology, Western Michigan Univ., Kalamazoo 49008.* Present address: *Michiana Area Council of Governments, County-City Bldg., South Bend, IN 46601.* *Accepted 15 Apr. 1976.*

SPECIAL REVIEW

JOHN OSTROM'S STUDIES ON *Archaeopteryx*, THE ORIGIN OF BIRDS, AND THE EVOLUTION OF AVIAN FLIGHT

Archaeopteryx lithographica is the most significant fossil species in the class Aves. Studies on *Archaeopteryx* have formed the basis for 3 generally accepted ideas about avian evolutionary history: (1) birds have their origins in reptiles, specifically within the pseudosuchian Thecodontia, (2) birds evolved their adaptive way of life—flight—from bipedal, arboreal ancestors, and (3) the origins of more modern avian taxa were post-Jurassic in time, *Archaeopteryx* being considered on the "main-line" of avian evolution or "close to it." *Archaeopteryx* has held this central position because it is the oldest fossil with obvious avian affinites and is represented by a number of well-preserved specimens. It is not surprising therefore that in addition to considerable work on the morphology of *Archaeopteryx*, many workers have attempted to reconstruct from that morphology much about the ecology and behavior of this species; and by inference these findings have been assumed to represent the avian ancestral condition. This controversial literature leads one to the important question of just how far historical analysis, which is highly inferential, can depart from the available evidence and yet remain "respectable" science, or alternatively to what extent can historical narrative explanation be regarded as "good" science? Indeed, this is one of the critical questions of paleontological methodology and I will return to it later.

The recent discovery of additional specimens of *Archaeopteryx* has created new interest in this species and in the larger problems mentioned above. Dr. John Ostrom of Yale University, a leading student of dinosaurs, was studying pterosaurs in 1970 and discovered that one specimen was actually referable to *Archaeopteryx*. His study of the other known specimens resulted in a series of papers (1970, 1972, 1973, 1974, 1975a, 1975b, 1976a) culminating in a large descriptive review (1976b). Ostrom's work focuses on two problems, the origin of birds and the origin of flight, and I believe that his solutions to these problems will almost certainly change contemporary viewpoints about *Archaeopteryx* and early avian evolution. I find most of his arguments persuasive, not in the sense that they are necessarily *true*, but that they "explain" far more than previous hypotheses. This is an important distinction, because arguments against Ostrom's viewpoints have not focused so much on his analysis of morphology and the hypotheses derived *directly* from it, but rather on alternative hypotheses that appear to have little evidentiary support.

Ostrom (1976b) presents a detailed comparative anatomical discussion, either refuting or calling into serious question many previous ideas about the morphology of *Archaeopteryx*. For example: (1) the pubis was probably not directed sharply backward as the Berlin specimen seems to indicate; (2) the hand and forelimb skeletons are not especially birdlike, and on the basis of comparisons with reptiles, Ostrom argues that the digits are numbers I, II, III; by implication this would be true for modern birds as well and thus contradicts the conclusions of some embryologists who have identified the digits as II, III, and IV; (3) x-ray studies indicate that there was proximal fusion of the metatarsals, and two proximal tarsal elements were co-ossified with the tibia and fibula, and at least two distal tarsals were fused to the metatarsus; (4) Ostrom believes that elements previously considered parts of the sternum are misidentified, and he concludes that an ossified sternum was not present.

Ostrom has made other notable discoveries about the morphology of *Archaeopteryx* that have significance when comparisons are made to modern birds and fossil reptiles. It is here that ornithologists owe Ostrom a particular debt, for it is doubtful whether any avian morphologist or paleontologist has as complete understanding of reptilian morphology as he does. This special knowledge has permitted him to undertake a broad comparative investigation, far surpassing efforts by previous authors. Which brings us to his two major conclusions, first about the relationships of *Archaeopteryx* and birds to reptilian taxa, and second, about the origin of flight.

Since its discovery in 1861, nearly all authorities have recognized the avian affinities of *Archaeopteryx*, yet its morphology was recognized as basically reptilian. Ostrom identifies two features as clearly indicating a relationship to birds: the possession of feathers and the fusion of the clavicles into a furcula. He also mentions other "birdlike" features, but does not make a strong attempt to use them as evidence of relationship. For example, the fusion of metatarsal elements and the fusion of tarsal elements with the tibia-fibula and metatarsals are characters shared with birds, though the theropod *Syntarsus* exhibits similar conditions. The tibia and fibula have become slender in *Archaeopteryx*, and especially in later birds, and both bones are elongated relative to the femur. Furthermore, Ostrom considers the orientation of the pubis to be intermediate between theropods and birds. All these features would seem to corroborate a phyletic relationship between birds and *Archaeopteryx* that excludes other vertebrates (but see comments below on *Syntarsus*).

Although not expressed entirely in Hennigian terminology, Ostrom's analysis very much follows the principles of phylogenetic systematics. He recognizes that "proof" of homology is not possible, therefore "the only reasonable working hypothesis remaining is that . . . resemblances are homologous in the absence of contrary evidence" (1976b:100). Contrary evidence would be, of course, support for a phylogenetic hypothesis requiring convergence in the characters under consideration. Ostrom also supports the notion that only derived character-states can be used to indicate relationships, shared primitive character-states lacking such information. For the most part, I believe Ostrom's conclusions and statements about systematics are well-founded and expressed in a logically consistent framework of phylogenetic reasoning. Unfortunately, we are all captives of our past—intellectually and psychologically—and Ostrom is no exception. When examined closely some of his statements lack clear meaning, but it must be said that all previous persons writing about *Archaeopteryx* fell into the same trap. As an example, consider the old argument about whether *Archaeopteryx* is (1) an aberrant form off the "main-line" of avian evolution, (2) on the "main-line" of avian evolution, or (3) the "direct ancestor" of birds (the second and third arguments are sometimes interchangeable). I doubt that there is a more pointless issue in the study of avian evolution than this. Ostrom (1975b:521) believes that considering *Archaeopteryx* as a "main-line" (never defined by him) transitional form is fundamental to his arguments about avian-*Archaeopteryx* affinities to theropods. Nothing could be further from the truth, because the conclusion to be drawn from his studies is that birds + *Archaeopteryx* are more closely related to theropod dinosaurs (and perhaps only a few genera of theropods) than to other reptiles; this conclusion can be reached whether *Archaeopteryx* is "main-line" or not. Thus, Ostrom has not yet escaped from some unnecessary doctrine of his paleontological training: "I personally believe *Archaeopteryx* lies very close to bird origins and probably is directly ancestral to all later birds" (1975a:61). It is questionable whether "very close" has any precise semantic or biological meaning as used here or whether "probability levels" are at issue. Nowhere does Ostrom (nor do paleontologists in general) present ways in which hypotheses of ancestral-descendant relationships can be tested. One necessary condition for an ancestor is that the ancestral species (only species can be ancestors) must have *all* primitive character-states relative to its descendants. Indeed, Ostrom considers the greatly shortened ischium as a unique (derived) feature of *Archaeopteryx.* If *A. lithographica* were the direct ancestor of birds it would be necessary to postulate reversals in the avian lineage for each derived character-state of *A. lithographica*, and this is less parsimonious than assuming that these derived states were evolved *after* the speciation event giving rise to birds on the one hand and *Archaeopteryx* on the other. But to repeat, I fail to see that these types of arguments have a fundamental bearing on Ostrom's major conclusions.

Following the discovery of *Archaeopteryx* in 1861 many morphologists and paleontologists wrote about the similarities of *Archaeopteryx* to different reptilian taxa. Many of these workers identified various dinosaur groups as the possible ancestors of *Archaeopteryx* and birds, and this view gained some acceptance. Later R. Broom and G. Heilman argued that dinosaurs and the *Archaeopteryx*-avian lineage were both derived from the same common ancestor, the pseudosuchian thecodonts. With few exceptions (particularly P. Lowe and N. Holmgren) this viewpoint of avian origins has been accepted dogma for over 50 years, and Ostrom's historical analysis (1976b:168–173) adds yet another example within avian systematics where a particular idea about relationships is maintained on the basis of authority rather than documented evidence.

Ostrom resurrects the theory of dinosaurian origins and convincingly demonstrates that the morphology of *Archaeopteryx* is extremely similar to that of theropod dinosaurs and very different from other reptilian groups, including pseudosuchians—on such comprehensive work are new dogmas born and sustained! Basically, Ostrom's argument is that theropods and *Archaeopteryx* share many derived character-states within reptiles and therefore his hypothesis of common ancestry seems well supported. Ostrom appears to have done a masterful job in this analysis, although it will take a specialist familiar with reptilian anatomy to be the final arbiter. Hecht (1976:357–360) criticizes Ostrom's list of shared derived characters because he believes they are "adaptive" or "fusion-reduction" characters and therefore of "low weight." Hecht's contentions are straws in the wind, for all significant taxonomic characters are "adaptive," and derived characters are either the result of common ancestry or independent origin (convergence). The only way to distinguish between these alternatives is by reference to a particular phylogenetic hypothesis. At best, all that Hecht offers is support for Bock (1965), who at that time accepted a pseudosuchian ancestry.

It is impossible here to summarize all the similarities between *Archaeopteryx* and theropods, but they are so substantial that without feathers *Archaeopteryx* would have been classified as a theropod. The similarities are strongest in the morphology of the forelimb, pectoral girdle, vertebral column, and skull. Of particular interest is the possibility, not discussed by Ostrom, that *Archaeoptryx* may be related to only one or a few genera of theropods rather than the entire group. For example, *Syntarsus* and *Archaeoptryx* appear to share some specializations absent in other theropods. This problem deserves further attention because it has obvious relevance for the analysis of avian origins and higher taxa in general.

As Ostrom correctly points out, the morphology of theropods and *Archaeopteryx* is the key to understanding the origin of birds and their flight mechanism, and his inferences from that morphology have led him to an unconventional, and controversial, hypothesis for the origin of avian flight. The literature on the origin of flight is an amalgam of good science and speculations bordering on science fiction. The latter are sometimes passed off as scientific because it is "historical narrative explanation," but the essential problem remains how to "describe" (one somehow hesitates to call this "explanation") the events of an admittedly interesting historical occurrence and yet not succumb to making inferences that exceed the available evidence.

The main outline of the different theories on avian flight extends back to 19th century workers. Basically there are two: flight originated from terrestrial, cursorial bipeds or from arboreal bipeds that passed through a gliding phase. The latter has been generally accepted by contemporary biologists and has had its clearest exposition by Bock (1965, 1969). Ostrom (1974, 1976a) resurrects the theory of terrestrial origin, but with a new twist. He argues as follows: (1) morphologically *Archaeopteryx* is a theropod, thus functional inferences should be based on that morphology with little emphasis given comparisons with modern birds; (2) *Archaeopteryx* was an active biped, and the hindlimb provides no indication of special adaptations for an arboreal habit; (3) the forelimb of *Archaeopteryx*, like that of closely related theropods, was a grasping appendage with strong powers of adduction and was adapted for predation and not climbing; (4) feathers evolved along with high metabolic activity and as a thermoregulatory control mechanism; (5) contour feathers of the forelimb were modified to aid in capturing prey and only later evolved flight functions.

Although many workers will be skeptical at first exposure to Ostrom's ideas—after all, the wings look like those of modern birds—once one confronts the totality of the evidence, his ideas become more and more acceptable *compared to the alternatives that have been suggested.* Ostrom is willing to construct hypotheses about the origin of avian flight only on the evidence presented by *Archaeopteryx.* Previous hypotheses—particularly the arboreal theory of flight—have been biased by expectations that *Archaeopteryx* should function as a bird. *But Archaeopteryx was a theropod dinosaur with feathers.* Personal prejudicies against the use of wings as capture devices should *not* be based on one's experiences with living birds—where the wing is clearly flight adapted—but on what might be expected of a feathered theropod. If non-feathered theropods were using forelimbs for predation, then might not *Archaeopteryx* have done likewise? In one of his most interesting papers, Ostrom (1976a) suggests that in *Archaeopteryx* the pectoralis minor (supracoracoideus) was a depressor of the arm, not an elevator as in birds, that the trunk skeleton was flexible, that the pectoral girdle was not rigidly fixed, that the sternum was probably cartilaginous, and that the forelimb skeleton exhibited no specializations usually attributed to avian flight. *Archaeopteryx* apparently could not elevate the humerus above shoulder level nor could the hand be folded back against the forearm. On the other hand, Ostrom claims that forelimb functions included rapid extension of the manus, powerful anteroventral flexion of the forearm toward the midline, and the capacity for extreme hyperextension of the wrist—all adaptations expected in a predator.

It seems to me that *Archaeopteryx* cannot be used to support an arboreal origin of avian flight. *Archaeopteryx* does not appear to have arboreal adaptations, and one wonders whether a species previously adapted for cursorial locomotion could move into the trees without such adaptations. Moreover, *Archaeopteryx* does not appear to possess a morphology indicating flight or even parachuting-gliding ability. If workers insist on building hypotheses based only on what we presently know, then we may be compelled to accept a terrestrial origin of avian flight. To invoke additional, unknown proto-avian stages is tantamount to the erection of *ad hoc* hypotheses. Nowhere does Ostrom deny the possibility of an arboreal origin (nor would I), but such a conclusion must await further discoveries. Surely there must have been a radiation of feathered coelurosaurs, and perhaps some of these were arboreal— but *Archaeopteryx* was not.

Historical narrative explanation typically does not involve direct deduction of historical events from natural laws, hence some philosophers of science claim that historical narration is not explanation, but merely description. Be that as it may, systematic hypotheses can be evaluated on the basis of how well they account for the available data and how consistent they are with known properties of organisms (physiology, genetics, etc.). In the case of the origin of avian flight, *Archaeopteryx* is about the only real evidence we have; to his credit, Ostrom is unwilling to extend himself much beyond that evidence.

I am not trying to create a bandwagon over Ostrom's papers, but they are exciting. Some of his findings may eventually be refuted, but there is no doubt that much of his meticulous work will last and that our ideas on avian evolution will be significantly influenced by his results. Ornithologists owe this non-ornithologist a great deal for this contribution.—JOEL CRACRAFT.

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ORNITHOLOGICAL LITERATURE

Proceedings of the 16th International Ornithological Congress. Edited by H. J. Frith and J. H. Calaby. Australian Academy of Science, Canberra, A.C.T., Australia, 1976: xvii + 765 pp., many black-and-white photographs, drawings, and charts. $50.00 Aust.—The 16th I.O.C. was held in Canberra, Australia, from 12–17 August 1974. The scientific program included 11 symposia with 61 papers, and an additional 131 papers in general sessions. Abstracts of the latter were published in *The Emu*, vol. 74, Supplement, 1975. The present volume contains only the papers from the symposia, and thus is a very incomplete representation of the meeting. In general it appears that the symposia papers are more reviews than research reports, while the general session papers are mainly of the latter type. There are some exceptions, however. Although the symposia cover a variety of topics, there is a strong emphasis on ecological and biogeographical subjects, especially in relation to the southern continents. Most of the papers present well prepared integrative summaries of the then current status of their subjects, but several differ little from other writings by their authors. A number of papers review the biology of Australasian birds, which must have been particularly interesting to non-Australians attending the congress.

The volume opens with several I.O.C. committee reports, and the presidential address by Jean Dorst on "Historical factors influencing the richness and diversity of the South American avifauna." Symposium No. 1 is titled *Origins of Australasian Avifauna*, and includes papers on paleogeography and paleoclimatology (J. Cracraft); the fossil record (P. V. Rich); protein evidence (C. G. Sibley); adaptive radiation in Meliphagidae (A. Keast); and the origins of Australian waterfowl as evidenced by their reproductive photoresponses (J. Kear & R. K. Murton). The symposium is unified by its consideration of the roles of immigration and isolation in the development of the Australasian avifauna.

Symposium No. 2, *Biology of Southern Hemisphere Species*, includes a general discussion by A. Keast; a study of the natural history of the emu (S.J.J.F. Davies); and a consideration of Australasia and the origin of the Phalacrocoracidae (G. F. van Tets). Papers on Australasian specialities include a comparative field study of Scrub-birds and Lyrebirds (G. T. Smith); evolution of the bowerbirds and birds of paradise (R. Schodde); osteology of Grallinidae, Cracticidae, and Artamidae (A. McEvey); and a review of the New Zealand Wattlebirds (G. R. Williams). A general conclusion from this symposium is that less is known about the biology and relationships of Australasian birds than about those of most other regions.

Symposium No. 3 concerns *The Value of Various Taxonomic Characters in Avian Classification.* W. J. Bock gives a general review of recent advances in avian systematics. Other papers include analyses of various kinds of taxonomic characters: external morphology (L. L. Short); fossil birds (P. Ballman); the digestive system (V. Ziswiler); behavior (K. Immelman—abstract only); oology (W. Meise); and bioacoustic characters (V. Ilyichev). I found this symposium disappointing. In his introduction E. Mayr identifies its main concerns as (1) the relationships of aberrent or isolated taxa, and (2) the mutual relationships of major avian groups. Few authors addressed these problems directly. It is remarkable that there is almost no discussion of the various systematic philosophies currently vying for predominance. Perhaps this is because the symposium was defined in terms of characters rather than the methods of their analysis.

Symposium No. 4, *Breeding Birds in Southern Continents*, includes studies on endogenous controls of reproductive rhythms (E. Gwinner & V. Dorka); breeding seasons of Australian waterfowl (L. W. Braithwaite); onset of breeding in African hornbills (A. C. Kemp); breeding of African birds in non-arid habitats (G. L. MacLean), and environmental control of breeding and movements in Australian birds (H. A. Nix).

Symposium No. 5 concerns *Biology of Crowned Sparrows (Zonotrichia) in Two Hemispheres.* Papers by B. B. deWolfe, J. R. King, M. L. Morton, F. Nottebohm, A. H. Meier, and D. S. Farner discuss the various environmental and internal factors controlling reproductive and related behaviors in several species.

Symposium No. 6 is titled *Structure of Feathers.* It includes papers on gross feather structure (E. Rutschke); structural adaptations of feathers (P. Stettenheim); structural colors (J. Dyck); taxonomic and evolutionary aspects of feather proteins (A. H. Brush); keratin synthesis (D. J. Kemp et al.); and the molecular structure of feather keratins (R. B. D. Fraser and T. P. Macrae). The symposium demonstrates that feathers; the most distinctive characteristics of birds, are the subject of active research at levels ranging from gross anatomy to biochemistry, and leads to the expectation of important advances in the near future.

Symposium No. 7, *Physiological and Behavioural Adaptations to Arid Zones* includes a general review by W. R. Dawson, and papers on the birds of Africa and South America (G. L. MacLean); Australia (S. J. J. F. Davies); Australian ducks (L. W. Braithwaite); and Sandgrouse (G. L. MacLean).

Symposium No. 8 considers the *Systematics of Australian Passerine Birds.* It includes studies of Australian and Pacific Island warblers (A. Keast); some monotypic genera of Australian oscines (R. Schodde & J. L. McKean); the Quail-thrushes (J. Ford); and protein studies of various forms (C. G. Sibley). It is clear that new approaches to systematic analysis promise to clarify the relationships of many enigmatic Australian passerines.

Symposium No. 9 examines the *Evolution of Island Land Birds.* A. Keast discusses general principles in relation to the specific case of isolated forest outliers in southern Australia, and F. Salomonson gives a theoretical analysis of the main problems concerning avian evolution on islands. Other papers include studies of population variation on islands (P. R. Grant); land-bridge islands (J. M. Diamond); the species-area relation within archipeligos (T. W. Schoener); and plant succession and avifaunal structure (C. Ferry et al.).

Symposium No. 10 deals with *Co-operative Breeding in Birds.* I am told by one who was there that many considered this to be the most exciting topic at the meeting. This is not so apparent from the papers, which deal mainly with surveys of co-operative breeding in various regions, including Australia (I. Rowley); Africa (L. G. Grimes); America (G. E. Woolfenden); and Eurasia (A. Zahavi). The symposium is important in bringing together in one place an enormous amount of data on the occurrence of co-operative breeding, but now a general synthesis is needed.

Symposium No. 11 concerns *Seabirds: Distribution, Speciation and Ecological Diversification at Sea.* Papers cover birds of the tropical "middle seas" (K. H. Voous); the North Atlantic Ocean (W. R. P. Bourne); South America and the North West Atlantic (R. G. B. Brown); the Australian sector of the Southern Ocean (G. W. Johnstone and K. R. Terry); and a general review by M. D. F. Udvardy.

Altogether this is a valuable collection of papers on a diverse group of topics, although as noted above it is only part of the proceedings of the 16th I.O.C., rather than the complete collection of papers that the title suggests. It should be a useful addition to any ornithological library.—ROBERT J. RAIKOW.

Bird Life. By Ian Rowley. The Australian Naturalist Library, Taplinger, New York, 1975. 284 pp., 28 plates of color and black and white photographs, 34 line drawings, maps and tables. $14.95.—This excellent book with a rather unfortunate title is part of a new series on Australian natural history, modeled after the Collins New Naturalist Library. If Rowley's contribution is typical of this new series, Australians and Australia buffs have a great deal to look forward to.

Most introductory ornithology books are written by Americans or Europeans for Northern Hemisphere readers. Rowley has now supplied Australians with an antipodean equivalent: an introduction to the ecology and behavior of birds, using examples from the Australasian fauna. It is also a highly interesting summary of recent field research on Australian birds, drawing from material that hitherto has been hidden in technical reports or journal articles not available to most readers—especially those in the Northern Hemisphere.

The first 5 chapters comprise a general introduction: how birds have evolved and adapted to Australia's unique environmental conditions. This is followed by 16 chapters of research-oriented accounts of single species or groups of related species that illustrate the introductory statements. Ten of these chapters deal with resident or sedentary birds such as the Superb Blue Wren (*Malurus cyaneus*), Australian Raven (*Corvus coronoides*), Australian Magpies (*Gymnorhina* spp.), Kookaburra (*Dacelo gigas*), Miners (*Manorina* spp.), and Mallee Fowl (*Leipoa ocellata*). The last six discuss migrant species (using an overly strict definition of the term) such as Tasmanian Mutton-birds (*Puffinus tenuirostris*) and nomadic species such as Brolgas (*Grus rubicundus*) and White-tailed Black Cockatoos (*Calyptorhynchus baudini*).

Rowley begins most accounts by stating who conducted the research, where and how it was done, and whether or not it is still in progress. He then summarizes the results in an interesting manner, successfully avoiding both the too technical and the too elementary. Much of the excitement of this book lies in reading about active research; one cannot help wondering whether some of the questions raised have been answered since the book was completed. For those who wish to read further about a given species, the accounts are well referenced.

The book ends with a chapter on economic ornithology and conservation problems, an appendix on methods of study (especially banding), another on books, journals, and societies, eight pages of references, and a good ten-page index.

As an American interested in Australian birds, but with only a few weeks of firsthand experience with the fauna, I found Rowley's book fascinating. He has done a particularly good job in describing the varied social systems—breeding regimens and movements—showing how they are adapted to the Australian climatic and ecological conditions that are so different from those in the Northern Hemisphere. Also of interest is the comparatively small number of migratory species in the Australian avifauna (approximately 8%) vs. residents (66%) and nomads (26%). The few transequatorial migrants are mostly waders and seabirds (no passerines). Other species migrate north-south within the Australo-Papuan region or between Tasmania and mainland Australia. A few may also be altitudinal migrants, but this is still poorly known. An American reader will be struck by the very different components of the Australian avifauna: the large number of nectivorous birds (lorikeets, sunbirds, silvereyes, and some 69 species of honeyeaters), and the many nomadic species. Most nomads breed seasonally, but may change the breeding locale from year to year. A few seem to be able to breed whenever conditions are favorable. Nomadic species are not just arid land birds affected by erratic rainfall in the interior of the continent. They are also forest and farmland species that follow a changing food supply. These latter include flower feeders (such as lorikeets and honeyeaters), insectivores (currawongs), fruit eaters (dicaeids), seed eaters (some cockatoos and grass finches), and scavengers (some corvids).

It is unfortunate that most ornithological research in Australia has had to be concerned only with economically important species: game birds, agricultural pests, etc. The CSIRO-conducted research has been of generally high quality but its limited scope has left serious gaps in the general knowledge of the avifauna. Fortunately private individuals and groups, particularly banders, are becoming increasingly active, so the serious research effort is becoming better balanced.

In a few instances Rowley's discussions have been outdated in information, or he has limited himself too much on a topic. His treatment of navigational theories is slightly behind the times, and in the section on zoogeography he begins with the Pleistocene, omitting mention of the important recent studies of plate tectonics and their effect on the origins of the Australian fauna. The book also should have been edited more tightly for grammatical errors: on p. 163 the word "data" is used both as a singular and plural in the same paragraph; on p. 108 one finds "orientate"; farther and further apparently are considered interchangeable; and in places the usage of commas, colons, and semicolons is quixotic.

The only serious fault of the book lies in the poor placement of the plates in relation to the text. For example, the plate showing nestling growth rates of Australian Ravens and 2 photographs of White-winged Choughs is inserted in the middle of the Kookaburra chapter, 24 pages after the raven account and 6 pages after the end of the choughs. The raven text is "illustrated" instead by a wren plate that belongs in the previous chapter. As the plates are not evenly spaced through the book, they could easily have been better coordinated with the text. It is also annoying to have the plates referred to only by number rather than by page, especially when they are so badly scattered.

These minor objections aside, considering his stated aims, Rowley has done an excellent job. This book will be enjoyed by anyone even slightly interested in the Australian avifauna or in the intricate adaptations of birds to their environment. The title is sadly undescriptive of the contents, but perhaps through listings such as "Bird Life [Australian]" that I saw recently in a dealer's catalog, this book will find its intended, and deserving, readership outside Australia.—MARY H. CLENCH.

AVIAN PHYSIOLOGY, 3rd Edition. Edited by Paul B. Sturkie. Springer-Verlag, New York, Heidelberg, Berlin, 1976: xiii + 400 pp., 77 tables, 102 figures. $23.80.—The prospect of having a current treatment of avian physiology in one volume is an attractive one, for the primarily physiological chapters of "Avian Biology" (D. S. Farner and J. R. King, editors; Academic Press) are distributed over 4 volumes and a 3 year interval (1972–75). Sturkie's book is thus timely and worth considering as to its adequacy as a reference work for ornithologists requiring physiological information in their studies. Authoritativeness has been assured in this volume through assemblage of a group of authors who have contributed chapters on their respective fields of interest: Nervous System (T. B. Bolton); Sense Organs (M. R. Kare and J. G. Rogers, Jr.); Blood: Physical Characteristics, Formed Elements, Hemoglobin, and Coagulation (P. D. Sturkie with P. Griminger); Heart and Circulation: Anatomy, Hemodynamics, Blood Pressure, Blood Flow, and Body Fluids (P. D. Sturkie); Heart: Contraction, Conduction, Electrocardiography (P. D. Sturkie); Respiration (M. R. Fedde); Regulation of Body Temperature (G. C. Whittow); Energy Metabolism (G. C. Whittow); Alimentary Canal: Anatomy, Prehension, Deglutition, Feeding, Drinking, Passage of Ingesta, and Motility (P. D. Sturkie); Secretion of Gastric and Pancreatic Juice, pH of Tract, Digestion in Alimentary Canal, Liver and Bile, and Absorption (P. D. Sturkie); Carbohydrate Metabolism (R. L. Hazelwood); Protein Metabolism (P. Griminger); Lipid Metabolism (P. Griminger); Kidneys, Extrarenal Salt Excretion, and Urine (P. D. Sturkie); Hypophysis (P. D. Sturkie); Reproduction in the Female and Egg Formation (P. D. Sturkie with W. J. Mueller); Reproduction in the Male, Fertilization, and early Embryonic Development (P. D. Sturkie with H. Opel); Thyroids (R. K. Ringer); Parathyroids, Ultimobranchial Bodies, and the Pineal (R. K. Ringer and D. C. Meyer); Adrenals (R. K. Ringer); Pancreas (R. L. Hazelwood). The chapters are well supplied with tables and figures that effectively supplement the text. Each of the chapters concludes with a list of the references cited in it, which should facilitate access to the original literature. The coverage of this literature extends mainly through 1974; only a handful of references later than this are included.

The various chapters are all quite informative. I found those on respiration; regulation of body temperature; carbohydrate, protein, and lipid metabolism; excretion; reproduction in the female; and various aspects of endocrinology of particular interest. The involvement of so many authors leads to only a few inconsistencies. For example, one derives quite different impressions of the state of knowledge concerning the avian pineal from the statements by P. D. Sturkie (p. 287) and by R. K. Ringer and D. C. Meyer (pp. 365–368).

My principal dissatisfaction with the third edition of "Avian Physiology" concerns the insufficient attention it devotes to the physiology of wild birds. The bulk of the available information on avian physiology does pertain to the domestic fowl, but a substantial body of literature exists on wild birds, which could permit broadly comparative treatments of a number of topics, something done very well in the volumes of "Avian Biology." Adequate use of this literature has been made in only a few of the chapters, notably those dealing with respiration, regulation of body temperature, energy metabolism, and excretion, which have a fairly strong comparative orientation. Further use of such an orientation would have led to improved coverage of a variety of processes important in the lives of birds, e.g., molt, migration (including its navigational aspects), winter fattening, reproductive timing, circadian periodicities, respiratory gas exchange and moisture loss in eggs. What comparative coverage does exist in many of the chapters is complicated by use of imprecise common species names (e.g., "sparrow") and/or omission of scientific names.

"Avian Physiology" will be a useful reference and text for individuals concerned with domesticated species. It also will be helpful to ornithologists seeking information on topics for which the domestic fowl is an adequate model species. However, the utility to this latter audience would have been increased by more extensive treatment of wild birds.—William R. Dawson.

The Birds of the Malay Peninsula, Vol. 5. By Lord Medway and David R. Wells, illus. by H. Grönvold. H. F. & G. Witherby Ltd., London, 1976: 448 pp., 25 color plates. £25.—Since the authors of this volume were my colleagues and since I had a deep personal interest from the inception of their work, I take pleasure in reviewing this important addition to the recorded knowledge of the birds of the Malay Peninsula. The careful understatements in the preface only hint at the struggle and pathos involved in the development and completion of the 5 volume work first conceived by H. C. Robinson, and later continued by F. N. Chasen, and in an unpublished form, by E. Banks. All of the first 3 authors died before the set could be completed, and its publication extended over a period of 5 decades. The first 4 volumes were published in 1927, 1928, 1938, and 1939.

When, in 1964, the plates for the final volume were discovered in the British Museum, David Wells told me that he and Lord Medway were contemplating completing the series both with enthusiasm and trepidation. They wished to duplicate the format of the previous 4 volumes, but realized that the costs would be much above the original. I do not know what the original volumes sold for, but they had become collector's items by 1958 when I bought my copies. There was no handbook or field guide for Malayan birds at that time, but Smythies "Birds of Borneo" encompassed most of the species and was very useful. The recent "A field guide to the birds of S. E. Asia" by King and Dickinson helps to fill the field guide needs for that area.

It is necessary for the reader to have at hand the previous 4 volumes before approaching the 5th critically. The authors have done a commendable job of recreating the format. Any criticism leveled at type form, color plates, book size, etc. must be tempered by knowledge of the objectives involved.

Use of the volume and its many local names is made easier by having a gazatteer of localities in the introductory section. Following the introduction are 3 chapters by David Wells (Resident Birds), Lord Medway (Migratory Birds), and Ian C. Nisbit (The Eastern Palearctic Migration System in Operation) based upon their research and observations. In these they summarize much of what has been learned of Malayan birds since the 1938 volume was published.

These introductory chapters take up the first 77 pages of the book. The remainder, over 325 pages, is devoted to a discussion of the 576 species recorded from Malaya. In this the taxonomy is brought up to date, progression of molt is indicated where known, migration information such as arrival and departure dates are given, and information on such topics as nesting, number of eggs, and a description of the voice is provided. Detailed biological descriptions are not given except where such data were inadequately reported in previous volumes. By this method a great mass of information is added to that already provided in the first 4 volumes, and knowledge is brought up to 1973 when the manuscript was closed for editing and publication.

The authors are to be highly commended for this authoritative and carefully prepared volume of great historical interest as well as value to the ornithology of Southeast Asia. —H. Elliott McClure.

Falcons Return. By John Kaufmann and Heinz Meng. Wm. Morrow and Co., New York, 1975: 128 pp., 106 black and white photos. $5.95.—Subtitled "Restoring an endangered species," this book is an account of the Peregrine Falcon and details its life history, its widespread destruction due to DDT poisoning, and efforts to restore the species by introducing captive-bred Peregrines back into the wild.

The first section is a description of the birds' external anatomy, nest sites, courtship, flight, and other aspects of Peregrine biology. The text is illustrated with black and white photographs ranging in quality from fair to excellent. Those of the Holt's Ledge eyrie are particularly good and show all aspects of the breeding biology of Peregrines. This section records the demise of the birds and concludes with a nontechnical discussion of pesticide poisoning and food chains.

Falconry is the subject of the second section. The history of the sport is described, and many falconry terms are defined. Capture, training, and flying of eyasses (young Peregrines removed from the nest) are described, and lure flying and hunting are examined. Although some conservationists may cringe at the mention of falconry, the authors contend that the only chance of bringing the Peregrine back depends upon the skillful use of the techniques of falconry. They suggest that hacking, an old method of raising eyasses so that they remain basically wild, but learn to fly and hunt on their own, is a possible means of replenishing the natural population.

The third section is devoted to the efforts of Heinz Meng to breed and raise Peregrines in captivity. The account of Meng's devoted and skillful work as the chicks' father is unnecessarily detailed and frequently melodramatic. Efforts by workers at Cornell University's Laboratory of Ornithology are also mentioned. Their capability of raising more than 200 Peregrines a year and placement of captive-bred chicks in eyries where parent birds fail to breed due to eggshell thinning, offer some glimmer of hope. However, the continued use of DDT and other pesticides in poorer countries of Central and South America where many birds winter continues to threaten the existence of Peregrines and other raptors. The book concludes with a brief bibliography.

Although this book is for general readers, particularly those with an interest in wildlife, it will also interest some ornithologists. It is a simply, but well-written and informative account of the Peregrine Falcon.—DAVID R. MAURER.

GEOGRAPHIC AND CLIMATIC RELATIONSHIPS OF AVIFAUNAS WITH SPECIAL REFERENCE TO COMPARATIVE DISTRIBUTION IN THE NEOTROPICS. By Paul Slud. Smithsonian Contributions to Zoology, No. 122, 1976; iii + 149 pp.—This massive study presents an extremely detailed analysis of bird distribution patterns throughout the world, although emphasis is placed on birds of the Neotropics. In addition, the bulk of the world's islands for which species lists exist are also examined. Dr. Slud has divided his book (for it is sufficiently lengthy to be so labeled) into four major sections: the Passerine-Nonpasserine Relationship; the Suboscine-Oscine Relationship; the Passerine-Nonpasserine Suboscine-Oscine Relationship; and Requirements for Further Research.

A too-detailed discussion as to why water birds should not be included in the analyses which will follow, and further interesting discussion on the separation of migrants and native land birds, lead into the first major subdivision detailing various properties of the world's Passerine-Nonpasserine relationships. Regarding migrants, the author's belief that migrants "complement the residents" (p. 9) rather than "compete with them" (p. 9) is not really borne out by Fig. 4, p. 10. Instead, migrants seem to have a difficult time existing in the complex and apparently highly competitive tropical rainforest as if there were no empty niche space to go around, or as if the highly specialized and competitive residents keep temporary migrants from coexisting in the community. Slud himself notes (p. 9) that, "Both in Africa and South America it is the richest biotope, the equatorial rain belt, that acts as a barrier which many migrants do not cross, very few enter, and the remaining ones skirt or pass over in order to winter in the southern third of the continent." Admittedly there is much rain forest north of Colombia (where the migrant percentage diverges from the native fauna, see Fig. 4, p. 9), but the data can realistically be interpreted both ways, as arguing for and against competitive interactions. In fact, the inverse correlation of percent migrants with total avifauna ($r = 0.99$, p. 8) also supports a competition hypothesis.

The author points out the similarity of the Passerine-Nonpasserine ratio in habitats throughout the world and notes that it is generally 2:1, with the ratio being higher in temperate areas and lower in tropical regions. The ratio then logically (and nicely) rises with altitude in the tropics. Figure 6 clearly illustrates the positive relationship of Passerine-Nonpasserine ratios with what is apparently overall physical environmental complexity, with the highest U.S. values being concentrated in the Southwest and adjoining Mexico. Slud discusses a "peninsular effect" of lowered ratios and specifically mentions Florida (0.89 P-N ratio) and the Yucatán Peninsula (1.03). He ignores Baja California (a physiographically complex peninsula) which has the highest ratio on the North American land mass!

Perhaps one of the most interesting sections is that dealing with birds on islands. "Insular avifaunas tend to correlate in size with the area of the island, but only in a general way" (p. 21). "Insular biotas, however, conform to no universal standard and their compositions are each the unique result of interplay among many factors that are differentially peculiar to islands: this makes islands synecologically nonintercomparable." (p. 21). With these statements a reader is led to think that perhaps the author has been isolated from the open literature for ten years and that the theories of island biogeography have slipped by him. But no, Slud has kept up with the literature. He is merely launching a low key attack on a number of studies that have dealt with avian insular biology, in particular, early work by Diamond, Terborgh and Faaberg, and MacArthur and Wilson. Slud is not speaking theoretically, but presents data on turnover rates, the effect of distance and colonization rates on islands. In particular, he reanalyzes earlier reported results with apparently more complete data and arrives at different conclusions. Slud notes, for example, that there is no evidence yet for believing that small far islands and large near islands have similar extinction rates of bird species. He also points out errors in previously published calculations of colonization rates and notes the difficulty of defining the species pool of potential colonizers in biogeographic studies. The author very likely places too much emphasis on anomalous little Cocos Island in the tropical eastern Pacific which has undergone no species turnover in about 70 years (no extinctions and no successful colonizations), and has an endemicity value of possibly 50%. One does not read this well-reasoned section and feel that the basic island biogeographic theory is shaken, for it is built on evidence from numerous and varied fields of study. One does, however, see a hard-working field biologist who gathers data carefully for years before publishing a monograph, challenging members of the "MacArthurian school" to bring a more solid data base into theoretical constructs. The "quick and dirty" techniques of idea biology have made large and exciting contributions to modern ecological theory, but such papers are open to attack by the very limited nature of their data. Perhaps fewer useless theories (which often tie up reasearchers who are committed to supporting or refuting such will-o-the-wisp hypotheses) would clutter the literature if more detailed empirical results were obtained before publishing. However, the spark of imagination is necessary if predictive syntheses are to be made and if one is going to be able to see the forest, rather than the individual trees, the rule, rather than the exception.

Trends in the Suboscine-Oscine ratio are discovered (it declines from about 60% in South America to about 20% in Mexico: it is lower in the dry tropics than in the humid tropics). The comparative Passerine-Nonpasserine:Suboscine-Oscine ratio is probably more useful. In particular, such a ratio can indicate whether or not a site is in the humid tropics (a low ratio), and allows comparisons of values obtained from highlands or higher latitudes (a higher ratio). As Slud notes, the ratio is most useful in site-oriented situations. The usefulness of ratios in surveys where time is limited (and some useful results can still be obtained) is pointed out in Figs. 32 and 33. The overall tone of the "Further Research" section seems to be artificially tacked onto the bulk of the publication, although the section is in itself informative. The data base for this study is presented in detailed tables at the end of the publication.

Basically, this is an enjoyable, if ponderous, work. There is much food for thought. The style is possibly too reportorial and I wish that the author had gone on to pursue other ramifications of the data, particularly from the evolutionary standpoint. One recalls (again) the MacArthur technique. Here are the data, now we need more ideas. —MICHAEL A. MARES.

THE BIOGEOCHEMISTRY OF BLUE, SNOW, AND ROSS' GEESE. By Harold C. Hanson and Robert L. Jones. Southern Illinois University Press, 1976: xviii + 281 pp., 266 figures, 45 tables. $15.00.—The purpose of this study is to show how elemental analyses of goose feathers can be used to determine the local origin of the birds. The book is divided into 8 chapters which cover a discussion of geographical origins of wild geese, sampling, analytical procedures, data analyses, soil and plant relationships, geology, soils, and feather mineral patterns. Data are also presented on the differences in feather mineral patterns and the origins of migrant and wintering geese. An adequate review of the previous literature on the chemical composition of feathers is also presented. Finally, the authors are able to discuss the biogeochemistry of feathers and wild geese and their chemical and mineral environment.

Detailed data for 12 elements in feathers (calcium, magnesium, sodium, potassium, phosphorus, iron, zinc, manganese, copper, boron, silicon, aluminum) are presented and discussed, while a less detailed discourse on sulfur is presented in an appendix.

The data were obtained by analyzing the vane portions of the pimary feathers, since these are more highly mineralized than the shaft. Optical emission spectroscopy was employed on ashed and subsequently liquefied samples using reference plant samples as standards.

Although it is not possible in a short review to mention all the important observations and conclusions obtained from this vast and important study, a few comments might serve to provide some concept of the variety of information that has been gleaned from this project.

Sodium is the dominant ion affecting the levels of absorption and excretion of calcium, magnesium, and potassium. Canada Geese, for example, have enough calcium and magnesium in their environment to exceed the excretory losses stimulated by their high sodium intake. The calcium content of feathers was the most important aid in distinguishing geese from the various colonies of Blue and Lesser Snow Geese. Coastal geese can be distinguished from inland populations of western Canada Geese on the basis of the high concentration of phosphorus in their primary feathers. A favored food of Canada Geese is one species of *Equisetum*, a zinc accumulator, which may account for the high zinc content of Canada Geese from the Belcher Islands. There is at least one species of *Equisetum* which is reputed to be a gold accumulator which Hanson and Jones might consider employing as a tracer as they continue to expand their study further.

In such an extensive study interelemental relationships arise which are quite important. Aluminum and silicon are closely related as is potassium with both these elements, reflecting their involvement with micaceous clays. Iron and manganese coherence are reminiscent of their association in soils as well as ore bodies. In addition, close significant relationships were observed between iron, silicon, and aluminum as well as between zinc and copper, reflecting the metalliferous areas over which birds have passed.

It is clear from this study that the chemical examination of feathers provides a sensitive record of environmental and metabolic relationships of elements. The concentration of these elements in feathers indicates the breeding grounds of geese of known and unknown origins.

This book is well worth reading, heavily illustrated, and nicely printed. It presents much valuable data of interest to avian biologists as well as general biogeochemists.—URSULA M. COWGILL.

BIRDS AND THEIR WAYS. By Alexander Dawes Du Bois with Charlotte A. Du Bois. T.S. Denison & Co., Minneapolis, Minnesota, 1976. 184 pp., 81 black and white photos. $8.95.—Intended as a companion to the author's earlier work, *Glimpses of Bird Life*, this book consists of two parts. Part I is an anecdotal and haphazard account of various species encountered during the author's lifelong pursuit of birds (one early account is on a horse drawn mail stage). Birds were observed in many parts of North America, although most observations are from around the author's Minnesota home or near Cornell University. Topics such as nesting, care of young, feeding, song, and sociality are discussed. Part II is a more detailed description of the lives of a dozen favorite species.

With the exception of a blurred kingfisher on p. 16, a spotted photo on p. 127, and a repetitive series of woodpecker holes, the photographs are of good quality and add to the text. These pictures, taken from a blind by the author, are illustrative of his devotion to birds and photography.

A major criticism is with the constant anthropomorphic interpretation of birds' actions: a bluebird "had sung to instill courage in his two fearful young, to give them promise of safety, and hope of food as a reward." A Red-headed Woodpecker showed so much grief at his wounded mate, "that I shot him also, out of compassion." Some of the wording is awkward: "All these hazards birds have no way of coping with," while other material is stilted: a bathing tanager is likened to "a flame trying to extinguish itself."

This book will have a limited appeal since it is neither visually impressive enough for the coffee table trade nor rigorously scientific.—DAVID R. MAURER.

THE BLUEBIRD: HOW YOU CAN HELP ITS FIGHT FOR SURVIVAL. By Lawrence Zeleny. An Audubon Naturalist Library Book, Indiana University Press, Bloomington, 1976: 170 pp., 7 color plates, 33 text figs., 3 tables. $7.95.—In this excellent book for conservationists and naturalists, Lawrence Zeleny gives a succinct and informative account of bluebird life history encompassing the breeding ranges of the three species, food habits, courtship behavior, nesting and care of the young, and migration. He makes the reader acutely aware of the problem of declining bluebird populations due to the effects of man's destruction of their natural habitat, and competition from Starlings and House Sparrows. Other contributing factors are a decline in bluebird winter food supplies, adverse weather conditions, and the indirect effects of insecticides. He also provides a listing of plants (by botanical and common name) that yield supplies of winter berries enjoyed by bluebirds.

After defining the scope of the problems, Zeleny presents solutions by which man can assist the bluebird in maintaining and increasing its present population size. He gives detailed directions and illustrations for the construction and placement of suitable roosting and nesting boxes. Based on a typical bluebird nesting timetable, the author explains how to monitor the nesting sites, and how to protect the bluebirds from predatory mammals, snakes, birds, and other cavity-nesting competitors. He also discusses various insects that are troublesome for bluebirds during the nesting period, and offers a table of insecticides that can be employed in the destruction of these pests, but that are unlikely to be noxious to the birds. He also gives the history, objective, construction, and management of bluebird trails that have been successful in helping the bluebirds to survive.

Throughout the book Zeleny ascribes the human attributes of love, happiness, sorrow, and altruism to the bluebird. The dispassionate scientist may criticize this anthropomorphic connotation, but after reading the heartwarming and delightful accounts of the author's handraising a brood of orphaned bluebirds to adulthood and seeing them and their offspring return to nature, one can only admire and think of the true beauty of God's creatures. This is a truly enjoyable book that I recommend most enthusiastically. —Edward V. Swierczewski.

ORNITHOLOGICAL NEWS

AARON M. BAGG STUDENT MEMBERSHIP AWARDS—1977

Student Membership Awards in the Wilson Ornithological Society have been made available through funds generously donated in the memory of the late Aaron M. Bagg, former president of the Society. The Student Membership Committee has designated the award recipients for 1977 as follows: Theresa M. Allen, University of Texas at Arlington; Jonathan L. Atwood, California State University at Long Beach; Albert Aulette, Michigan State University; Bruce M. Beehler, Princeton University; Keith L. Bildstein, Ohio State University; Erik J. Bitterbaum, University of Florida; Roderick N. Brown, McGill University; Kelly B. Bryon, Sam Houston State University, Texas; William D. Clark, University of Illinois; Leon J. Folse, Jr., Texas A&M University; Eric D. Forsman, Oregon State University; Kimball L. Garrett, University of California at Los Angeles; Ralph J. Gutierrez, University of California at Berkeley; Geoffrey G. Hogan, Brock University, Ontario; Ronald L. Kalinoski, Syracuse University; Walter D. Koenig, University of California at Berkeley; Scott M. Lanyon, State University of New York at Geneseo; Howard Levenson, Humbolt State University, California; Douglas W. McWhirter, Michigan State University; Michael C. Moore, Indiana University; Gerald R. Meyers, Kent State University; Barry R. Noon, State University of New York at Albany; Douglas O. Norman, State University of New York at Stony Brook; Gary L. Nuechterlein, University of Minnesota; Richard T. Reynolds, Oregon State University; Douglas G. Richards, University of North Carolina; Kim M. Riddell, University of Florida; Wanda K. Rola-Pleszcynska, University of Toronto; Mark R. Ryan, Iowa State University; Josef K. Schmutz, University of Alberta; Bonita M. Smith, Miami University, Ohio; Donald L. Sparling, University of North Dakota; Gail E. Spealer, University of Florida; Michael N. Weinstein, California Polytechnic State University—Douglas James, Chairman, Student Membership Committee.

EBBA RESEARCH GRANT

The Eastern Bird-Banding Association is offering a $250 Memorial Grant in aid of research. The applicant must be an undergraduate or graduate student and must be using bird banding as part of his or her research. Applications must be completed before 1 March 1978. For further information write to the Chairman: Dr. Bertram G. Murray, Jr., c/o Biology-Livingston, Kilmer Campus, Rutgers University, New Brunswick, N.J. 08903.

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in The Wilson Ornithological Society are available because of funds generously donated in the memory of Aaron M. Bagg, a former president of the Society. Application forms for the awards to be granted in 1978 may be obtained from James R. Karr, Dept. of Ecology, Ethology, and Evolution, Vivarium Building, Univ. of Illinois, Champaign 61820. The deadline for applying is 1 December 1977. An Aaron M. Bagg Student Membership Award provides a 1-year gratis new membership in The Wilson Ornithological Society for selected exceptional students in the field of ornithology.—James R. Karr, Chairman, Student Membership Committee.

Erratum.—On p. 187, paragraph 5, line 1 of the March issue (Vol. 89, No. 1), the word "distant" should be "distinct."

THE PRESIDENT'S PAGE

The Wilson Ornithological Society comprises a balanced blend of members from the ranks of both amateurs and professionals united by a common interest in avian biology. It is advantageous to preserve this balance. But, it is particularly important too for the Society to develop programs that will attract student members because these constitute the potential ornithologists of the future. A few years ago the Society adopted the present policy permitting student members, upon graduating, to apply toward a regular life membership the total dues paid when they were students. Maybe this has not been publicized enough, or perhaps the financial status of a new graduate prevents the grasping of opportunities no matter how attractive. Whatever the reason, not many students have accepted this life membership option and its financial benefits. More recently, the Aaron M. Bagg Student Membership Awards have provided pre-paid first-year memberships to especially talented students, and this program has been very successful. Also, the Alexander Wilson Prize has recognized the best student paper presented at annual meetings. Finally, research support to graduate students has been allocated annually in the form of Louis Agassiz Fuertes Grants.

But more needs to be accomplished and I will regularly communicate to the membership concerning these actions, and also concerning other new executive initiatives of general society interest, or on other matters, particularly those requiring views expressed from the membership. This time I want to stress the matter of assistance to student research through the Fuertes Grants. In recent years the Fuertes Fund Committees have become more and more vocal concerning the difficulty of the task in selecting 1 or 2 recipients from among the increasing number of excellent applications received. There simply have not been enough funds available to award all those who deserve the aid and recognition. Of course, it is unrealistic to expect that there will ever be enough money available to reward every deserving person, but a higher proportion should receive recognition than now is the case.

There are some who have argued that indeed the recognition is really the only importance of the grants because the amounts awarded are not presently enough to be essential to graduate research. True enough, it is an honor to receive these grants and the recipients can be proud to include mention of them in their resumés the rest of their careers. On the other hand, I know of many cases in which an amount of a few hundred dollars, such as a Fuertes Grant, has been extremely important to the successful completion of both master's and doctoral research programs. With the continuing decline in federal and state funds to support such research, through default this activity becomes increasingly thrust upon other resources such as the Fuertes Fund.

Thus, I recommend that new funds be sought to increase the number of Fuertes Awards given annually. I recognize that the primary responsibility of an organization such as the Wilson Ornithological Society is to maintain the viability of a respected research journal, and that almost all operating funds are allocated for that purpose. If the number of Fuertes Grants are to be increased this means finding ways to independently supplement that fund. Therefore, I have appointed a special committee to study this matter and make recommendations to the Executive Council at the West Virginia meeting next May. This committee is chaired by Dr. C. J. Ralph. A second charge to the committee concerns revising the application and selection process. I invite members to send their opinions on either matter to Dr. Ralph addressed to the Institute of Pacific Islands Forestry, 1151 Punchbowl Street, Honolulu, Hawaii 96813.—DOUGLAS JAMES.

PROCEEDINGS OF THE FIFTY-EIGHTH ANNUAL MEETING

George A. Hall, Acting Secretary

At the invitation of the Department of Zoology and the Department of Wildlife and Fisheries of Mississippi State University, the Oktibbeha Audubon Society, the Mississippi Ornithological Society, and the Noxubee National Wildlife Refuge, the Fifty-eighth Annual Meeting of the Wilson Ornithological Society was held on the campus of Mississippi State University near Starkville, Mississippi, from Thursday 19 May to Sunday 22 May 1977. The Executive Council met on Thursday evening in Harned Hall. Business sessions, and scientific papers' sessions were held in McCool Hall on Friday and Saturday.

On Thursday evening members were entertained at a reception at the Lakeside Country Club. A session of 3 motion pictures (Atchafalaya, At the Crossroads, Life in a Weaverbird Colony) was held on Friday evening.

The Annual Banquet was a buffet dinner held on Saturday evening at the Mississippi State Union. After a few announcements including the announcement of the award winners the group moved to McCool Hall for the showing of a most impressive movie on the Harpy Eagle presented by Neil Rettig, Wolfgang Salb, and Alan Degan.

On Friday and Saturday mornings, field trips were held to the Noxubee National Wildlife Refuge, where the feature was a nesting Red-cockaded Woodpecker who performed beautifully for all, and to the Cliftonville Heronry, a colony of Little Blue Herons and Cattle Egrets. On Sunday a somewhat longer trip was taken to Noxubee Refuge, and many of the members participated in a canoe trip on the Tombigbee River. A display of ornithological art was on exhibition at the University library and in the MSU Union. Trips were arranged to a local clock factory and to some antebellum homes. A star gazing session was also held on Thursday and Friday nights.

FIRST BUSINESS MEETING

The session was called to order at 9:15, Friday 20 May by Local Chairman J. A. Jackson. He introduced Dr. J. C. McKee, Vice-President for Research and Graduate Study at Mississippi State University, who made a short speech of welcome. President Andrew J. Berger then responded for the Wilson Society and called to order the first business meeting.

The minutes of the 1976 meeting at Ithaca, New York were approved.

Acting Secretary G. A. Hall summarized the actions taken by the Executive Council on Thursday evening:

1. The Council heard reports from the officers and committee chairmen, copies of which follow.

2. The Council unanimously re-elected Dr. Jerome A. Jackson as editor of the Wilson Bulletin.

3. The 1978 meeting will be held at Jackson's Mill, West Virginia, on 4–7 May 1978. No definite commitments for subsequent meetings have been made but tentatively the 1979 meeting will be in Duluth, Minnesota, the 1980 meeting will be a joint meeting with the Cooper Society, and the 1981 meeting may be in Charleston, South Carolina.

4. The Council is exploring the proposals made by the Council of the A.O.U. to produce a combined membership list for the 3 ornithological societies. Treasurer Ernest E. Hoover summarized the report of the Treasurer. The full report follows.

THE WILSON ORNITHOLOGICAL SOCIETY

REPORT OF THE TREASURER

Year Ending December 31, 1976

GENERAL FUNDS

Balance as of last report December 31, 1975			$21,088.95

RECEIPTS

Membership Dues			
Active for 1976	$ 4,203.00		
Active for 1977	11,640.00		
Total Active		$15,843.00	
Sustaining for 1976	135.00		
Sustaining for 1977	570.00		
Total Sustaining		705.00	
Subscriptions to *The Wilson Bulletin*			
For 1976	1,963.50		
For 1977	6,580.00		
Total Subscriptions		8,543.50	
Advance Renewals		419.50	
Sales of Back Issues of *The Wilson Bulletin*		1,140.00	
Interest and Dividends on Savings & Investments			
Income from General Endowment Fund	4,758.71		
Income from G. M. Sutton Colorplate Fund	1,761.14		
Interest on Endowment Savings Account	423.97		
Interest on Regular Savings Account	368.85		
Total Interest and Dividends		7,312.67	
Royalties from Microfilming Back Issues of *The Wilson Bulletin*		185.24	
Contributions from Authors and Others		1,878.00	
Transfer from Regular Savings Account		7,000.00	
Total Receipts			$43,026.91

DISBURSEMENTS

The Wilson Bulletin (Printing & Engraving)	27,578.23	
The Wilson Bulletin (Mailing & Maintenance)	2,351.08	
Colorplate Processing Expense	2,201.80	
Editor's Expense	1,703.26	
Secretary's Expense	86.09	
Treasurer's Expense	1,636.38	
Committee Expense	302.32	
Annual Meeting Expense	300.67	

International Council for Bird Preservation	30.00	
Miscellaneous Expense	2.00	
Total Disbursements		$36,191.83
Excess of Receipts Over Disbursements		$ 6,835.08

GENERAL CASH FUND

Checking Account	$18,978.39
Savings Account	$ 2,464.86
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1976	$21,443.25

Josselyn Van Tyne Memorial Library Fund

Balance as of Last Report December 31, 1975	$ 804.27

RECEIPTS

Sale of Duplicates and Gifts	1,041.70

DISBURSEMENTS

Purchase of Books	1,437.76
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1976	408.21

Louis Agassiz Fuertes Research Fund
Margaret Morse Nice Fund
Edwards and W.O.S. Paper Funds

Balance as of Last Report December 31, 1975	$ 313.00

RECEIPTS

Contributions	2,634.00

DISBURSEMENTS

Grant-In Aid		
To Charles R. Brown	$100.00	
To Richard O. Bierragard	200.00	
To Susan Hannon	200.00	
To Stephen T. Emlen	200.00	
To Arthur J. Wiseman	100.00	
To Stephen Borecky	100.00	
Total		$ 900.00
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1976		$ 2,047.00

Aaron Moore Bagg
Student Membership Award Fund

Balance as of Last Report December 31, 1975	$ 400.00

RECEIPTS

Contributions	$ 200.00

DISBURSEMENTS

Student Membership Grants	$ 176.00
Balance in Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1976	$ 424.00

Endowment Funds

General Endowment Fund

Balance in Endowment Savings Account, Old Kent Bank and Trust Co., Grand Rapids, Michigan as of Last Report, December 31, 1975		$ 6,990.00

RECEIPTS

Life Membership Payments		$ 2,550.00
Balance in Endowment Savings Account, Old Kent Bank and Trust Co., Grand Rapids, Michigan, December 31, 1976		$ 9,540.00
Investments Held as of December 31, 1976		
United States Government Bonds	$ 5,393.75	
International Bank Bonds	9,810.00	
Canadian Provincial Bonds	4,100.00	
Corporate Bonds	19,975.00	
Convertible Corporate Bonds	2,625.00	
Convertible Preferred Stocks	14,245.00	
Common Stocks	53,733.50	
Uninvested Principal	1,885.70	
Total Investments		$111,767.95
Total General Endowment Fund December 31, 1976		$121,307.95

George Miksch Sutton Colorplate Fund

Investments Held as of December 31, 1976		
International Bank Bonds	$ 1,090.00	
Canadian Provincial Bonds	4,587.50	
Corporate Bonds	10,000.00	
Common Stocks	9,050.00	
Total Investments		$ 24,727.50
Total Combined Wilson Ornithological Society Endowment Funds December 31, 1976		$146,035.45

Ernest E. Hoover, *Treasurer*

Chairman C. E. Braun summarized the report of the Conservation Committee. The full report will appear later in *The Wilson Bulletin.*

Editor J. A. Jackson gave his report.

REPORT OF THE EDITOR—1976

From 1 January through 31 December 1976, I received 183 new manuscripts; this figure does not include book reviews and news items. I received 78 new manuscripts during 1977 through 17 May. Rejection rate for manuscripts received during 1975 and processed to some definite outcome was 34.9%. For manuscripts received thus far in 1977, the rate has been 37.5%. Turn-around time for both notes and papers is presently about 15 months from date of acceptance to date of publication and is improving. Processing time (time from receipt to acceptance of papers published in volume 88—including time needed for revision by the author) averaged 87.8 days for notes and 147.4 days for major papers. Time from receipt to rejection of manuscripts averaged 47.6 days.

Through the generosity of George M. Sutton, it was possible to include a color plate in each issue of volume 88. Volume 88 included 721 pages and was the largest volume published to date; this increased size was made possible by generous contributions from a number of Society members. Editing of volume 88 was facilitated by the assistance of nearly 200 referees, by the hard work of my editorial assistants, and by the patience, hard work, and expertise of my secretary, Lyda Eubanks. I gratefully acknowledge the efforts of all of these individuals.

Jerome A. Jackson, *Editor*

The composition of the following committees had been previously announced: Nominating—O. S. Pettingill, Chairman, H. L. Batts, P. S. Street; Resolutions—R. D. Burns, Chairman. S. A. Gauthreaux. S. F. Spofford; Auditing—J. F. Ponshair, G. M. Wickstrom. President Berger appointed R. C. Banks, J. A. Mosher. R. W. Schreiber, and R. C. Whitmore as a committee to judge student papers for the Alexander Wilson Prize.

A list of new members was posted for inspection by the membership.

REPORT OF THE MEMBERSHIP COMMITTEE—1976–77

A major task for the Membership Office this past year was the preparation of the new membership list. Our experience with the 1974 list had led us to believe that we had a system that could generate the product with a minimum of time and effort. Such was not the case! Despite frequent correspondence with the Treasurer and diligent efforts to keep up-to-date files, we found many errors—and our membership found more following publication. Although we continue to believe that the membership list is a proper function of this office rather than of the Treasurer, it is clear that a better form of filing must be devised.

Since the last annual meeting, we have added 240 new members. Against these we count losses of 11 through death and 209 by suspension, leaving a net gain of 20. The number of suspensions is unusually large and includes professional and foreign members of long standing. We hope their loss will prove temporary.

Fifty-one members used the space provided on the dues notice to suggest one or more possible new members. We do not have complete figures, but at least 17 of these suggestions led to successful recruitments.

As a side interest this year, we kept track of membership migration. Our membership proved to be highly mobile. Two-hundred-fifty-five of them moved; 19 moved twice. Because each address change involves a certain amount of paper work and expense, we would like to encourage those members who know that they may move about frequently but have a reasonably stable base of operations, e.g. an academic department, to use that locus as their address for the Society.

Abbot S. Gaunt, *Chairman*

REPORT OF THE STUDENT MEMBERSHIP COMMITTEE—1976

Letters requesting membership nominations of college students interested in ornithology and inviting application from exceptional students to be considered for Aaron M. Bagg Student Membership Awards were sent to all members affiliated with educational institutions in the Wilson Ornithological Society and American Ornithologists' Union (duplications eliminated). This totaled approximately 850 letters mailed. The Cooper Ornithological Society was not included because the new membership list was issued after the mailing deadline. This activity resulted in 147 student nominations including 61 nominated for membership awards of which 34 were selected as award recipients. The award recipients will be announced in *The Wilson Bulletin.*

Also, letters requesting nominations of promising pre-college students were mailed to the natural history and conservation organizations and institutions in 9 northeastern states. This resulted in 36 pre-college nominations. In keeping with the practice of the past, this procedure will progress from region to region on a yearly basis.

In total, combining college and pre-college students, the committee processed 183 student nominations. Evaluation of the number of these that actually joined was not pursued.

Douglas James, *Chairman*

REPORT OF THE CONSERVATION COMMITTEE—1976

Activities in 1976–77 centered around review of management practices on National Wildlife Refuges in the United States and preparation of a report dealing with the problems involved. The committee's report on refuge management practices will be published in a future issue of *The Wilson Bulletin.*

Considerable demand for copies of previous Conservation Committee reports on eagles, Sandhill Cranes and sagebrush avifauna continued in 1976–77 with over 50 requests being processed. The Conservation Committee contributed to the Environmental Impact Statement analyzing livestock grazing in Wyoming, provided reference sources and suggestions concerning effects on birds of spraying with insecticides for control of spruce budworm in New Brunswick, and contributed to a request for data on the status of Sandhill Cranes in British Columbia. By far, most correspondence received in 1976–77 concerned refuge management practices.

Clait E. Braun, *Chairman*
Keith W. Harmon
Jerome A. Jackson
Carroll D. Littlefield

REPORT OF THE LIBRARY COMMITTEE—1976

During calendar 1976, the Josselyn Van Tyne Memorial Library continued to grow and prosper. Janet Hinshaw (very capably relieved for a time by Elizabeth Strauch) continued to make good progress with the ongoing problems of sorting, filing, shelving, and the correction of remaining discrepancies in lists and records, along with the day-to-day affairs of mailing, receiving, and correspondence, and handling of back issues of *The Wilson Bulletin.*

The New Book Fund was put to good use in some 44 judicious purchases of books and journals, while being considerably bolstered by the sale of duplicates. Sixty-eight loans were made to 50 members: in all, 204 books, journals, reprints, translations, and photocopies. Through 110 exchanges for the *Bulletin*, we received 135 journals, news letters, and reprints. Complimentary subscriptions and gifts raised the total of periodicals received to about 160.

Donations are once more most gratefully acknowledged: 1068 items in all, from 32 members and organizations. These included 682 reprints, 268 journals, 84 books, 1 thesis, 5 translations, 18 reports, abstracts, and pamphlets, from the following: W. H. Behle, A. J. Berger (over half the items, most being reprints), G. R. Brody estate (50 items), California Dept. Fish and Game (by R. M. Jurek), C. T. Collins, J. Cooper, Delaware Museum of Natural History, P. B. Hamel, F. Haverschmidt, E. Hoover, D. W. Johnston, L. Kelson, C. Kendeigh, LGL. Ltd. (by W. J. Richardson). Linnaean Society of N.Y. (by R. W. Dickerman), H. G. Lumsden, H. F. Mayfield, M. E. Morse estate (42 items), R. B. Payne, A. R. Phillips, R. A. Romanes, W. Southern, P. Stettenheim, Mrs. W. C. Stone, J. G. Strauch, Tamarack Press, Welder Wildlife Foundation, L. Wolf, Col. L. R. Wolfe, M. Wood, Yale University Press, R. L. Zusi.

Your support is most gratifying. May it continue. Contribute as you are able; purchase duplicate items offered for sale; most of all, make use of our fine Library collections for your own profit and pleasure.

William A. Lunk, *Chairman*

SECOND BUSINESS MEETING

President A. J. Berger called the Second Business Session to order at 15:00 on 21 May 1977.

The following report of the Auditing Committee was read and accepted.

AUDITOR'S REPORT

We have examined the treasurer's records. bank statements, cancelled checks, account books, and other financial records of the Society covering transactions occurring during the past fiscal year. The financial status of the Society is substantially as set forth in the Treasurer's Report dated 31 December 1976.

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

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

The list of new members previously posted was voted on and the persons listed were formally accepted as members of the Society.

Chairman O. S. Pettingill presented the following slate of officers as proposed by the Nominating Committee; President, Douglas A. James; First Vice-President, George A. Hall; Second Vice-President, Abbot S. Gaunt; Secretary, James Tate, Jr.; Treasurer, Ernest E. Hoover; Elective Member of the Council, term to expire in 1978, Sidney A. Gauthreaux, Jr.; Elective Member of the Council. term to expire in 1980, Clait E. Braun. This report was accepted. and there being no other nominations from the floor, the Secretary was instructed to cast a unanimous ballot for the slate.

Chairman E. D. Burns and member S. A. Gauthreaux of the Resolutions Committee presented the following resolutions which were adopted by the membership.

WHEREAS, the United States Government is currently funding a number of water projects of doubtful economic value, of questionable safety, and destructive to natural environments, and,

WHEREAS, many of these water projects currently under construction would eliminate or severely damage much essential habitat for certain low density or localized bird populations, particularly in the Southwest, and.

WHEREAS, the economic and environmental values of these projects are currently being carefully, reexamined by the President of the United States,

THEREFORE, BE IT RESOLVED that the Wilson Ornithological Society opposes the construction of all water projects that are detrimental to the environment and of dubious value to human welfare, and urges that full and careful consideration be given to environmental concerns before approval of future water projects. and

BE IT FURTHER RESOLVED that the Society commends President Carter for proposing the review and possible cancellation of unsound water projects.

WHEREAS, certain agencies within the Federal Government have become increasingly interested in research on and management of non-game species of wildlife, particularly birds, and

WHEREAS, there is pending legislation that would increase funds for work on non-game wildlife, by Federal and State Agencies,

THEREFORE, BE IT RESOLVED that the Wilson Ornithological Society commends the Fish and Wildlife Service, the Forest Service, and the Bureau of Land Management for their increased interest in non-game species of wildlife and,

BE IT FURTHER RESOLVED that the Society urges passage of the pending legislation that would further increase support for work on non-game species of wildlife by Federal and State Agencies.

WHEREAS, the recent general interest and concern for the environment has frequently resulted in a number of published accounts of the locations of breeding and roosting areas of rare and endangered species in journals, newspapers, environmental impact statements, and other places, and

WHEREAS, this has too often resulted in increasing visitations by humans to certain locations and, thereby, further threatens the future survival of certain rare and endangered species,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society strongly discourages publication of detailed descriptions and/or photographs of breeding and roosting locations of rare and endangered species, and that authors, editors and compilers of such information make every attempt to protect these areas from undue human interference,

AND BE IT FURTHER RESOLVED that each and everyone of us be reminded that we are stewards of our natural world. and whether it be visiting, studying, photographing, or providing directions to the locations of rare and endangered species, that we be ever mindful of the consequences of our actions.

WHEREAS, the Fifty-eighth Annual Meeting of the Wilson Ornithological Society convened on the campus of Mississippi State University has been a smashing success, and

WHEREAS, the scientific program has been of high quality, the field trips were well organized and thoughtfully conducted. and in addition, the culinary talents of the Local Committee on Arrangements plus their gracious southern hospitality was out-performed only by the cooperativeness of the local Red-cockaded Woodpeckers,

BE IT THEREFORE RESOLVED that the Wilson Ornithological Society gratefully acknowledges and thanks the Local Committee on Arrangements and its Chairman, Jerry

Jackson, for their many efforts and long hours of toil which have made this meeting a memorable success.

The meeting adjourned at 15:25.

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

Louis Agassiz Fuertes Awards

Ernest E. Stevens, "The significance of the geographic variation in the rictal flange color of the parasitic Brown-headed Cowbird (*Molothrus ater*)"

Dale Lewis, "Environmental influence on the population structure and social behavior of *Plocepasser mahali*"

Margaret Morse Nice Award

David P. Hendricks, "Breeding range and distribution of the Brown-capped Rosy Finch"

Edwards Prize

Glen A. Fox, "Eggshell quality: its ecological and physiological significance in a DDE-contaminated Common Tern Population"

Edwards Prize, Second Place

Douglas W. Mock, "Pair-formation displays of the Great Blue Heron"

Alexander Wilson Prize

David R. Maurer, "The appendicular myology and phylogenetic affinities of the alcediniform Coraciiformes, the trogons and sub-oscines"

At this time it is appropriate to list the winners of the Alexander Wilson Prizes for 1975 and 1976 which have not been previously published in the Proceedings.

1975 Douglas W. Mock, "Vocabulary shifts during pair-formation in Great Blue Herons"

1976 Stephen R. Borecky, "The appendicular myology and phylogenetic affinities of the birds of paradise (Paradisaeidae) and the bowerbirds (Ptilonorhynchidae)"

PAPERS SESSION

Travis McDaniel, Noxubee National Wildlife Refuge, Mississippi, *An introduction to Noxubee National Wildlife Refuge.*

Richard Bradley, Florida State Museum, Gainesville, Florida, *Hybridization in* Calypte *hummingbirds.*

Richard C. Banks, U.S. Fish and Wildlife Service, Washington, D.C., *Nomenclature of the Black-bellied Whistling (Tree) Duck.*

J. W. Hardy, University of Florida, *Reproductive behavioral ecology of the Southern San Blas Jay* Cyanocorax s. sanblasiana.

Glen E. Woolfenden, University of South Florida, Tampa, *Growth and survival of young Florida Scrub Jays.*

G. Thomas Bancroft, University of South Florida, Tampa, *Molt and breeding in Florida Scrub Jays.*

D. Bruce Barbour, University of South Florida, Tampa, *Territorial vocalizations of the Florida Scrub Jay.*

Lester L. Short, American Museum of Natural History, New York, *Introductory Remarks.*

Walter J. Bock, Columbia University, New York, *Morphology of the feeding apparatus of woodpeckers.*

H. Winkler, Austrian Academy of Sciences, Vienna, *Vocal and other behavior in the Strickland's Woodpecker.*

Ernest E. Hoover, 1044 Webster St. NW, Grand Rapids, Michigan, *Iris color changes in the Hairy Woodpecker.*

Lawrence Kilham, Dartmouth Medical School, Hanover, New Hampshire, *Nesting behavior of Yellow-bellied Sapsucker.*

Luis F. Baptista, Occidental College, Los Angeles, California, *Revision of the Mexican* Piculus *complex.*

Jerome A. Jackson, Mississippi State University, Mississippi State, *Home range, interspecific competition, and management for the Red-cockaded Woodpecker.*

Lester L. Short, American Museum of Natural History, New York, *Burdens of the picid hole-nesting habit.*

Alexander Cruz, University of Colorado, Boulder, Colorado, *Ecology of the Jamaican Woodpecker* (Melanerpes radiolatus).

Randall Breitwisch, University of Miami, Coral Gables, Florida, *The ecology and behavior of the Red-bellied Woodpecker*, Melanerpes carolinus, *in South Florida.*

Joseph B. Williams, Pepperdine University, Malibu, California, *Competition among bark-foraging birds in central Illinois: Experimental evidence.*

W. Wilson Baker, Tall Timbers Research Station, Tallahassee, Florida, *Roosting behavior of Red-cockaded Woodpeckers in north Florida.*

Robert G. Hooper, Michael R. Lennartz, and Richard F. Harlow, Southeastern Forest Experiment Station, Clemson, South Carolina, *Territory and home range sizes of the Red-cockaded Woodpecker.*

Virginia Kirby, University of Arizona, Tucson, *Adaptive modifications in the ribs of woodpeckers (Picidae).*

Richard N. Conner, Virginia Polytechnic Institute and State University, Blacksburg, *Bill and body size differences in woodpeckers: An alternate view.*

Curtis S. Adkisson, Virginia Polytechnic Institute and State University, Blacksburg, *A comparison of the vocal behavior of Red and White-winged crossbills.*

Irvine D. Prather, Virginia Polytechnic Institute and State University, Blacksburg, *Behavioral relationships between Black Vultures and Turkey Vultures.*

John N. Mugaas, Southwestern at Memphis, Memphis, Tennessee, *Microclimatic analysis of Black-billed Magpie habitat using equivalent blackbody temperatures: Implications for thermal budgeting and behavioral thermoregulation.*

Larry J. Miller, Louisiana State University, Baton Rouge, *The effects of altered photoperiod upon the migratory orientation in the White-throated Sparrow*, Zonotrichia albicollis.

Bette J. Schardien, Mississippi State University, Mississippi State, *A comparative study of nestling development in Mockingbirds and Brown Thrashers.*

David R. Maurer, University of Pittsburgh, Pittsburgh, Pennsylvania, *The appendicular myology and phylogenetic affinities of the alcediniform Coraciiformes, the trogons and the sub-oscines.*

Ronald D. Drobney, University of Missouri-Columbia, Puxico, Missouri, *Feeding ecology of Wood Ducks in Missouri.*

Alexander Cruz, University of Colorado, Boulder, Colorado, *Adaptive evolution in the Jamaican Blackbird*, Nesopsar nigerrimus.

Elliot J. Tramer and Thomas R. Kemp, University of Toledo, Toledo, Ohio, *Foraging ecology of migrant warblers and vireos in the highlands of Costa Rica.*

James R. Karr, University of Illinois, Champaign, *Intercontinental variation in the evolution of tropical rainforest avifaunas.*

Noel O. Wamer, Florida State University and Tall Timbers Research Station, Tallahassee, *Avian diversity and habitat in Florida: An analysis of a peninsular diversity gradient.*

Robert C. Whitmore and E. James Harner, West Virginia University, Morgantown, *Analysis of multivariately determined community matrices using cluster analysis and multidimensional scaling.*

Chandler S. Robbins and Danny Bystrak, U.S. Fish and Wildlife Service, Laurel, Maryland, *Recent changes in bird populations revealed by breeding bird survey.*

Joseph M. Meyers, University of Georgia, Athens, *Effect of selected transmissionline rights-of-way treatments on forest bird communities.*

T. Scott Taylor, University of Missouri-Columbia, Puxico, Missouri, *Avian use of moist soil impoundments.*

James G. Dickson and Charles A. Segelquist, Southern Forest Experiment Station, Nacogdoches, Texas, *Breeding bird populations in pine and pine-hardwood forest stands in east Texas.*

ATTENDANCE

ALABAMA: *Birmingham*, Fred Carney, Walter F. Coxe, Joseph A. Imhof, Thomas A. Imhof, Elberta G. Reid, Robert R. Reid, Jr.; *Jacksonville*, Bill Summerour; *Tuscaloosa*, Richard K. Crawford; *University*, David T. Rogers, Jr.

ARIZONA: *Tucson*, Virginia Kirby.

ARKANSAS: *Fayetteville*, Douglas James.

CALIFORNIA: *Los Angeles*, Luis F. Baptista, Ralph W. Schreiber; *Malibu*, Joseph B. Williams.

COLORADO: *Boulder*, Alexander Cruz; *Fort Collins*, Clait E. Braun.

FLORIDA: *Coral Gables*, Randall Breitwisch; *Gainesville*, Erik J. Bitterbaum, Richard Bradley, John W. Hardy, Barbara Kimball, Sarah Sloane, Thomas A. Webber; *Lake Placid*, Fred E. Lohrer; *Orlando*, Richard V. Demmer; *Tallahassee*, Wilson W. Baker, Noel E. Wamer; *Tampa*, G. Thomas Bancroft, Douglas B. Barbour, Jim Rodgers, Glen B. Woolfenden; *Winter Haven*, Peggy MacQueen.

GEORGIA: *Athens*, Joseph M. Meyers, *Atlanta*, Franklin McCamey; *Augusta*, Emil K. Urban.

HAWAII: *Honolulu*, Andrew J. Berger.

ILLINOIS: *Champaign*, James R. Karr; *Momence*, Mr. and Mrs. William T. Lory; *Rockford*, John T. Bergstrom.

INDIANA: *Richmond*, Timothy Brush, Alan Simon.

KANSAS: *Hays*, Charles A. Ely, Pat Lattas, Ren Lohoefener.

KENTUCKY: Ethel Woolfenden, Lester B. Woolfenden.

LOUISIANA: *Baton Rouge*, J. W. Eley, Dick Ferrell, Robert B. Hamilton, Robert S. Kennedy, Dwight J. LeBlanc, Dr. *and* Mrs. George H. Lowery, Jr., Christina Lusk, Larry Miller, Mr. & Mrs. Bob Newman, Robert E. Noble, John P. O'Neill, John S. Sylvest, Dan Tallman, Erika Tallman; *Eunice*, Harland D. Guillory; *Franklin*, Jack H. Deshotels; *Monroe*, David Kee; *Shreveport*, Horace H. Jeter.

MAINE: *Wayne*, Olin S. Pettingill, Jr.

MARYLAND: *Boyds*, Mary Schaefer; *Cumberland*, Bruce Lawson; *Frostburg*, James Mosher, Susan Mosher; *Laurel*, Chandler S. Robbins, Eleanor C. Robbins; *Lonaconing*, William J. Devlin.

MASSACHUSETTS: *Manomet*, Kathleen S. Anderson.

MICHIGAN: *Ann Arbor*, Janet Hinshaw, Stephen Hinshaw; *Grand Rapids*, Ernest Hoover; *Jackson*, Robert A. Whiting; *Pleasant Lake*, Hubert P. Zernickow, Norene E. Zernickow.

MINNESOTA: *Duluth*, P. B. Hofslund.

MISSISSIPPI: *Cleveland*, Mr. and Mrs. J. S. White; *Clinton*, DeAnne Smith, Marita Smith; *Columbus*, Thelma Barnes, William S. Parker; *Greenville*, Ed Alexander, Ginger Alexander; *Gulfport*, Jay Toups, Judith Toups; *Jackson*, Stephen W. Peterson, Annie C. Turcotte, W. H. Turcotte; *Kosciusko*, Rebecca W. Davis, Walter V. Davis, Ray E. Weeks; *Mississippi State*, Martha B. Hays, Jerome A. Jackson, Nancy Jackson, Wilma Mitchell, Patricia Ramey, Bette Schardien, Wayne Weber, Wendy Weber, Pat Shindala, Glenn Liming, Mike Christensen, Ardis Christensen, David Werschkul, Sue Werschkul, Oskar Zernickow, Keith Parsons, Joe Ferguson, Frances Fortenberry, Martha Ward, Tom Morrow, Glenn Clemmer, Sherry Clemmer, Ann McWhorter, Bob Esher, Kathy Esher, Courtney Hackney, Lois Kilgore, Lawrence Croft, Elsie Croft, Frances Windham, Arlie Wilson, Ethel Wilson; *Monticello*, Carl Bauer, Florence Bauer; *Shaw*, Nona Herbert; *Starkville*, E. W. Permenter, Bonnie Turner, Bill Hughes, Nellie Hughes, Florence Dunn, Burton S. Webster, Marjorie Webster, Caroline Bennett, Mrs. Gifford Bull, Julia Broyles, Travis McDaniel, Willena Ratliff; *Vicksburg*, Louis P. Cashman, Jr.

MISSOURI: *Cape Girardeau*, William R. Eddleman, Marie Heye, Paul L. Heye; *Columbia*, Jeffrey Brawn, Larry Vangilder; *Puxico*, Ronald Drobney, Judy Sherpelz, T. Scott Taylor.

NEW HAMPSHIRE: *Lyme*, Jane Kilham, Lawrence Kilham.

NEW JERSEY: *East Millstone*, John Jubon, Mary Jubon; *Mt. Holly*, Katherine Price.

NEW YORK: *Mamaronick*, Robert Arbib; *New York*, Susan R. Drennan, Lester L. Short.

NORTH CAROLINA: *Chapel Hill*, Helmut C. Mueller.

OHIO: *Columbus*, Abbot S. Gaunt, Sandra Gaunt; *Gambier*, Robert D. Burns; *Lakewood*, Nancy R. Klamm, William A. Klamm; *Waterville*, Harold Mayfield, Virginia Mayfield.

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This issue of *The Wilson Bulletin* was published on 30 September 1977.

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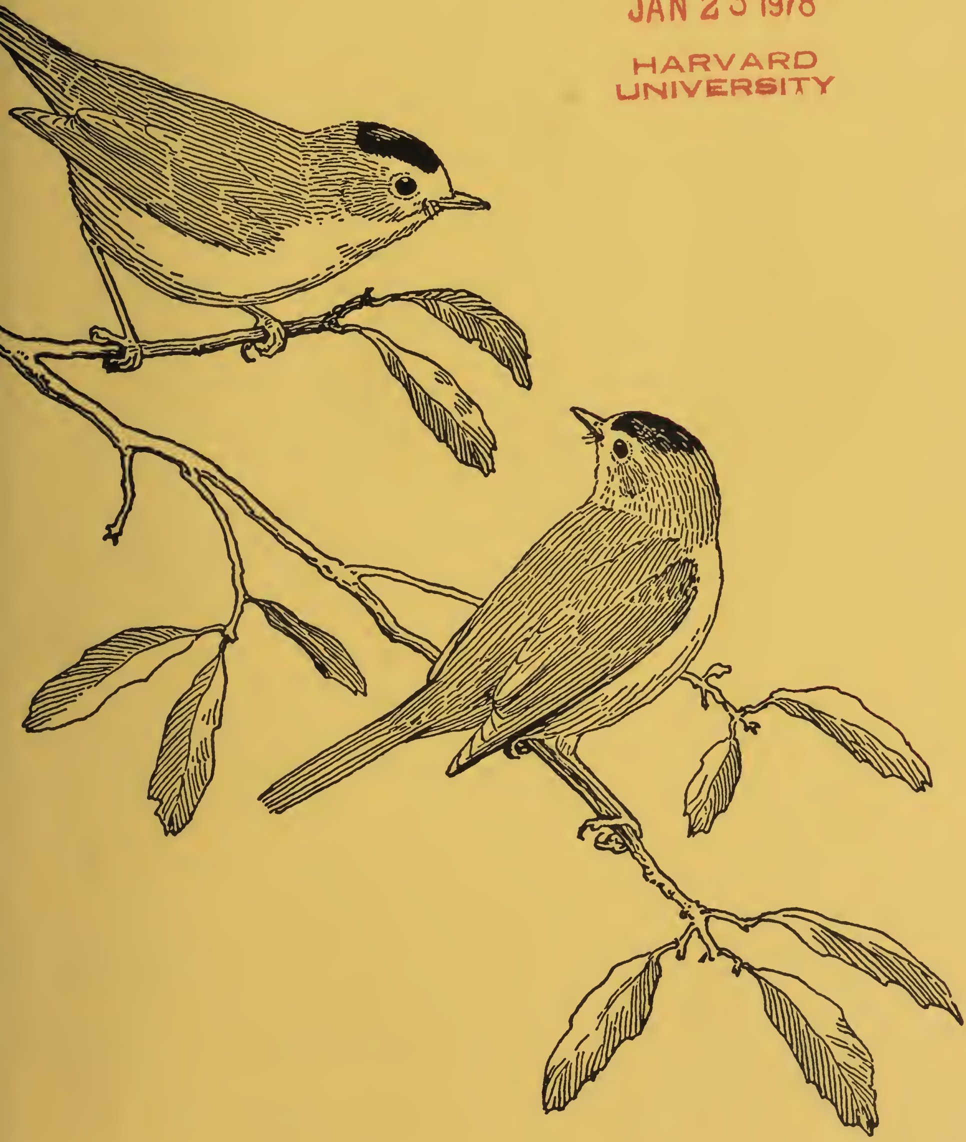

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Lesser Prairie Chicken *(Tympanuchus pallidicinctus)*,
photographed 26 April 1975 in Roosevelt County, New Mexico
by Keith Giezentanner.

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THE LESSER PRAIRIE CHICKEN'S INFLATABLE NECK SACS

GEORGE MIKSCH SUTTON

In the fall of 1932, in the vicinity of Arnett, Ellis County, western Oklahoma, I first saw and handled the Lesser Prairie Chicken (*Tympanuchus pallidicinctus*). The species was common at that time in the "shinnery oak" country thereabouts, especially on the Davison Ranch a few kilometers southeast of the city (Sutton, Ann. Carnegie Mus., 24:11–12, 1934). A detailed watercolor sketch that I made of the head and foot of an adult male bird shot that year on 6 October shows the neck sac to be light cinnamon-buff, a color that contrasted sharply with the bright, slightly ochraceous orange-yellow of the comb above the eye.

Noting that Florence M. Bailey (Birds of New Mexico, New Mexico Dept. of Fish and Game, Santa Fe, 1928:207) described the neck sacs as "yellow in the breeding season," I fell to believing that the sacs brightened to yellow in spring and summer and reverted to cinnamon-buff (or some such comparatively dull shade) in fall and winter. When, in 1936, I spent about 6 weeks at Arnett (early May to mid-June), I observed Lesser Prairie Chickens almost daily, for in certain parts of the "shinnery country" thereabouts they were common. Repeatedly I made a point of driving to one or more "gobbling grounds," where I observed the performing males at remarkably close range from my car. Convinced that the neck sacs were not at all yellow, I made a point of collecting 2 males early in the day on 25 May and drawing them in detail before the colors of the fleshy parts had had a chance to fade. In each of these drawings the neck sac is light, somewhat reddish brown, again in sharp contrast to the bright orange-yellow of the comb above the eye. I made a third detailed sketch of an adult male bird later that summer but did not record the date.

To my surprise I found that authors continued to describe the color of the neck sacs inadequately. Friedmann (*in* Ridgway, U.S. Natl. Mus. Bull. 50, Pt. IX, 1941:220), who may have been following Bailey (*supra*), stated that the "gular sacs" were "yellow in the breeding season." Ligon, in "New Mexico Birds and Where to Find Them" (Univ. New Mexico Press, Albuquerque, 1961:89), called the sacs "orange-colored." Peterson, in his "Field Guide to the Birds of Texas" (Houghton Mifflin Co., Boston, 1960:74), came much closer to accuracy when he described the sacs as "dull red rather than orange," though I continue to feel that *red* is the wrong word. Robbins, Bruun, and Zim, in their "A Guide to Field Identification Birds of North America" (Golden Press, N.Y., 1966:86), described the sacs as "reddish," but the illustration on the opposite page is hopelessly misleading since the color shown there approaches pale lilac or violet. I suspect that Arthur Singer, whose excellent drawings illustrate this work, was advised to make clear that the color of the neck sac was very different from that in the Greater Prairie Chicken (*T. cupido*), and he may have heard or assumed that the proper color was close to that of the neck sac of the Sharp-tailed Grouse (*Pedioecetes phasianellus*).

In any event, now that I have been observing the Lesser Prairie Chicken off and on for 45 years, I am convinced that its neck sacs are never yellow or purple at any season; nor are they orange, the color-word that best describes the sacs of the Greater Prairie Chicken. I would call them *tan*, were not that word so widely used commercially for a variety of shades. The accompanying colorplate, which is based on photographs taken by my friend and former student, Keith Giezentanner, now Development Supervisor for the New Mexico Department of Game and Fish at Santa Fe, shows the color of the inflated air sacs admirably. The photographs were taken on the morning of 26 April 1975 at a well established booming ground 13 km east of Milnesand, Roosevelt County, southeastern New Mexico.

STOVALL MUSEUM OF SCIENCE AND HISTORY, UNIV. OF OKLAHOMA, NORMAN 73019. ACCEPTED 28 JUNE 1977.

NESTING HABITAT OF CANADA GEESE IN SOUTHEASTERN MICHIGAN

Richard M. Kaminski and Harold H. Prince

Habitat selection by birds is guided by instinctive and learned responses to stimuli from the physical environment, conspecifics, and other species within the environment (Hilden 1965). Whitmore (1975) reviewed studies that described species preferences and differences in habitat use based on certain features of the landscape and vegetation; however, most earlier studies were largely qualitative and failed to reveal which parameters were most important among several that affect habitat selection. Recent studies of passerines, employing multivariate analyses (Anderson and Shugart 1974, Cody 1968, James 1971, Sturman 1968, Whitmore 1975), have revealed differences between species-specific habitat types within particular communities. Crawford and Bolen (1976) used multiple regression analysis to correlate factors of vegetation and land-use with spring and fall population levels of Lesser Prairie Chickens (*Tympanuchus pallidicinctus*).

Little attempt has been made to quantitatively show differences within species between used and unused portions of the available habitat. Although Klebenow (1969) attempted unsuccessfully to differentiate (using discriminant function analysis) between habitat that was used and not used by Sage Grouse (*Centrocercus urophasianus*) for nesting and brood rearing, similar studies with other bird species, including waterfowl, are unavailable. This study investigates factors which separated used from unused nesting wetlands and nesting sites of Canada Geese (*Branta canadensis*) in southeastern Michigan in order to better understand nesting habitat selection by this species.

STUDY AREA, METHODS, AND ANALYSIS

The study area (9065 km^2) lies within the Huron River Valley of southeastern Lower Michigan which Hanson (1965) includes as part of the breeding range of giant Canada Geese (*B. c. maxima*). A morainic topography, resulting from the Wisconsin glacier, contains numerous kettle hole lakes and marshes. Kaminski (1975) presented a more detailed description of the study area's wetlands and vegetation.

Morphological measurements (culmen length and width, tarsus length, middle-toe length, and body weight) of molting geese (1 year and older) were made to determine subspecies identity of the Huron River Valley flock. Mean values for these measurements were similar to those documented by Hanson (1965) for giant Canada Geese (Kaminski 1975).

Between 15 April and 25 April 1974 for 8 days (08:00–16:00), we conducted a helicopter survey of the study area in order to estimate numbers of nesting Canada Geese. Quarter sections (65 ha each) were chosen as the sampling unit; the boundaries of which were easily identified from the air. Topographic maps of the study area were used to enumerate all quarter sections containing any wetland (pond, lake, river, marsh, and waste treatment lagoon) that could potentially provide nesting habitat for Canada Geese. A total of 6275 quarter sections contained at least 1 of these wetlands. A 5% sample (n = 310) was randomly selected (using a table of random numbers) and positioned on county maps by their appropriate legal description and then systematically searched for nesting geese. Ground searches of other wetlands revealed additional nests for study.

Wetlands that contained nesting geese were characterized by a shoreline development index (Reid 1961) which is based on shoreline configuration (a value of 1 denotes a perfectly round shoreline), percent residential and/or recreational shoreline occupancy, area of permanent open water, and area of emergent vegetation within the nesting quarter section. These data were obtained from aerial photos and from an inventory of Michigan's lakes prepared by Humphrys and Green (1962).

Williams and Nelson (1943), Miller and Collins (1953), and others suggested that Canada Goose nesting sites should be elevated to provide good visibility, afford protection, be near water, and provide a firm foundation. On the basis of these criteria, appropriate parameters were measured to evaluate the magnitude of difference between muskrat (*Ondatra zibethica*) lodges and islands selected as nesting sites, and similar unused sites. Nest site type dictated the parameters that were measured. Parameters measured on and around muskrat lodge nest sites were: (1) width of lodge top, (2) percent occurrence of cover, (3) lodge height above standing water, (4) distance from the lodge to open water, (5) average height of emergent aquatic vegetation, and (6) distance from the lodge to the nearest shoreline. The same measurements were recorded for the nearest muskrat lodge devoid of nesting Canada Geese. We assumed that the geese had a choice between the sites independent of social interactions between conspecific pairs. This assumption did not appear to be violated because of the low average density (0.08/65 ha) of nests in 1974. Data for percent occurrence of cover and height of vegetation were collected at 0.1 m intervals along transect lines (0.05 m × 10 m) extending from the base of each lodge in the 4 cardinal directions. Only vegetation (dead annuals plus live and dead perennials) that was presumed to be available to Canada Geese selecting nest sites and that intersected and/or overshadowed the transect line was counted. Parameters measured on islands used by nesting geese and islands not used were: (1) % slope at the highest point on the island, (2) density of vegetation, (3) distance from the island to the nearest shoreline, (4) island length, and (5) average height (up to 3 m) of all understory vegetation. Percent slope was measured with a Haga altimeter. Distance measurements were made with a range finder. A density board, described by DeVos and Mosby (1969), was used to estimate the density of vegetation. Four readings, corresponding to the cardinal directions, were taken within 3 m of the shore-water interface on all islands plus at the nest site on islands used by nesting Canada Geese. Replicated measurements (taken within 1 circular plot (0.03 ha) circumscribing the nest and within 1 randomly placed plot positioned adjacent to the shore on islands not used by nesting Canada Geese) were used to estimate vegetation height.

Data from nest sites were analyzed using a multivariate discriminant function analysis modified from Cooley and Lohnes (1971). The goal of discriminant function analysis is to maximize among-group variation thereby assigning individuals to a group on the basis of data peculiar to the group (Lachenbruch 1975). Green (1971) presented an excellent discussion on the statistical theory and ecological application of discriminant function analysis. In our analysis, one discriminant function was calculated because $g - 1$ (g = number of groups contrasted) was less than p, the number of elements of the vector variable (Cooley and Lohnes 1971) and it accounted for 100% of the among-group variance. Variation about reported mean values is denoted by 95% confidence limits. All percent data were transformed using arcsine values (Sokal and Rohlf 1969) prior to analysis.

RESULTS AND DISCUSSION

Twenty-six active nests were located during the survey of quarter sections. We estimated there were 526 ± 231 active nests on the study area at the time of the survey. The design of the aerial survey did not exclude any wetland size class; hence quarter sections containing wetlands were surveyed in relation to their abundance. As a result, the survey concentrated on searching small wetlands (Fig. 1). Wetlands with nesting Canada Geese had shoreline development values averaging 1.4 ± 0.2 ($n = 30$). This type of shoreline configuration (nearly circular) is common to most wetlands in southeastern Michigan. Shoreline development values for nesting wetlands differed significantly ($P < 0.01$) when stratified by nest site type (muskrat lodge, island, or floating mat of vegetation) suggesting that the presence of suitable nest sites was more important to Canada Geese selecting nesting wetlands than was the shape of the shoreline. The area of emergent aquatic vegetation (predominately *Typha latifolia* and *Scirpus* spp.) within nesting quarter sections ranged from 0 to 40 ha and did not appear to directly influence habitat choice by nesting geese. Nesting wetlands having little or no emergent vegetation contained one or more islands which were virtually inaccessible to mammalian predators, alleviating the necessity for nest concealment by emergent cover. Nesting wetlands covered by more emergent vegetation usually contained muskrat lodges which were the most frequently used nest site type in the study area (Kaminski 1975). Cooper (1973) stressed the important commensal relationship between muskrats and the use of emergent cover by nesting Canada Geese at Marshy Point, Manitoba. Twelve (40%) nesting wetlands had 10% or more of their shorelines occupied residentially and/or recreationally, suggesting that Canada Geese will tolerate some human habitation when selecting nesting wetlands in southeastern Michigan. The most important factor affecting use of wetlands by nesting geese appeared to be the area of permanent open water. Ninety-two percent of all nests located during the aerial survey were situated on wetlands having 2 or more hectares of open water (Fig. 1). The greatest proportion (42%) of nesting pairs used wetlands for nesting that contained more than 25 ha of open water. This is similar to Hanson's (1965) observations that although Canada Geese demonstrate a wide adaptability for various nesting habitats, these must be available in large blocks and contain bodies of water of moderate to large size.

The difference between selected nest sites and ones not used by Canada Geese was evaluated using a discriminant function analysis. A multivariate analysis of variance yielded a highly significant ($P < 0.001$) discrimination

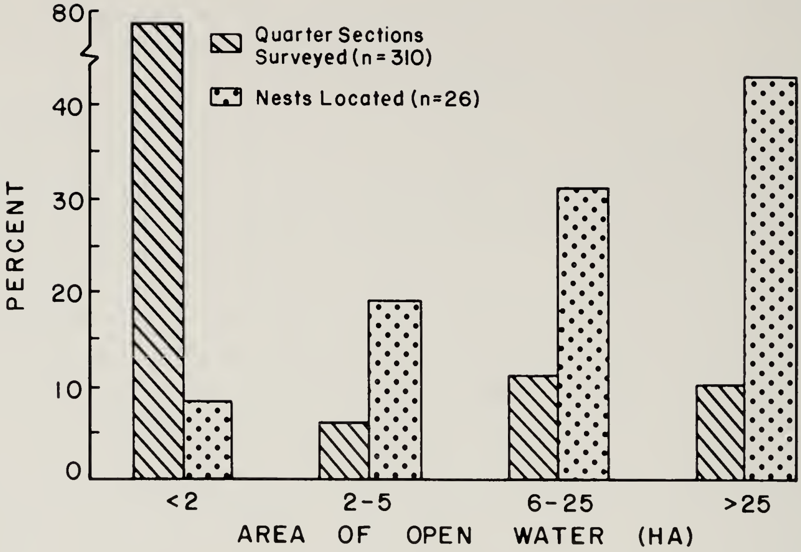

FIG. 1. Percentages of Canada Goose nests in relation to the area of open water associated with nesting wetlands in 1974.

between both categories of muskrat lodge and island sites. Width of muskrat lodge top had the highest scaled eigenvector coefficient (Table 1) indicating it was most influential in separating lodges used by nesting geese compared to ones not used. All lodges used by nesting Canada Geese exceeded 1 m in top width while only 2 met this criterion in the unused category. Rienecker (1971) observed that Canada Geese more readily accepted artificial nesting structures having large (0.9 m–1.2 m) platforms. Although percent occurrence of cover, surrounding muskrat lodges, was not significantly different ($P > 0.05$) among lodges with goose nests, percent occurrence of cover was significantly different ($P < 0.05$) among lodges not used by nesting geese. This suggests that Canada Geese selected muskrat lodges for nest sites that were surrounded by a similar amount of cover. Although percent occurrence of cover ranked second in discriminatory ability (Table 1), it contributed similarly to the discriminant function along with lodge height above standing water and distance from the lodge to open water. These 4 parameters are probably important cues used by Canada Geese in selecting muskrat lodges as nest sites and should be measured when field evaluating lodges as potential nest sites for this species. Discriminant scores for all muskrat lodges were computed using a grand mean of 50 (S.D. = 10). Histograms of these scores depict the relative difference between muskrat lodges used and not used by

TABLE 1

MEAN (95% C.I.) AND SCALED EIGENVECTOR COEFFICIENTS FOR PARAMETERS MEASURED ON AND AROUND MUSKRAT LODGES USED AND NOT USED BY CANADA GEESE AS NESTING SITES IN 1974

Parameter	Used lodges (n = 23)	Unused (n = 23)	Scaled eigenvector coefficient[1]
Width of lodge top (m)	1.6 (1.4– 1.8)	0.88 (0.80–0.96)	–2.535
% occurrence of cover	35.1 (32.4–39.4)	30.2 (25.0–35.5)	–0.786
Lodge height above water (m)	0.34 (0.30–0.38)	0.27 (0.21–0.33)	–0.718
Distance from lodge to open water (m)	17.5 (9.6–25.4)	25.7 (5.7–45.7)	+0.556
Average height of vegetation (m)	0.82 (0.75–0.89)	0.80 (0.70–0.90)	–0.294
Distance from lodge to nearest shoreline (m)	58.7 (39.3–78.1)	58.9 (39.0–78.8)	–0.289

Root of $W^{-1}A = 1.046$
Wilk's lambda = 0.489; df = 6,39; F = 6.79; ($P < 0.001$)

[1] The largest absolute value is most important.

nesting Canada Geese (Fig. 2). Although lodges within the 46–55 range could not be clearly assigned to 1 of the 2 groups with much confidence, each distribution is comparatively distinct with used lodges occupying the lower ranges of discriminant scores. The minimal overlap between the distributions suggests that those lodges selected by nesting geese were superior nesting sites.

Five parameters were measured on islands used and not used by nesting

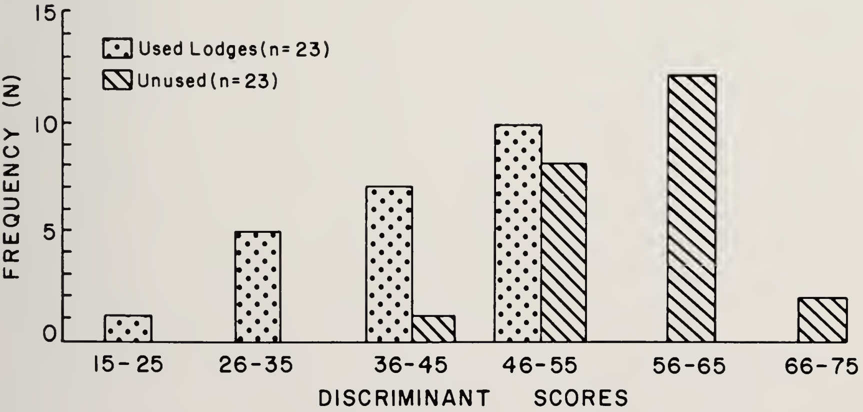

FIG. 2. Histograms of discriminant scores from parameters measured on and around muskrat lodges used and not used by Canada Geese as nesting sites in 1974.

TABLE 2

MEAN (95% C.I.) AND SCALED EIGENVECTOR COEFFICIENTS FOR PARAMETERS MEASURED ON ISLANDS USED AND NOT USED BY CANADA GEESE AS NESTING SITES IN 1974

Parameter	Used islands (n = 37)	Unused (n = 37)	Scaled eigenvector coefficient[1]
Island relief (% slope)	15.7 (13.4–18.1)	8.4 (6.2–10.9)	+24.352
Island vegetation density (%)	45.7 (36.1–55.3)	62.9 (53.3–72.0)	–16.607
Vegetation density at nest site (%)[2]	17.1 (11.8–23.1)	———	——
Distance from island to nearest shoreline (m)	73.2 (61.1–85.3)	61.4 (45.1–77.7)	+11.788
Island length (m)	65.9 (39.0–92.8)	85.1 (50.8–119.4)	–11.501
Average height of vegetation (m)	1.7 (1.5– 1.9)	2.0 (1.6– 2.4)	–10.836

Root of $W^{-1}A = 0.439$
Wilk's lambda = 0.695; df = 5,68; F = 5.96; ($P < 0.001$)

[1] The largest absolute value is most important.
[2] Not included in discriminant function analysis.

Canada Geese (Table 2). Percent slope of island relief had the highest relative power for discrimination being 7% greater on the average for islands used by nesting geese compared to unused islands. Hanson and Eberhardt (1971) observed that Canada Geese did not use islands that had low profiles for nesting in the Columbia River of Washington. Islands having more relief not only facilitate nest vigilance but render nests less vulnerable to fluctuating water levels. The density of vegetation was significantly lower ($P < 0.01$) on all islands used by nesting geese compared to islands not used. Furthermore, the density of vegetation at the immediate nest site was significantly lower ($P < 0.01$) than the average vegetation density on the remaining area of the nesting island. Sherwood (1968) reported that most Canada Geese nesting at the Seney National Wildlife Refuge in northern Michigan selected islands that were free of dense, high brush which enhanced visibility and accumulated less snow. Barry (1962), Cooper (1973), and Ryder (1967) observed that snow cover on the breeding grounds delayed nest initiation in Atlantic Brant (*Branta bernicla*), Canada Geese, and Ross' Geese (*Chen rossii*) respectively; because suitable nest sites were not available. Although all variables contributed cumulatively to the discriminant function, distance from the island to the nearest shoreline, island length, and the height of vegetation differed slightly in their order of magnitude (Table 2) suggesting a reduced contribution to the separation. Percent slope of island relief and the density of island vegetation were the most important parameters, among those measured, affecting island use by nesting Canada Geese. Increasing island relief and thinning dense stands of vegetation should improve the

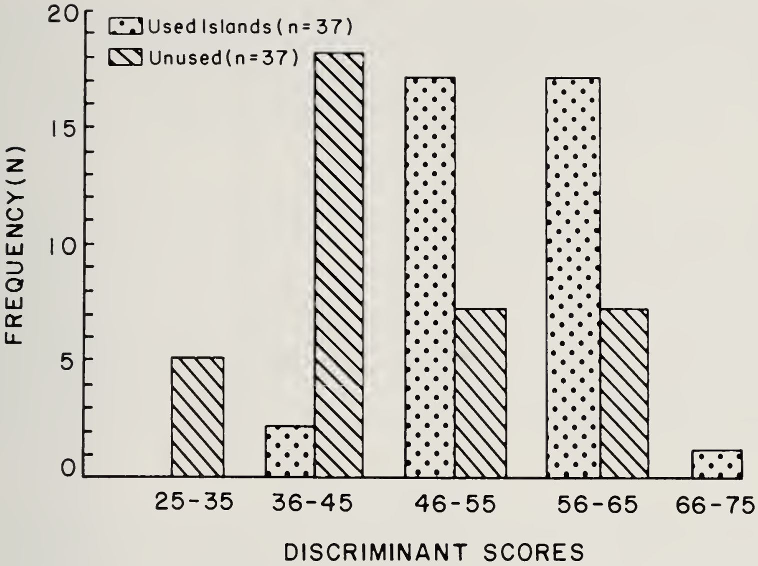

Fig. 3. Histograms of discriminant scores from parameters measured on islands used and not used by Canada Geese as nesting sites in 1974.

suitability of islands for nesting in southeastern Michigan. Discriminant scores, forming frequency distributions (Fig. 3), from both island groups show the greatest overlap in the 46–65 range making it difficult to accurately predict if an island having a score within this range will be used by nesting Canada Geese in southeastern Michigan. The less distinct separation between these frequency distributions may reflect the preference that Canada Geese show for insular nest sites throughout their breeding range.

Although an absolute separation was not obtained in either case, the analyses show that certain physiognomic characteristics delineated selected nest sites from sites not chosen. Those parameters, most significant in the discrimination, were probably important proximate cues (Hilden 1965) affecting site selection by Canada Geese. Klopfer and Hailman (1965) stated that if a bird species recognizes and distinguishes between suitable and unsuitable habitats, its reproductive efficiency could be enhanced. This should theoretically contribute to the fitness of reproducing individuals.

Information obtained in this study is valuable for predicting potential nest site availability, for providing guidelines in the manipulation of habitat, and for the effective construction and positioning of artificial nesting structures for Canada Geese. Experimental manipulation of nest site quality along with the density of breeding pairs as they affect site selection would be a logical advancement of this study. Similar research with other species whose nest sites lend themselves to discriminant function analysis would augment our understanding of factors affecting species-specific nest site selection and provide an opportunity to evaluate their strategies of habitat selection.

SUMMARY

Nesting habitat of Canada Geese in southeastern Michigan is described. Most nesting pairs (92%) preferred wetlands that contained 2 or more hectares of open water. Data were collected from both muskrat lodges and islands used and not used by Canada Geese as nesting sites. These data were analyzed using a discriminant function analysis to determine which factors best separated used from unused nesting sites. Top width of muskrat lodges and percent slope of island relief along with the density of island vegetation were most important in the discrimination. This approach provides a quantitative technique for evaluating the potential availability of nesting habitat along with revealing species-specific nest site preferences.

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RESIDUES OF ENVIRONMENTAL POLLUTANTS AND SHELL THINNING IN MERGANSER EGGS

Donald H. White and Eugene Cromartie

There is little information regarding the types and concentrations of environmental pollutants in mergansers. However, the reports that are available indicate that residues of certain toxic chemicals are high in eggs and tissues of Common (*Mergus merganser*), Red-breasted (*Mergus serrator*), and Hooded mergansers (*Lophodytes cucullatus*) from southern Canada, Michigan, and Wisconsin (Fimreite et al. 1971, Vermeer and Armstrong 1972, Faber and Hickey 1973, Vermeer et al. 1973, Fimreite 1974). Also, significant eggshell thinning has been detected in Common and Red-breasted mergansers from Wisconsin and Michigan (Faber and Hickey 1973).

Mergansers feed mostly on fishes and invertebrates (Munro and Clemens 1939, Timken and Anderson 1969, Bellrose 1976) and are more susceptible to chemical contamination than species feeding at lower trophic levels. This study was conducted (1) to determine the levels of environmental pollutants in merganser eggs, mainly those of Hooded Mergansers, as factors contributing to possible population declines and (2) to compare eggshell thickness with eggs of earlier collections. Hooded Merganser eggs were more readily available than those of Common or Red-breasted mergansers since Hooded Mergansers commonly use nest boxes on many federal and state refuges throughout their breeding range.

METHODS AND MATERIALS

Federal and state biologists assisted us in collecting clutches of merganser eggs in 1973 and 1975 (see Table 1 for collecting sites). Cooperators were sent insulated containers for shipment of eggs with instructions to collect only fresh whole clutches. So that hens would have time to renest, eggs were collected early in the nesting season and kept refrigerated until shipment to the Patuxent Wildlife Research Center, Laurel, Maryland. Most of the clutches were complete and only a few contained addled eggs or eggs with developing embryos.

Each egg was opened at its equator after determining its weight, length, breadth, and volume (by water displacement). One egg from each clutch was randomly selected for chemical analysis since eggs within a particular clutch usually contain similar residue levels (Klaas and Swineford 1976). The egg contents were stored frozen in chemically cleaned jars until analysis.

Eggshells were dried at room temperature for at least 30 days, then weighed and measured with the shell membranes left intact. Three thickness measurements were taken randomly around the equator using a Starrett Model 1010 M micrometer and a mean shell thickness was calculated for each egg. Similar procedures were used in measuring museum egg collections except that measurements were taken at the blow-hole of each egg. Mean clutch thickness values were calculated by averaging clutch means from each locality within a collecting region and not by averaging individual egg measurements (Klaas et al. 1974); this method gives an indication of average shell thickness by population as opposed to individual hens. In comparing clutch means, all shell measurements used were from fresh or early incubated eggs, therefore stage of incubation did not significantly bias the data. Historical collections of merganser eggs were measured at the American Museum of Natural History, Museum of Vertebrate Zoology at Berkeley, Philadelphia Academy of Sciences, and the Western Foundation of Vertebrate Zoology.

Contents of each egg were homogenized with a Virtis homogenizer. A 10 g aliquot was mixed with anhydrous sodium sulfate in a blender and extracted for 7 h with hexane in a Soxhlet apparatus. An aliquot of the extract was cleaned up by gel permeation chromatography or on a florisil column. Pesticides and polychlorinated biphenyls (PCB's) were separated into 3 fractions on a Silicar column and analyzed by gas chromatography. The limit of quantification was 0.1 ppm for pesticides and 0.5 ppm for PCB's on a wet-weight basis. The analytical procedures have been described in detail by Cromartie et al. (1975). Residues in 10% of the samples were confirmed with a gas chromatograph/mass spectrometer. All residues were corrected for moisture loss as suggested by Stickel et al. (1973). Lipid content in eggs of Hooded, Red-breasted, and Common mergansers averaged 16%, 16%, and 14%, respectively. Residue arithmetic means and geometric means were very similar, therefore only arithmetic means were reported.

Egg contents were analyzed for total mercury at the Environmental Trace Substances Research Center, Columbia, Missouri. An aliquot of the homogenized sample was digested under reflux conditions with concentrated nitric acid. Stannous chloride was added to reduce the ionic mercury to elemental mercury which was measured photometrically on an atomic absorption spectrophotometer. The limit of quantification was 0.02 ppm on a wet-weight basis.

RESULTS

Hooded Merganser eggs.—Residues of DDE, DDT, DDD, dieldrin, PCB's, and mercury in Hooded Merganser eggs are presented in Table 1. Residues varied greatly within and among localities. Of 96 eggs, DDE was found in 92, dieldrin in 22, and PCB's in 82. Eggs collected in 1973 from Necedah National Wildlife Refuge (NWR), Wisconsin had the highest mean of DDE; the highest mean of DDE for 1975 occurred in eggs from Iroquois NWR, N.Y. Sample sizes from these localities were small (2) however, and may not reflect overall contamination levels in the breeding populations. All collections from the Northeast (Maine, New Hampshire, New York, Vermont) had mean levels of DDE greater than 0.1 ppm. The highest mean level of dieldrin was in eggs from the Upper Mississippi NWR, Iowa. Usually dieldrin was detected in only 1 or 2 eggs from a locality, therefore mean levels are not indicative of all the breeding birds. The highest mean PCB level was found in eggs from New Hampshire; all eggs from this locality contained PCB's as did eggs from the other localities in the Northeast. Of the 90 Hooded Merganser eggs analyzed for mercury, 89 contained detectable residues. The highest mean level of mercury occurred in eggs from Big Lake NWR, Arkansas.

TABLE 1

RESIDUES AND SHELL THICKNESS OF HOODED MERGANSER EGGS[1]

State—year (Location)	N[2]	Mean clutch thickness (mm)	Residues, ppm wet weight					
			DDE	DDT	DDD	Dieldrin	PCB's[3]	Mercury
Arkansas—1975 (Big Lake NWR)	6	0.630 ± 0.006 (56)[4]	0.53 ± 0.10 (6)[5]	0.14 ± 0.05 (2)	0.14 ± 0.06 (2)	0.19 ± 0.05 (3)	0.83 ± 0.26 (2)	1.49 ± 0.36 (6)
Arkansas—1975 (White River NWR)	5	0.621 ± 0.002 (55)	1.12 ± 0.33 (5)	0.27 ± 0.12 (3)	0.12 (1)	0.17 (1)	0.80 ± 0.09 (3)	0.48 ± 0.06 (5)
Idaho—1975 (Kootenai NWR)	2	0.589 ± 0.007 (13)	0.63 ± 0.24 (2)	ND[6]	ND	ND	0.55 ± 0.12 (2)	0.16 ± 0.06 (2)
Iowa—1975 (Upper Mississippi NWR)	3	0.564 ± 0.006 (28)	0.84 ± 0.24 (3)	0.08 (1)	ND	1.34 ± 1.13 (2)	1.15 ± 0.12 (3)	0.75 ± 0.31 (3)
Maine—1975 (Central)	10	0.583 ± 0.008 (106)	1.45 ± 0.36 (10)	0.21 ± 0.09 (4)	0.18 ± 0.06 (2)	0.21 ± 0.07 (3)	3.50 ± 1.28 (10)	0.97 ± 0.16 (10)
Michigan—1973 (Seney NWR)	6	0.565 ± 0.010 (33)	1.26 ± 0.54 (6)	1.39 (1)	ND	0.23 (1)	1.59 ± 0.37 (6)	no analysis
Michigan—1975 (Seney NWR)	9	0.574 ± 0.002 (66)	0.86 ± 0.22 (9)	0.19 ± 0.10 (2)	ND	0.37 ± 0.15 (4)	3.03 ± 1.08 (9)	0.53 ± 0.09 (9)
Minnesota—1975 (Rice Lake NWR)	1	0.650 (2)	0.07 (1)	ND	ND	ND	1.59 (1)	0.25 (1)
Missouri—1973 (Mingo NWR)	10	0.612 ± 0.021 (36)	4.90 ± 2.68 (10)	13.90 (1)	7.38 ± 2.86 (2)	0.37 (1)	1.86 ± 0.96 (4)	0.74 ± 0.13 (10)

TABLE 1 (*continued*)

State—year (Location)	N[2]	Mean clutch thickness (mm)	Residues, ppm wet weight					
			DDE	DDT	DDD	Dieldrin	PCB's[3]	Mercury
Missouri—1975 (Mingo NWR)	7	0.617 ± 0.002 (43)	0.35 ± 0.07 (7)	ND	ND	0.11 (1)	0.85 ± 0.06 (7)	0.92 ± 0.12 (7)
New Hampshire—1975 (Central)	10	0.546 ± 0.004 (105)	1.84 ± 0.50 (10)	0.51 (1)	0.19 (1)	0.15 ± 0.07 (2)	4.91 ± 1.56 (10)	1.11 ± 0.23 (9)
New York—1975 (Iroquois NWR)	2	0.589 ± 0.006 (14)	3.24 ± 1.94 (2)	0.56 (1)	0.10 (1)	0.20 (1)	2.37 ± 0.82 (2)	1.44 ± 0.30 (2)
North Dakota—1975 (Clark Salyer NWR)	8	0.593 ± 0.006 (41)	0.67 ± 0.40 (5)	ND	ND	0.14 (1)	1.10 ± 0.24 (8)	0.73 ± 0.09 (8)
Oregon—1975 (W. L. Finley NWR)	2	0.604 ±0.012 (12)	0.34 ± 0.13 (2)	ND	ND	ND	0.93 ± 0.46 (2)	0.53 ± 0.09 (2)
Tennessee—1975 (Hatchie NWR)	10	0.620 ± 0.004 (71)	1.06 ± 0.18 (10)	0.18 ± 0.03 (9)	ND	0.19 (1)	0.90 ± 0.09 (9)	0.94 ± 0.18 (10)
Vermont—1975 (Northwestern)	3	0.598 ± 0.008 (24)	1.54 ± 0.21 (2)	ND	ND	ND	2.37 ± 0.40 (3)	0.53 ± 0.17 (3)
Wisconsin—1973 (Necedah NWR)	2	0.584 ± 0.011 (6)	13.20 ± 9.77 (2)	2.42 (1)	1.77 (1)	0.27 (1)	0.44 (1)	0.56 ± 0.21 (2)

[1] Values are means ± standard errors.
[2] N = total no. of clutches collected; one egg per clutch was analyzed.
[3] PCB's are quantified on the basis of Aroclor 1254.
[4] Total no. of eggs in clutches that were measured.
[5] No. of eggs having detectable residues.
[6] ND = not detected.

TABLE 2

RESIDUE COMPARISONS OF POOLED SAMPLES OF HOODED MERGANSER EGGS FROM 3 REGIONS, 1975

		Residues, ppm wet weight[1]		
Regional pool	N[2]	DDE	PCB's	Mercury
Northeast	25	1.77 ± 0.29[a]	3.84 ± 0.08[a]	1.01 ± 0.12[a]
(Maine, New Hampshire, New York, Vermont)		(24)[3]	(25)	(24)
Midwest	20	0.79 ± 0.16[b]	1.97 ± 0.52[a]	0.64 ± 0.07[b]
(Iowa, Michigan, North Dakota)		(18)	(20)	(20)
South-central	28	0.78 ± 0.10[b]	0.86 ± 0.04[b]	0.62 ± 0.12[b]
(Arkansas, Missouri, Tennessee)		(28)	(21)	(28)

[1] Values are means ± standard errors.
[2] N = total no. of samples in the pool.
[3] No. of samples in the pool having detectable residues.
[ab] Significant differences exist between means having different superscripts ($P < 0.01$, *t*-test).

In addition to the chemicals listed in Table 1, certain other toxicants were detected in some Hooded Merganser eggs at much lower levels. Heptachlor epoxide was found in 6 eggs, 1 each from Iowa and New Hampshire and 2 each from Maine and Michigan, but residues were low, ranging from 0.14 to 0.48 ppm. One egg each from Vermont and Michigan contained mirex at 0.08 and 0.18 ppm, and 4 of 10 eggs from Maine contained mirex, ranging from 0.15 to 0.66 ppm. Chlordane isomers were detected in 6 eggs, 2 from New Hampshire and 4 from Maine, ranging from 0.09 to 1.8 ppm. Toxaphene occurred in only 2 eggs, at 0.17 ppm in an egg from Seney NWR, Michigan and 0.10 ppm in an egg from Big Lake NWR, Arkansas. Hexachlorobenzene (HCB) was detected at 0.19 ppm in an egg from Seney NWR, Michigan.

We pooled residue data from localities within major regions if they were not statistically different ($P > 0.05$) from one another in order to compare DDE, PCB's, and mercury in Hooded Merganser eggs on a regional basis. Residues in eggs from Oregon and Idaho were not pooled because of very small sample sizes and mean differences. Means of pooled residues are shown in Table 2. DDE residues were significantly higher ($P < 0.01$, *t*-test) in eggs from the Northeast than in those from the Midwest or South-central states. However, these are relative comparisons based on specific localities and are not representative of whole areas. PCB's were significantly higher ($P < 0.01$) in the Northeast and Midwest samples than in those from the South-central region, probably resulting from heavy industrial use of PCB's in those regions. Mercury was significantly higher ($P < 0.01$) in eggs from the Northeast

Table 3

Residues and Shell Thickness of Red-breasted and Common Merganser Eggs, 1975[1]

	Red-breasted Merganser (Door County, Wisconsin)	Common Merganser (Door County, Wisconsin)	Common Merganser (Seney NWR, Michigan)
N[2]	18	2	1
Mean shell thickness (mm)	0.302 ± 0.004 (178)[3]	0.314 ± 0.006 (16)	0.346 (6)
DDE	15.73 ± 1.39 (18)[4]	24.44 ± 4.72 (2)	9.85
DDT	0.62 ± 0.10 (18)	0.70 (1)	ND
DDD	0.40 ± 0.04 (17)	0.34 ± 0.08 (2)	ND
Dieldrin	1.00 ± 0.11 (18)	0.64 ± 0.10 (2)	1.39
Heptachlor epoxide	0.31 ± 0.04 (18)	0.27 ± 0.09 (2)	0.17
Mirex	0.42 ± 0.15 (8)	ND[5]	ND
Chlordane isomers	0.57 ± 0.06 (18)	0.82 ± 0.32 (2)	0.34
HCB	0.11 ± 0.01 (16)	ND	ND
Toxaphene	0.26 ± 0.04 (3)	ND	ND
PCB's	44.67 ± 6.06 (18)	79.43 ± 9.02 (2)	24.19
Endrin	0.33 (1)	ND	ND
Mercury	0.56 ± 0.06 (18)	0.56 ± 0.26 (2)	0.52

[1] Values are means ± standard errors.
[2] N = total no. of clutches collected; one egg per clutch was analyzed.
[3] Total no. of eggs in clutches that were measured.
[4] No. of eggs having detectable residues.
[5] ND = not detected.

than in those from the Midwest or South-central regions, although eggs from a locality in Arkansas had the highest overall mean of mercury (Table 1).

Red-breasted and Common merganser eggs.—In general, residues of DDE, dieldrin, and PCB's were higher in Red-breasted and Common merganser eggs, and other chemicals occurred more frequently, than in eggs of Hooded Mergansers (Table 3). A high of 29 ppm DDE was detected in a Common

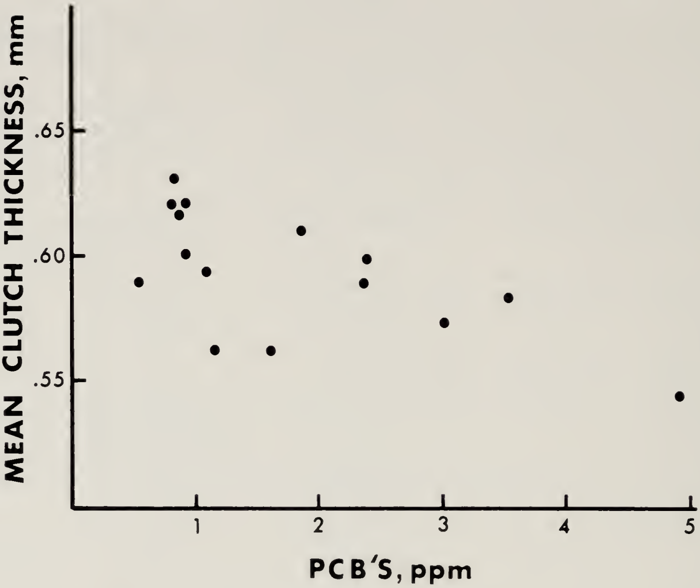

FIG. 1. Relationship of PCB's in Hooded Merganser eggs and mean clutch thickness on a population basis. (Spearman's rank correlation, r = –0.63, P < 0.01)

Merganser egg from Door County, Wisconsin; a Red-breasted Merganser egg from the same locality had a high of 113 ppm PCB's. Residue levels in eggs of the 2 species were similar except that mirex, HCB, and endrin were not detected in Common Merganser eggs. Mercury residues were similar to those found in Black-crowned Night Heron (*Nycticorax nycticorax*) eggs from Lake St. Clair (Stendell et al. 1976).

Eggshell measurements and shell thickness changes.—Clutch thickness means by locality are shown in Table 1 for Hooded Mergansers, and in Table 3 for Red-breasted and Common mergansers. There was wide geographic variation in mean thicknesses among Hooded Merganser clutches (Table 1); clutch means ranged from a low of 0.546 mm in New Hampshire to a high of 0.630 mm in Arkansas (Minnesota mean excluded because of only 2 eggs in the sample). According to Klaas et al. (1974), variation in eggshell thickness among clutches (at least in some species) depends on many factors, including: differences related to clutch size and stage of incubation, genetic and physiological differences among females, differences in diet of the various females, and differences in environmental conditions between years.

There was a negative correlation (r = –0.28, Spearman's rank correlation,

TABLE 4

COMPARISONS OF EGGSHELL MEASUREMENTS FROM EARLY MUSEUM COLLECTIONS AND 1973, 1975 COLLECTIONS

		Mean clutch thickness ± standard error, mm		
Species	Collection region	1880–1927	1973–1975	Percent change
Hooded Merganser	Iowa, Michigan, Minnesota, North Dakota, Wisconsin	0.628 ± 0.025 (6/55)[1]	0.576 ± 0.005 (28/174)	–8.3
Red-breasted Merganser	Michigan, Wisconsin, south Manitoba	0.367 ± 0.001 (8/105)	0.302 ± 0.004 (18/178)	–17.7[a]
Common Merganser	Michigan, Wisconsin, south Manitoba	0.426 ± 0.011 (3/33)	0.326 ± 0.015 (3/22)	–23.5[a]

[1] Total number of clutches/total number of eggs within clutches.
[a] Percent change highly significant ($P < 0.001$, analysis of variance).

Snedecor and Cochran 1967) between DDE residues and mean clutch thickness for each locality, but the relationship was not significant ($P > 0.05$). However, PCB's and mean clutch thickness also were negatively correlated ($r = -0.63$) on a locality basis and the relationship was highly significant ($P < 0.01$) (Fig. 1).

Regression analysis showed that a significant relationship ($r = 0.61$, $P < 0.05$) existed between DDE and PCB's, but when DDE and PCB's were combined and compared with mean clutch thickness by population, there was no significant ($P > 0.05$) relationship. It appears that PCB's were contributing more to the negative relationship between residues and mean clutch thickness than DDE. The results must be viewed with caution however, because of the wide variety of factors that may contribute to geographic variation in shell thickness of Hooded Merganser eggs. Controlled experimental studies are needed to clarify these findings. In order to test for possible eggshell thinning, we compared eggshell measurements from our collections with those of early museum collections (Table 4). Data from each major region were combined if the clutch means did not differ significantly ($P > 0.05$) from one another. For Hooded Mergansers, we were able to obtain comparable data only from certain midwestern states, therefore comparisons with collections from the Northeast and South-central regions could not be made. Clutches of Hooded Merganser eggs were 8.3% thinner than earlier collections from the same general area (Table 4) however, the difference was not significant ($P > 0.05$).

Highly significant shell thinning ($P < 0.001$) was detected in the Red-breasted Merganser eggs. The clutch means were 17.7% thinner than those from early museum collections from the same general area (Table 4). Faber and Hickey (1973) found that Red-breasted Merganser eggs from Wisconsin in 1969 were 17.0% thinner than pre-1947 collections from the same area. Although their comparisons were made on an individual egg basis rather than on clutch means, the results were strikingly similar to ours.

Highly significant shell thinning ($P < 0.001$) also was detected in Common Merganser eggs. The 1975 collections were 23.5% thinner than early museum collections from the same region (Table 4); only 3 clutches were available from each time period for comparisons, but the results proved significant. Faber and Hickey (1973) also reported shell thinning in Common Merganser eggs from Michigan and Wisconsin; collections made in 1970 were 15.8% thinner than pre-1947 collections.

DISCUSSION

In general, residues of organochlorines in Hooded Merganser eggs were considered to be low. Geographical differences were detected however; residues of DDE, PCB's, and mercury were higher in the Northeast than in the other regions. It is doubtful that these relatively low levels of organochlorines could be responsible for overall population declines of Hooded Mergansers, but some hens with moderate to high levels of toxicants could experience poor reproductive success. Also, mercury averaged about 1 ppm in eggs from the Northeast and about 0.63 ppm at other localities; these levels may be sufficient to cause aberrant behavior in ducklings (Heinz 1975).

Most of the Red-breasted and Common merganser eggs contained potentially dangerous levels of DDE and possibly PCB's. In addition, mercury and a wide array of other toxic organochlorines were present in the eggs. Both species exhibited significant eggshell thinning. Mergansers are top predators, and consequently are highly subjected to contamination from their food sources. This is especially true for Red-breasted and Common mergansers, which feed almost exclusively on fishes of various types. Hooded Mergansers take fewer fish and more invertebrates than the other species; this may explain the lower residues in their eggs.

The effects cumulative concentrations of toxic chemicals in eggs might have on reproduction and survival of wild birds are unknown. A toxicant load of the magnitude found in Red-breasted and Common mergansers might cause reproductive failure or otherwise threaten the survival of merganser populations. Experimental studies with DDE have shown that reproductive impairment may be induced in Mallards (*Anas platyrhynchos*) and Black Ducks (*A. rubripes*) at residues similar to those found in some of the Red-breasted and Common mergansers (Longcore et al. 1971, Haegele and Hudson 1974). Also, in experimental studies with methylmercury, Heinz (1975) found that aberrant behavior of Mallard ducklings resulted when eggs accumulated 1 ppm or less of mercury. In our study, residues of mercury in Red-breasted and Common merganser eggs averaged 0.56 ppm and ranged up to 1.2 ppm. Field studies are needed to document reproductive success of mergansers in the Door County, Wisconsin area. Further, these data demonstrate the persistence and prevalence of DDT, DDE, and dieldrin in the environment, even though the use of technical DDT was suspended in December 1972 and the use of dieldrin was suspended in October 1974.

SUMMARY

Clutches of merganser eggs were collected in 1973 and 1975 to determine whether levels of organochlorines and mercury might be responsible for possible population declines and to compare eggshell measurements with those of early museum collections. One egg per clutch was selected randomly for chemical analysis. Overall, residues of DDE, PCB's, and mercury were low in Hooded Merganser eggs; locality means for DDE ranged from 0.07 to 13.2 ppm, PCB means ranged from 0.44 to 4.91 ppm, and mercury means ranged from 0.16 to 1.49 ppm on a wet-weight basis. Residues of DDE and PCB's appeared to be high in Red-breasted and Common merganser eggs. DDE averaged 15.7 ppm in Red-breasted Merganser eggs and PCB's averaged 44.6 ppm; Common Merganser eggs contained an overall mean of 19.5 ppm DDE and 61.0 ppm PCB's. Hooded Merganser eggs from the Midwest had thinned 8.3%, but the change was not significant. Highly significant shell thinning was detected in Red-breasted and Common merganser eggs; Red-breasted Merganser eggs were 17.7% thinner and those of Common Mergansers were 23.5% thinner than museum collections.

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BREEDING BIRD SURVEY COUNTS AS RELATED TO HABITAT AND DATE

Wayne C. Weber and John B. Theberge

The Breeding Bird Survey (hereafter BBS) is a standardized technique designed to measure year-to-year changes in numbers of breeding birds (Robbins and Van Velzen 1967, 1969; Van Velzen and Robbins 1971). It has been carried out over much of North America each year since 1966. The factors causing variability in BBS counts, such as time of day, weather, and time of year, have been briefly discussed by Robbins and Van Velzen (1967). However, no detailed analysis has yet been made of the effects of these factors, nor of the relationship between BBS counts and habitat. In this paper, we describe some of these relationships for an area of southern Ontario, Canada.

We used the BBS to study breeding bird populations during 1971 in Waterloo County, Ontario (now the Regional Municipality of Waterloo). Our chief aim in conducting the study was to obtain an index to bird populations against which future changes could be measured and compared with changes in land use or other factors. Our purposes in this paper are: (1) to show that the BBS method, when considered together with land use data, is useful in relating bird populations to habitat; (2) to describe some of the bird-habitat relationships evident in our study area; and (3) to outline some of the problems in using the BBS as a technique for estimating bird populations, and particularly to evaluate the effect of time of year on numbers of birds recorded.

The field work for the study was done by Weber, but both of us participated in its planning and in the analysis of results.

STUDY AREA AND METHODS

Study area.—Waterloo County, located in southern Ontario about 100 km west-southwest of Toronto (Fig. 1), has an area of 1336 km^2 and a human population of 254,037 (1971 Canadian census). There are 2 large metropolitan areas in the county—Kitchener-Waterloo, with a population of 151,000, and Galt-Preston-Hespeler (recently amalgamated under the name of Cambridge), with a population of 62,000—as well as several smaller towns and villages. Urban growth in the county is extremely rapid (an increase of 46.4% from 1961 to 1971).

The area consists of old glacial outwash plains and rolling moraines, with an elevation of about 240 to 430 m; it lies entirely within the drainage basin of the Grand River. Soils range from coarse glacial sands and gravels to fine alluvial deposits along the rivers. The area is in a transition zone between the Great Lakes-St. Lawrence and Deciduous Forest Regions (Rowe 1972); the climax forests were dominated by sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), with some conifers such as eastern

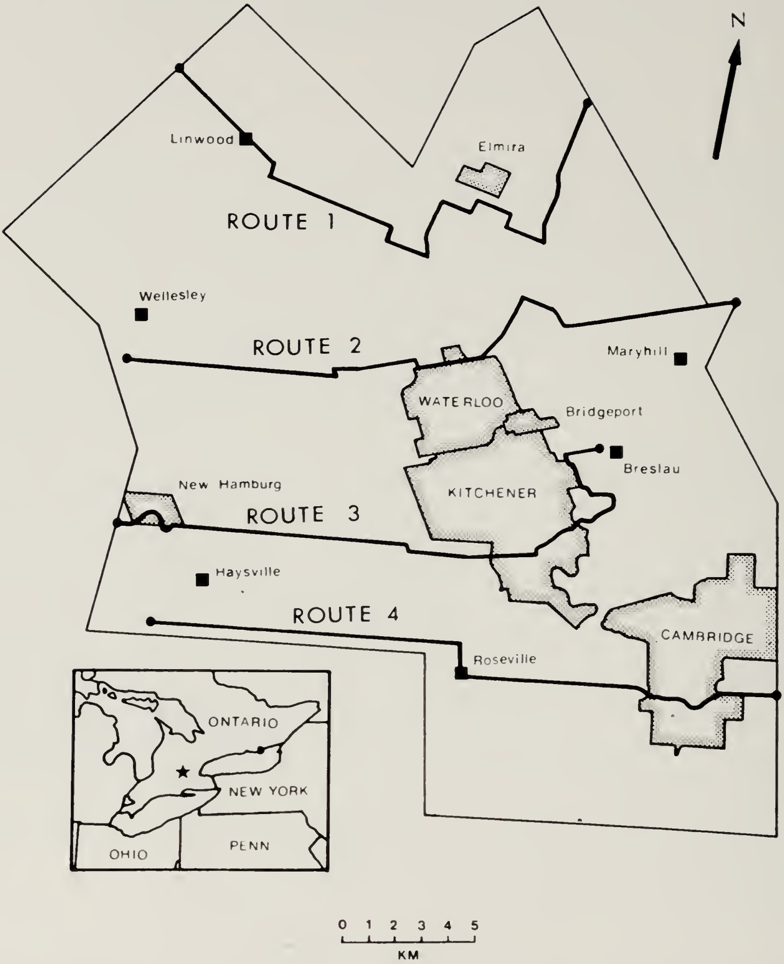

FIG. 1. Waterloo County, Ontario, showing locations of Breeding Bird Survey routes. Inset map shows general location of county in southern Ontario.

hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobus*). Only about 10% of the land is now forested (less than in most surrounding areas), and most of this consists of small second-growth woodlots, often in pockets of swampy or poorly-drained soil unsuitable for farming. The county supports a fairly intensive agriculture dominated by dairying and the raising of crops such as corn, oats, barley, wheat, and hay.

We divided habitats in the county into 4 major categories: fields, forest, urban habitats, and "miscellaneous" habitats (including wetlands and gravel pits). These were subdivided into 20 habitat types. This classification was intended not to correspond with plant communities, but to reflect major physical and vegetational features of the habitat which are probably important to birds. Our habitat types were:

Fields.—These included: (1) pasture, hayfields, and alfalfa fields; (2) brushy pasture (not grazed or mowed for several years, usually with numerous shrubs or small trees); (3) cornfields; (4) other grains—mainly oats and barley (often mixed), some wheat; (5) other crops, mainly potatoes; and (6) bare earth.

Forest.—These included: (1) upland deciduous forest—mainly sugar maple-American beech forest, in various successional stages, but mostly young; (2) upland coniferous forest—plantations of red pine (*Pinus resinosa*) and eastern white pine; (3) upland mixed forest—like upland deciduous, but with eastern hemlock or eastern white pine also present (deciduous trees always dominant); (4) riparian deciduous forest—mainly willows (*Salix* spp.), also balsam poplar (*Populus balsamifera*), American elm (*Ulmus americana*), etc., along streams; (5) swamp coniferous forest—mainly northern white-cedar (*Thuja occidentalis*) and/or tamarack (*Larix laricina*); (6) swamp mixed forest —red maple (*Acer rubrum*), American elm, black ash (*Fraxinus nigra*), tamarack, northern white-cedar, eastern hemlock, etc.; (7) orchards (included under forests for lack of a better alternative).

Urban.—These included: (1) commercial—business districts, i.e., stores and offices; (2) industrial—factories, warehouses, railway yards, etc. (newer areas often interspersed with fields); (3) residential—both "estate" areas with widely-spaced houses and many trees, and more typical areas with more houses and fewer trees; (4) cemeteries and parks —usually with many trees.

Miscellaneous.—These included: (1) lakes and ponds; (2) marshes—both cattail (*Typha latifolia*) and shrub-willow (*Salix* spp.) marshes; (3) gravel pits.

Methods.—The BBS technique was developed by Chandler S. Robbins of the U.S. Fish and Wildlife Service from similar methods used for many years by wildlife biologists in surveys for American Woodcock, Ruffed Grouse, and other gamebirds. A survey route consists of 50 stops spaced at 0.8 km (½ mile) intervals; thus each route is 39.4 km (24.5 miles) long. The survey is begun ½ h before local sunrise. The observer spends 3 min at each stop and records all birds heard at any distance, and all seen within 0.4 km (¼ mile). In the continent-wide BBS, supervised by the U.S. Fish and Wildlife Service and Canadian Wildlife Service, each route is covered only once a year; in southern Canada, this may be done between 1 June and 7 July. For more details, see Robbins and Van Velzen (1967).

We set up 4 BBS routes in Waterloo County, spanning the county from east to west at intervals of about 12 km (Fig. 1). Each route was surveyed 8 times between 18 May and 16 July 1971. Direction of coverage was reversed in alternate weeks. Although surveys were continued for 8 weeks, only 5 weeks' results (28 May to 4 July) were used in the analysis (see Discussion for reasons).

In conjunction with the bird surveys, we estimated the area covered by each of the 20 habitat types along the survey routes. At each stop, the percentage covered by each type within a 0.4 km radius was estimated in the field to the nearest 10%. These data were then summed to give totals for each route.

We also noted the presence and importance at each stop of hedgerows (rows of trees or shrubs), scattered trees, farm buildings, and streams. Based on the habitat composition and the importance of hedgerows and scattered trees at each stop, we assigned it an "edge rating," as a rough index to the amount of forest-field edge present. These ratings ranged from 0, for little or no edge, to 2, for much edge. For example, a stop where forest and fields each covered 30% or more of the area was assigned a 2, whether or not hedgerows and scattered trees were present. If a stop was 100% fields but deciduous

TABLE 1

HABITAT COMPOSITION ALONG BREEDING BIRD SURVEY ROUTES

	Survey route[2]				
Habitat	1	2	3	4	Overall
FIELDS	85.2%	70.8%	70.0%	67.8%	73.5%
Pasture	30.0	26.4	29.2	22.4	27.0
Brushy pasture	–	0.2	1.8	5.2	1.8
Corn	22.6	22.6	24.6	26.8	24.2
Other grains	28.4	17.4	13.4	13.0	18.1
Other crops	–	4.0	0.2	–	1.1
Bare earth	4.2	0.2	0.8	0.4	1.4
FOREST	10.4	21.2	8.2	16.8	14.2
Upland deciduous	4.8	12.0	4.4	9.0	7.6
Upland coniferous	0.2	–	0.2	0.4	0.2
Upland mixed	–	3.4	0.4	0.4	1.1
Riparian deciduous	2.0	4.4	0.8	0.8	2.0
Swamp coniferous	1.4	1.0	0.4	0.6	0.9
Swamp mixed	2.0	0.2	1.2	5.6	2.3
Orchard	–	0.2	0.8	–	0.3
URBAN	3.4	6.6	20.4	14.6	11.3
Commercial	–	–	2.2	2.0	1.1
Industrial	0.2	0.8	5.8	1.6	2.1
Residential	3.2	5.8	12.2	10.2	7.9
Cemeteries and parks	–	–	0.2	0.8	0.3
MISCELLANEOUS	1.0	1.4	1.4	0.8	1.1
Lakes and ponds	–	0.4	–	–	0.1
Marsh	0.4	1.0	–	0.8	0.6
Gravel pits	0.6	–	1.4	–	0.5

[1] For brief descriptions of habitat types, see "Study Area."
[2] Route 1—Linwood to North Woolwich (see Fig. 1); Route 2—Ariss to New Prussia; Route 3—New Hamburg to Breslau; Route 4—Galt to Haysville.

hedgerows were important, the edge rating was 2; if both hedgerows and scattered trees were present but unimportant (covering a small area, or far from the observation point), the edge rating was 1; and if both were absent, the rating was 0. Edge ratings for individual stops were then summed to give a total for each route, ranging from a minimum possible 0 to a maximum possible 100.

RESULTS

Habitat composition along survey routes.—The percentage of area occupied by each habitat on the 4 survey routes is shown in Table 1. Fields occupied an average of 74% of the area, ranging from 68% on Route 4 to 85% on Route 1. Forest occupied only 14% of the area overall, but was more impor-

TABLE 2

TOTAL NUMBERS OF BIRDS (SELECTED SPECIES) RECORDED ALONG BREEDING BIRD SURVEY ROUTES, 28 MAY TO 4 JULY 1971

	Survey route			
Species	1	2	3	4
FIELD SPECIES				
Killdeer	102	85	74	88
Horned Lark	124	65	49	34
Bobolink	123	106	53	77
Savannah Sparrow	470	346	336	275
URBAN SPECIES				
Chimney Swift	28	41	55	60
Purple Martin	–	3	20	–
FOREST SPECIES				
Black-capped Chickadee	2	20	4	13
Veery	1	12	2	6
Red-eyed Vireo	25	35	23	30
FOREST-EDGE SPECIES				
Gray Catbird	5	18	2	34
Brown Thrasher	3	14	6	13
Yellow Warbler	17	49	9	34
Song Sparrow	163	213	138	190

tant on Routes 2 and 4 (21% and 17%, respectively) than on Routes 1 and 3 (10% and 8%). Urban habitats took up 20% on Route 3 and 15% on Route 4, and averaged 11% over the 4 routes.

Comparison of bird numbers among routes.—Weber recorded 101 bird species (not including 6 migrants and non-breeders) on the 4 routes between 28 May and 4 July. For many species, differences in total numbers among routes showed a close relationship with habitat composition; some of these species are included in Table 2. (See appendix for scientific names of all birds mentioned in this paper.) Several birds characteristic of fields (Killdeer, Horned Lark, Bobolink, Savannah Sparrow) were most abundant on Route 1, which was 85% fields; another species, the Upland Sandpiper, occurred only on Route 1. Two highly urban species, the Purple Martin and Chimney Swift, reached peak numbers respectively on Routes 3 and 4, the routes with most urban habitat. Numbers of Field Sparrows paralleled the extent of brushy pasture on the survey routes.

Many forest and forest-edge species were numerous on Routes 2 and 4, which had many wooded areas, but scarcer on Routes 1 and 3. Fig. 2 shows

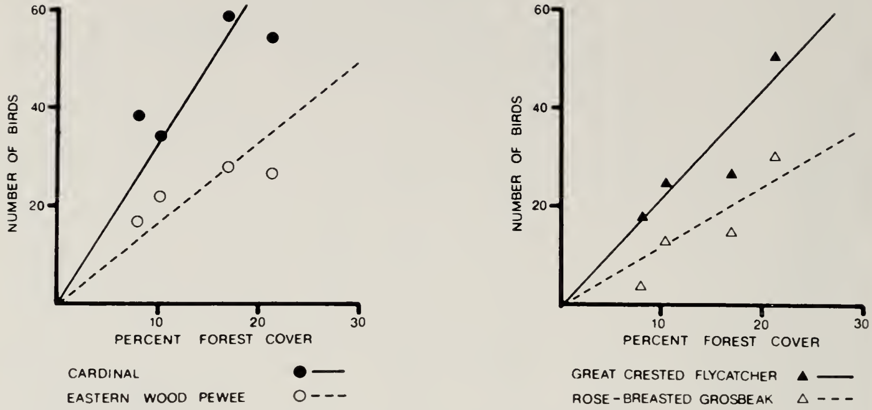

Fig. 2. Comparison of numbers of birds recorded, 28 May to 4 July, with percent forest cover on survey routes.

graphs for 4 forest species—Great Crested Flycatcher, Eastern Wood Pewee, Cardinal, and Rose-breasted Grosbeak—whose numbers showed particularly close relationships with percent forest cover. Fig. 3 does the same for 4 forest-edge species—Mourning Dove, Common Flicker, House Wren, and Indigo Bunting—using the "edge rating" for each route instead of percent forest cover. Edge ratings were 50, 67, 54, and 66 for Routes 1, 2, 3, and 4 respectively. These ratings refer only to forest-field edge; other types of edge (urban-field, urban-forest) were far less extensive.

As the amount of edge on each route was roughly proportional to the amount of forest, bird species whose numbers closely reflected edge ratings would also closely reflect percent forest cover. To determine whether a bird was best considered a forest or forest-edge species, we relied both on published information and on our own observations during the study. Of our "forest" birds, the Great Crested Flycatcher and Cardinal also occur to some extent in non-forested habitats; but Dow (1970) in Ontario and Emlen (1972) in Texas found that Cardinal densities increased with vegetation density. Hespenheide (1971) considered the Eastern Wood Pewee a forest-edge species, but in comparison with, for instance, the Eastern Kingbird, a more typical edge species, we would still consider the Wood Pewee a forest bird. Bird species display a complete spectrum from those preferring dense forest to those inhabiting treeless fields, and the distinction between "forest" and "forest-edge" species must sometimes be arbitrary.

The lines in Figs. 2 and 3 were fitted by eye. Those for forest birds (Fig. 2) were drawn through the origin, on the assumption that numbers

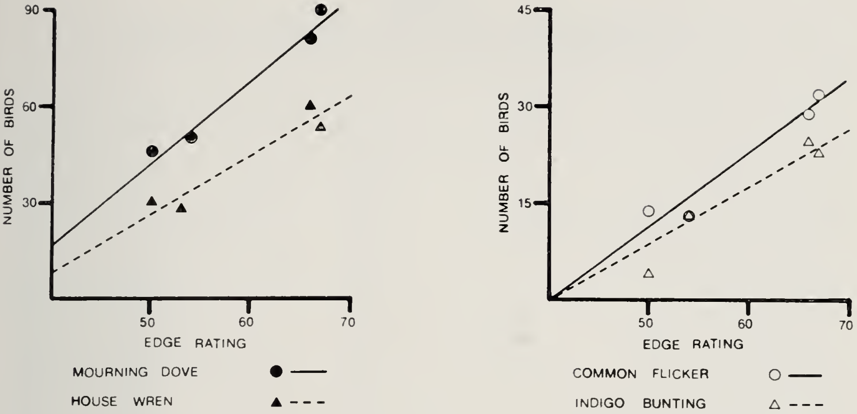

Fig. 3. Comparison of numbers of birds recorded, 28 May to 4 July, with edge ratings on survey routes.

of forest birds should decline to 0 only when forest cover approaches 0. However, edge rating is a much less precise measure than percent forest cover, and is relative rather than absolute. Notice that the lines for Common Flicker and Indigo Bunting (Fig. 3) decline to 0 birds with an edge rating of about 40.

Comparison of bird numbers in different habitats.—The data in Table 3, comparing the abundance of the commoner bird species in each major habitat category, were obtained by a stop-by-stop tabulation of the number of birds at selected stops over the 28 May to 4 July period. A total of 47 stops in fields, 11 in forest, and 19 in urban areas were used; thus only 77 of the total of 200 stops were included in this analysis. For fields, we included only those stops which were 100% fields; but for forest and urban habitats, because of their small extent, we included all stops which were 60% or more forest or urban, respectively.

The 40 species recorded in largest numbers accounted for 97.1% of the total birds recorded at the selected stops. Of these 40, 6 species, comprising 43.0% of total individuals, were considered characteristic of urban areas and farm buildings; 18 (30.4% of individuals) were forest-edge species; 7 (21.8% of individuals) were field species; 7 (3.2% of individuals) were forest species; and 2 (1.6% of individuals) were water-associated species.

Because of the nature of the habitats, the majority of stops selected for analysis contained some "edge." The field stops, although none included any forest or urban habitat, nearly all contained some hedgerows and scattered trees which attracted numerous "edge" birds. Both the forest and urban

Table 3

Abundance of Birds in Different Habitats (Birds per 100 Stops)

Species	Habitat			
	Overall	Fields	Forest	Urban
1. Starling (U)[1]	416.3	514.9	67.3	384.2
2. House Sparrow (U)	371.6	528.9	101.8	412.6
3. Red-winged Blackbird (W, FI)	160.1	131.1	78.2	22.1
4. Common Grackle (E)	151.3	137.0	103.6	178.9
5. Savannah Sparrow (FI)	142.7	211.9	29.1	38.9
6. Rock Dove (U)	95.3	173.6	25.5	85.2
7. American Robin (E)	88.8	66.8	89.1	117.9
8. Common Crow (E)	77.9	74.9	85.5	42.1
9. Song Sparrow (E)	70.4	52.3	89.1	18.9
10. Brown-headed Cowbird (E)	55.7	49.8	41.8	38.9
11. American Goldfinch (E)	41.8	36.2	36.4	28.4
12. Eastern Meadowlark (FI)	36.0	27.2	12.7	22.1
13. Bobolink (FI)	35.9	46.8	5.4	–
14. Vesper Sparrow (FI)	35.2	46.4	32.7	1.1
15. Killdeer (FI)	34.9	48.1	9.1	10.5
16. Chipping Sparrow (E)	32.4	26.0	9.1	58.9
17. Bank Swallow (W)	29.4	17.0	14.5	6.3
18. Horned Lark (FI)	27.2	48.9	1.8	5.3
19. Mourning Dove (E)	26.7	15.3	36.4	24.2
20. Barn Swallow (U)	21.4	29.8	5.4	6.3
21. Cedar Waxwing (E)	19.6	8.9	41.8	37.9
22. Cardinal (FO)	18.4	7.7	41.8	16.8
23. Chimney Swift (U)	18.4	5.1	16.4	116.8
24. Northern Oriole (E)	18.0	11.1	27.3	11.6
25. House Wren (E)	17.1	2.6	29.1	10.5
26. Eastern Kingbird (E)	13.9	13.2	9.1	4.2
27. Great Crested Flycatcher (FO)	12.1	3.0	43.6	4.2
28. Red-eyed Vireo (FO)	11.3	4.2	50.9	6.3
29. Yellow Warbler (E)	10.9	–	7.3	8.4
30. Cliff Swallow (U)	9.7	2.6	–	6.3
31. Eastern Wood Pewee (FO)	9.4	0.4	54.5	5.3
32. Blue Jay (FO)	9.1	0.9	25.5	2.1
33. Warbling Vireo (E)	8.8	1.3	7.3	6.3
34. Common Flicker (E)	8.8	3.0	9.1	9.5
35. Indigo Bunting (E)	6.5	1.3	32.7	11.6
36. Rose-breasted Grosbeak (FO)	6.3	0.9	38.2	1.1
37. Gray Catbird (E)	5.9	–	14.5	3.2
38. Spotted Sandpiper (W)	5.1	7.2	7.3	–
39. Willow/Alder flycatcher (E)[2]	4.8	0.4	7.3	1.1
40. Black-capped Chickadee (FO)	3.9	0.4	32.7	1.1

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[1] Letters in parentheses after species name designate major habitat type considered "typical" for species (i.e., where it reaches highest densities). E = forest-edge; FI = fields; FO = forest; U = urban areas and farm buildings; W = water (lakes, streams, and their edges).

[2] Both Willow and Alder flycatchers were present along the routes, in about equal numbers, but were not always recorded separately.

TABLE 4

COMPOSITION OF BREEDING AVIFAUNA IN DIFFERENT HABITATS

Group of birds	Habitat		
	Fields	Forest	Urban
FIELD BIRDS			
No. of species[1]	7	3	4
Individuals per 100 stops[1]	560.4	140.0	93.6
Individuals as % of total	24.0%	11.1%	5.5%
FOREST-EDGE BIRDS			
No. of species	11	11	15
Individuals per 100 stops	491.5	612.8	604.0
Individuals as % of total	21.1%	48.3%	35.1%
FOREST BIRDS			
No. of species	1	8	1
Individuals per 100 stops	7.7	319.9	16.8
Individuals as % of total	0.3%	25.2%	1.0%
URBAN AND FARM-BUILDING BIRDS			
No. of species	4	3	5
Individuals per 100 stops	1247.2	194.6	1005.1
Individuals as % of total	53.5%	15.3%	58.4%
WATER-ASSOCIATED BIRDS			
No. of species	2	–	–
Individuals per 100 stops	24.2	–	–
Individuals as % of total	1.0%	–	–
TOTAL INDIV. (25 commonest spp.)	2331.0	1267.3	1719.5
TOTAL INDIV. (all spp.)	2375.3	1600.0	1790.5

[1] Out of 25 commonest species in each habitat.

stops included other habitats, mostly fields; thus "edge" was also present there: Only 72.7% of the area at "forest" stops was actually forested, and only 78.9% of the area at "urban" stops was actually urban. Only one of the 200 stops was 100% forest.

At the 47 stops in fields (Table 4), only 7 of the 25 commonest species (24.0% of individuals) were true "field" birds, nesting on the ground and carrying out all other activities in fields. Three of the 4 commonest species —House Sparrow, Starling, and Rock Dove—were associated with, and nested in, farm buildings. These 3 are often considered urban birds (Weber 1972), but in Waterloo County, their total numbers in rural areas almost

TABLE 5

COMPARISON OF NUMBERS OF EDGE BIRDS IN FIELDS WITH AND WITHOUT DECIDUOUS HEDGEROWS

Species	Number of birds per 100 stops[1] Fields overall	Fields with hedgerows	Fields without hedgerows
Mourning Dove[2]	15.3	14.3	12.7
Eastern Kingbird[2]	13.2	18.6	14.5
Common Crow[2]	74.9	74.3	61.8
American Robin[2]	66.8	65.7	50.9
Cedar Waxwing[2]	8.9	5.7	16.4
Red-winged Blackbird[2]	131.1	155.7	112.7
Northern Oriole[2]	11.1	15.7	5.5
Common Grackle[3]	137.0	115.7	125.5
Brown-headed Cowbird[2]	49.8	64.3	50.9
American Goldfinch[2]	36.2	45.7	29.1
Chipping Sparrow[3]	26.0	18.6	21.8
Song Sparrow[2]	52.3	62.9	40.0
TOTALS—12 edge species	622.6	657.2	541.8
TOTALS—all species	2375.3	2332.4	2314.1

[1] Data based on 47 stops for fields overall; 14 stops for fields with hedgerows; and 11 stops for fields without hedgerows.

[2] Species characteristic of deciduous hedgerows.

[3] Species characteristic of coniferous hedgerows.

certainly exceeded those in cities, even if their densities were lower. Forest-edge birds were also important in fields (11 out of 25 species, 21.1% of individuals).

In forest, only 8 of the 25 commonest species, and 25.2% of individuals, were true forest birds; forest-edge birds (11 species) accounted for 48.3%. This is a result of the unavoidable inclusion of some fields in the forest stops analyzed, plus the edge created by the road rights-of-way. Even farm-building birds (3 species, 15.3% of individuals) and field birds (3 species, 11.1% of individuals) crept into the top 25 forest species.

In urban habitats, only 5 of the top 25 species were typical urban birds, but they made up 58.4% of individuals. Forest-edge birds accounted for 15 species, though only 35.1% of individuals; their importance is not surprising, as many urban areas (at least residential areas) consist, in effect, of almost continuous "edge." Five species of field and forest birds also entered the urban list, but were relatively unimportant.

Effect of deciduous hedgerows on bird numbers in fields.—Forest-edge birds are numerous in fields, as we have noted. However, the Ontario

TABLE 6

COMPARISON OF NUMBERS OF FARM-BUILDING BIRDS IN FIELDS WITH AND WITHOUT FARM BUILDINGS

Species	Number of birds per 100 stops[1]		
	Fields overall	Fields with farm buildings	Fields without farm buildings
Rock Dove	173.6	234.3	92.0
Barn Swallow	29.8	30.0	28.0
Starling	514.9	512.9	560.0
House Sparrow	528.9	695.7	300.0
TOTALS—4 farm-building species	1247.2	1472.9	980.0
TOTALS—all species	2375.3	2573.0	2300.0

[1] Data based on 47 stops for fields overall; 14 stops for fields with farm buildings; and 5 stops for fields without farm buildings.

Department of Agriculture has advocated more intensive use of farmland, including removal of hedgerows. To evaluate the significance of hedgerows to birds, we compared numbers of birds at 14 stops in fields where deciduous hedgerows were important with those at 11 stops in fields where they were lacking (Table 5). All stops containing coniferous hedgerows were excluded from this analysis.

Twelve species of "edge" birds totalled 541.8 individuals per 100 stops without hedgerows, and 657.2 (21.1% higher) with hedgerows; 9 of the 12 were commoner with hedgerows. Nevertheless, even where hedgerows were absent, many "edge" birds were supported by scattered trees or by forest-field edge beyond the 0.4 km radius (from which birds were counted if heard).

Of the 3 edge species not positively associated with deciduous hedgerows, 2 (Common Grackle and Chipping Sparrow) preferred coniferous hedgerows, which were excluded from this analysis. The third species, the Cedar Waxwing, was commoner without hedgerows for reasons unknown—perhaps merely the small sample size.

Effect of farm buildings on bird numbers in fields.—Like hedgerows, farm buildings have a great effect on numbers of birds recorded in fields. Table 6 compares bird numbers at 5 stops where no farm buildings were present within 0.4 km with those at 14 stops where farm buildings were important (close to the observation point, or 2 or more farmsteads present within 0.4 km). Total numbers of 4 "farm-building" species were 50.3% higher with farm buildings than without them (1473 versus 980 per 100 stops); Rock Doves and House Sparrows were more than twice as abundant. Starlings

TABLE 7

DIVERSITY AND DENSITY OF BIRDS IN DIFFERENT HABITATS

Habitat	No. of stops	Total no. of species	Species per stop	Individuals per stop
Fields	47	56	9.61	23.7
Forest	11	71	11.60	16.0
Urban	19	50	7.62	17.9

would undoubtedly have shown the same pattern had surveys been done earlier in the season, before wandering flocks of juveniles appeared.

DISCUSSION

Diversity and density of birds in different habitats.—Diversity will be discussed only in terms of numbers of species. Out of 101 species (excluding migrants and non-breeders) recorded on the survey routes from 28 May to 4 July, we recorded 50 species at urban stops, 56 at field stops, and 71 at only 11 forest stops (Table 7). Another indication of diversity is the mean number of species per stop, which varied from 7.6 in urban habitats to 11.6 in forest. Although these figures may be inflated by the inclusion of some edge habitat in each category, forests clearly have more species than either fields or urban habitats.

A similar pattern was found by Speirs et al. (1967, 1970, 1975) in a comprehensive census-plot study of bird populations in Ontario County, Ontario, about 130 km east-northeast of Waterloo County. They found a total of 30 species on 11 10-ha study plots in fields; 79 species on 11 forest plots; and 52 species on 10 urban plots. Their low species count in fields is explained by the fact that they largely excluded trees, shrubs, and farm buildings (Speirs and Orenstein 1967); for example, they recorded no Rock Doves, Bank Swallows, Common Crows, House Sparrows, or Northern Orioles in fields.

As the BBS does not measure absolute density, the trends in avian density suggested by our data are misleading. From Table 7, it would appear that the highest densities (individuals per stop) are in fields. This results merely from the observer's ability to see and hear birds at much greater distances in fields than elsewhere. In forest and urban areas, trees and buildings impede the detection of distant birds, and noise from traffic and other sources further reduces detectability in urban areas. Speirs et al. (1970) give mean total bird densities for Ontario County of 240 pairs per 100 ha in fields, 613 in forest, and 1005 in urban areas; the same trend undoubtedly holds true in Waterloo County. Even allowing for the birds added by farm buildings and hedgerows (largely excluded by Speirs et al.), fields unquestionably have lower densities than any other habitat.

Critique on the method.—The BBS technique is not a reliable indicator of the relative abundance of different species because of differences in conspicuousness among species. Emlen (1971) has quantified conspicuousness as the coefficient of detectability (CD)—the proportion of individuals in an area which is ordinarily detected by an observer. Not only does CD differ greatly among species, but the CD value for each species varies with habitat. For instance, though we made no measurements, our guess is that the mean detection distance in forest is about ⅓ that in fields. As a result, differences among habitats in a species' numbers may be over- or underestimated.

One advantage of the BBS is that it inevitably samples "edge" habitats as well as "pure" habitats; in fact, it is considerably biased toward edge habitats, as roadsides usually create an edge situation. In contrast, the usual approach in census-plot studies is to include only "pure" habitats, and to deliberately avoid mixed habitats and "edge." As an illustration of this, the Common Crow, a typical edge species which ranked 8th in abundance on our surveys, was not even listed among the commoner species in Ontario County by Speirs et al. (1970), whose plot censuses covered all the major pure habitat types. Pure habitats, unmixed with edge, do not cover any extensive areas in southern Ontario. Thus the BBS records a segment of the bird population hardly touched by traditional census-plot methods.

The factors causing variability in BBS counts are discussed by Robbins and Van Velzen (1967:6–12). These include the observer, time of day, weather, and time of year. As all our surveys were conducted by one observer, only the other 3 factors need concern us here.

Most species of birds sing less frequently as the morning progresses, although the rate of decrease varies with the species (Robbins and Van Velzen 1967:11). This becomes particularly noticeable when the direction of coverage is reversed in alternate weeks, as we did. A cogent example is the number of Mourning Doves recorded on Route 1. Mourning Doves sing frequently for about an hour after sunrise, but much less frequently thereafter. Most of the forest-edge on Route 1, hence most of the Mourning Doves, were near the east end of the route. When the survey was begun at the east end, a mean of 12.5 Mourning Doves was recorded. When it was begun at the west end, only 4.3 were recorded; the birds at the east end had stopped singing by the time the observer arrived there.

BBS routes are generally not surveyed during rain, steady drizzle, or fog, or when winds exceed Beaufort force 3 (19 km/h). Within these constraints, however, weather affects counts less than we had anticipated. A case in point is the survey of 1 July, which was begun under marginal weather conditions

TABLE 8

WEEKLY COUNTS (ALL SURVEY ROUTES COMBINED) OF COMMON BIRD SPECIES

	Week[1]								
Species	1	2	3	4	5	6	7	8	CV[2]
Killdeer	70	63	61	74	76	75	96	58	.10
Rock Dove	102	177	147	248	237	144	244	272	.26
Mourning Dove	39	64	42	45	55	61	38	71	.18
Chimney Swift	26	39	37	31	44	33	24	14	.14
Eastern Kingbird	39	30	29	27	23	30	41	46	.11
Great Crested Flycatcher	15	29	23	30	20	19	7	7	.21
Eastern Wood Pewee	4	15	21	21	17	20	20	16	.14
Horned Lark	63	60	56	55	58	43	48	37	.12
Bank Swallow	36	56	40	68	43	87	164	192	.33
Barn Swallow	54	60	33	27	39	55	67	90	.33
Cliff Swallow	0	16	4	7	20	50	113	52	.94
Blue Jay	40	48	13	11	12	7	10	12	.92
Common Crow	110	152	143	150	171	163	147	154	.07
House Wren	15	31	31	25	42	42	32	34	.22
American Robin	156	189	157	163	195	184	196	226	.09
Cedar Waxwing	8	9	60	42	36	49	47	30	.49
Starling	485	688	1000	775	955	745	1133	1611	.16
Red-eyed Vireo	6	22	17	27	21	26	12	17	.18
Yellow Warbler	19	22	22	22	23	20	12	10	.05
House Sparrow	607	657	726	726	816	791	1006	936	.08
Bobolink	90	73	65	65	79	75	57	38	.09
Eastern Meadowlark	82	64	63	81	79	73	67	53	.12
Red-winged Blackbird	335	304	304	338	344	311	271	327	.06
Northern Oriole	63	41	37	33	44	25	17	23	.21
Common Grackle	346	298	300	286	381	253	287	522	.16
Brown-headed Cowbird	122	124	117	104	110	102	85	55	.08
Cardinal	26	37	33	40	35	39	23	29	.07
American Goldfinch	143	124	67	66	74	87	76	107	.29
Savannah Sparrow	213	230	257	276	318	346	336	310	.16
Vesper Sparrow	69	60	66	70	84	72	69	61	.13
Chipping Sparrow	53	55	63	71	74	61	58	66	.12
Song Sparrow	130	135	120	147	153	149	150	175	.10
TOTAL INDIVIDUALS (all species)	3838	4227	4344	4360	4920	4484	5206	5873	
TOTAL SPECIES	92	87	82	82	79	81	82	79	

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[1] Weeks are as follows: Week 1, 18 to 21 May; Week 2, 28 May to 1 June; Week 3, 4 to 9 June; Week 4, 10 to 18 June; Week 5, 19 to 23 June; Week 6, 28 June to 4 July; Week 7, 7 to 10 July; Week 8, 12 to 16 July.

[2] CV = coefficient of variation (standard deviation divided by mean) for Weeks 2 to 6 (28 May to 4 July).

(low clouds, wind 16 km/h) and was halted by heavy rain after 12 stops (it was completed the next day). On these 12 stops, 234 birds of 38 species were recorded, compared with a mean of 248 birds of 36 species—almost identical—on 5 previous coverages of this section of the route. We conclude, as does Anthony J. Erskine (pers. comm.), that weather during a survey generally has little effect on counts if rain and strong winds are avoided.

Time of year had a very noticeable effect on counts for most species. Table 8 shows week-by-week total counts for the 32 commonest species. A Friedman non-parametric analysis of variance (Siegel 1956:166) showed that time of year had a significant effect on counts ($p < .05$). Much of the variation was contributed by Week 1 (18 to 21 May) and Weeks 7 and 8 (7 to 16 July); for most species, counts during these 3 weeks tended to be either higher or lower than those during Weeks 2 to 6 (28 May to 4 July). For 30 of the 32 commonest species, at least 1 of the counts during Weeks 1, 7, and 8 lay outside the range of those in Weeks 2 to 6; for 15 of the 32, all 3 counts in Weeks 1, 7, and 8 lay outside this range.

During Week 1 (18 to 21 May), high counts were recorded for several species (e.g. Blue Jay, Bobolink, and Northern Oriole), probably because they were still migrating in numbers. Interestingly, a sizable Blue Jay migration was noted on 18 and 19 May, the same dates when Weir (1972) reported an influx at Prince Edward Point, Ontario, about 305 km to the east. On the other hand, numbers of several insectivorous species (e.g. Great Crested Flycatcher, Eastern Wood Pewee, House Wren, Cedar Waxwing, and Red-eyed Vireo) were low, presumably because many individuals had not yet arrived from the south. During Week 2 (28 May to 1 June), Blue Jays were still migrating, and most Cedar Waxwings still had not arrived. Even during Week 3 (4 to 9 June), a few migrants were recorded. The presence of migrants in June may be unusual, however, as April and May 1971 were abnormally cold in southern Ontario, and bird migration was noticeably delayed as a result (Fairfield 1971, Goodwin 1971, Weir 1972).

During Weeks 7 and 8 (7 to 16 July), a number of species (e.g. Great Crested Flycatcher, Red-eyed Vireo, Yellow Warbler, Bobolink, Cardinal) were recorded less often because they had stopped singing or sang less often. Most of these are species usually detected by ear. In fact, at least 3 species (Horned Lark, Brown Thrasher, and Northern Oriole) had noticeably decreased their song frequency even by Week 6 (28 June to 4 July). In contrast, a number of visually-conspicuous species (e.g. Eastern Kingbird, Bank and Barn swallows, American Robin, Starling, House Sparrow) showed peak counts in Weeks 7 and 8; this is attributable to the presence of fledged young and of noisy, highly visible family groups or flocks.

Restricting our attention to Weeks 2 to 6 (28 May to 4 July), we found that counts varied little for most species, although the coefficients of variation ranged from .05 for the Yellow Warbler to .94 for the Cliff Swallow. Two species, the Blue Jay and Cedar Waxwing, showed high coefficients (.92 and .49) only because migratory movements occurred in Weeks 2 and 3; later counts of these species were quite consistent. There was a tendency for highly-localized or colonial species (e.g. Cliff and Bank swallows, Rock Doves) to have high coefficients, although there were exceptions to this. Nevertheless, the median coefficient of variation for the 32 species was only .135, indicating that, for most species, one count in the period 28 May to 4 July is almost as reliable as 5 counts.

We conclude from these data that the period 28 May to 4 July is best for conducting Breeding Bird Surveys in southern Ontario. This is 3 or 4 days earlier than the period of 1 June to 7 July recommended by the U.S. Fish and Wildlife Service for southern Canada, but southern Ontario lies farther south than other parts of southern Canada, and undoubtedly the nesting season is correspondingly earlier.

Finally, we wish to offer some suggestions concerning the continent-wide Breeding Bird Survey. We believe that the value of the Survey would be greatly enhanced by the collection of data similar to ours on land use along survey routes. Land use data could be collected either on the ground, by individual Survey cooperators, or possibly by centralized interpretation of data from high-level aerial photography. Such data need not be collected annually, but perhaps only once every 3 or 4 years.

The main stated purpose of the Survey is to measure year-to-year changes in the abundance of breeding birds (Robbins and Van Velzen 1967, Erskine 1970). We suspect that changes in land use will be the most important single factor responsible for long-term changes in bird numbers; but without information on land use along the actual survey routes, it will be difficult to determine whether changes in numbers have resulted mainly from land use changes or from other, more subtle causes like pesticides. This is especially true in areas sparsely sampled by BBS routes, such as most of the western United States, where land use along BBS routes may not reflect land use over the area as a whole. Before information on land use can be gathered, however, a classification of habitats usable throughout North America is needed. This classification must reflect important features of both natural and man-altered habitats, and must be easily comprehensible to amateur ornithologists, but its development would be well worth the effort.

Even if it does not prove practicable to collect land use data on a continent-wide basis, we hope that our approach will be useful to others who wish to study changes in bird populations in a localized area such as the one we studied.

SUMMARY

We used the Breeding Bird Survey technique to study breeding bird populations in relation to habitat in Waterloo County, Ontario, in 1971. Four survey routes across the county were each covered 8 times between 18 May and 16 July. In conjunction with these surveys, we devised a classification of habitat types and estimated the coverage of each type at each sampling point.

We compared bird numbers among survey routes, and found that numbers of several species were closely related to the extent of particular habitat types. We also compared bird numbers in 3 major habitat categories (fields, forest, and urban areas), based on results from selected sampling points. Because of the nature of the sampling and of the habitats themselves, all 3 contained a high proportion of forest-edge birds. Our data support those of others showing that forests have the most species of birds and urban areas fewest, and are consistent with a pattern of densities highest in urban areas and lowest in fields.

In a critique on the method, we looked at the effects of time of day, weather, and especially time of year on bird counts. Counts in the third week of May were high for some species which were still migrating in large numbers, and low for others which were still arriving. Counts after 4 July were high for some visually-conspicuous species which congregate in family groups or flocks, and low for other species because of a decrease in song. Between 28 May and 4 July, however, counts varied little for most species.

We conclude that interpretation of the significance of changes in bird numbers shown by Breeding Bird Surveys would be facilitated if complementary data on land use were gathered. We recommend the development of a classification of habitats usable throughout North America, and its application in conjunction with the continent-wide Breeding Bird Survey.

ACKNOWLEDGMENTS

Several people provided helpful advice and information during our work, especially Robert S. Dorney of the School of Urban and Regional Planning, University of Waterloo, as well as several Planning graduate students (particularly Derek Coleman and Ray Smith) and a number of local naturalists including Craig A. Campbell, Larry Lamb, and Willard Schaefer. Anthony J. Erskine and Chandler S. Robbins advised us on methods before the study began, and gave helpful comments on an early draft of the manuscript, as did Jerome A. Jackson and J. Murray Speirs. We wish to thank all these people, and also the National Research Council of Canada, which financed the study through a grant to Theberge.

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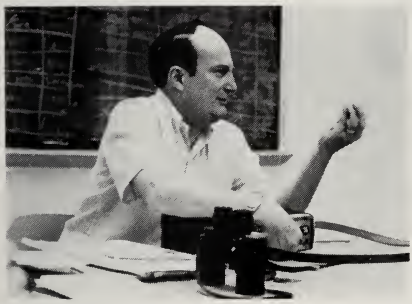
APPENDIX: SCIENTIFIC NAMES OF BIRDS MENTIONED IN TEXT AND TABLES

Ruffed Grouse, *Bonasa umbellus*; Killdeer, *Charadrius vociferus*; American Woodcock, *Philohela minor*; Upland Sandpiper, *Bartramia longicauda*; Spotted Sandpiper, *Actitis macularia*; Rock Dove, *Columba livia*; Mourning Dove, *Zenaida macroura*; Chimney Swift, *Chaetura pelagica*; Common Flicker, *Colaptes auratus*; Eastern Kingbird, *Tyrannus tyrannus*; Great Crested Flycatcher, *Myiarchus crinitus;* Willow Flycatcher, *Empidonax traillii*; Alder Flycatcher, *Empidonax alnorum*; Eastern Wood Pewee, *Contopus virens*; Horned Lark, *Eremophila alpestris*; Bank Swallow, *Riparia riparia*; Barn Swallow, *Hirundo rustica*; Cliff Swallow, *Petrochelidon pyrrhonota*; Purple Martin, *Progne subis*; Blue Jay, *Cyanocitta cristata*; Common Crow, *Corvus brachyrhynchos*; Black-capped Chickadee, *Parus atricapillus*; House Wren, *Troglodytes aedon*; Gray Catbird, *Dumetella carolinensis*; Brown Thrasher, *Toxostoma rufum*; American Robin, *Turdus migratorius*; Veery, *Catharus fuscescens*; Cedar Waxwing, *Bombycilla cedrorum*; Starling, *Sturnus vulgaris*; Red-eyed Vireo, *Vireo olivaceus*; Warbling Vireo, *Vireo gilvus*; Yellow Warbler, *Dendroica petechia*; House Sparrow. *Passer domesticus*; Bobolink, *Dolichonyx oryzivorus*; Eastern Meadowlark, *Sturnella magna*; Red-winged Blackbird, *Agelaius phoeniceus*; Northern Oriole, *Icterus galbula*; Common Grackle, *Quiscalus quiscula*; Brown-headed Cowbird, *Molothrus ater*; Cardinal, *Cardinalis cardinalis*; Rose-breasted Grosbeak, *Pheucticus ludovicianus*; Indigo Bunting, *Passerina cyanea*; American Goldfinch, *Carduelis tristis*; Savannah Sparrow, *Passerculus sandwichensis*; Vesper Sparrow, *Pooecetes gramineus*; Chipping Sparrow, *Spizella passerina*; Field Sparrow, *Spizella pusilla*; Song Sparrow, *Melospiza melodia.*

NEW LIFE MEMBER



Robert D. Burns has become a life member of the Wilson Ornithological Society. Dr. Burns is presently a professor of biology at Kenyon College in Gambier, Ohio. His principal interests in ornithology are primarily in the area of population ecology; he has published several studies on the Cardinal. Dr. Burns is also a member of the AOU, The American Society of Mammalogists, and other natural history organizations. He has been very active in the Wilson Society and has served as an elected council member and a member of WOS committees. Dr. Burns is married and has two children.

ANALYSIS OF MATERIALS IN CLIFF AND BARN SWALLOW NESTS: RELATIONSHIP BETWEEN MUD SELECTION AND NEST ARCHITECTURE

Delbert L. Kilgore, Jr. and Kathy L. Knudsen

Studies of the mud nests of Cliff (*Petrochelidon pyrrhonota*) and Barn swallows (*Hirundo rustica*) have heretofore emphasized nest-site selection and nest-building activity (e.g., Emlen 1952, 1954, Mayhew 1958, Samuel 1971, Jackson and Burchfield 1975). While it is usually acknowledged in these studies that a "proper consistency of mud" is essential for nest construction, there are no specific data available on the actual texture or consistency of such materials. Furthermore, it is not known if or how the design of nests constructed by these species may affect the selection of building materials; Cliff Swallows build nests which are enclosed and retort-shaped, whereas Barn Swallows construct simple cup-shaped nests (Samuel 1971). The purposes of this study were to analyze the materials used by these swallows in nest construction and to determine if there are interspecific differences which may be related to nest construction or design.

MATERIALS AND METHODS

Collecting sites.—Three Cliff and 3 Barn swallow nests were collected at each of 11 sites in western Montana (Fig. 1). At 7 of these sites (1, 3, 4, 8, 9, 10, 11), nests of both species were found within a few meters of each other on the same structure (concrete or wooden bridge, barn, or highway overpass). At the remaining 4 sites, nests of both species were located on different structures, but were never more than 400 m apart.

Analyses.—Samples of each nest were analyzed for texture (% sand, % silt, % clay), sand size, organic matter, and water content. Texture refers to the type and relative numbers of particles in the sample (Baver et al. 1972).

Two 50 g samples of dried mud from each nest were analyzed for texture by the hydrometer method described by Bouyoucos (1936). In intact nests (5 Cliff, 7 Barn) 1 sample was taken from the area of attachment (base), while the other was selected from the rim or opening of the nest. In other nests, the samples were not selected from specific regions. Because the amount and kind of organic matter in the samples varied considerably, they were not routinely treated with hydrogen peroxide. Instead, conspicuous pieces of organic matter were removed by hand.

The suspension remaining after the textural analysis was washed through 4 brass sieves, sizes 20, 32, 60, and 120. The mesh openings of these sieves are 0.841, 0.557, 0.250, and 0.125 mm, respectively. The portions of the suspension which were retained in the sieves were air dried and weighed on a semi-microbalance. Non-sand materials were eliminated from the residue before weighing. Sand remaining in the size 20 sieve was classified as very coarse sand, that in the size 32 sieve as coarse sand, that in the size 60 sieve as medium sand, and that in the size 120 sieve as fine sand (USDA 1951).

An additional 15 g sample from each nest was air dried at 110°C for 24 h and then

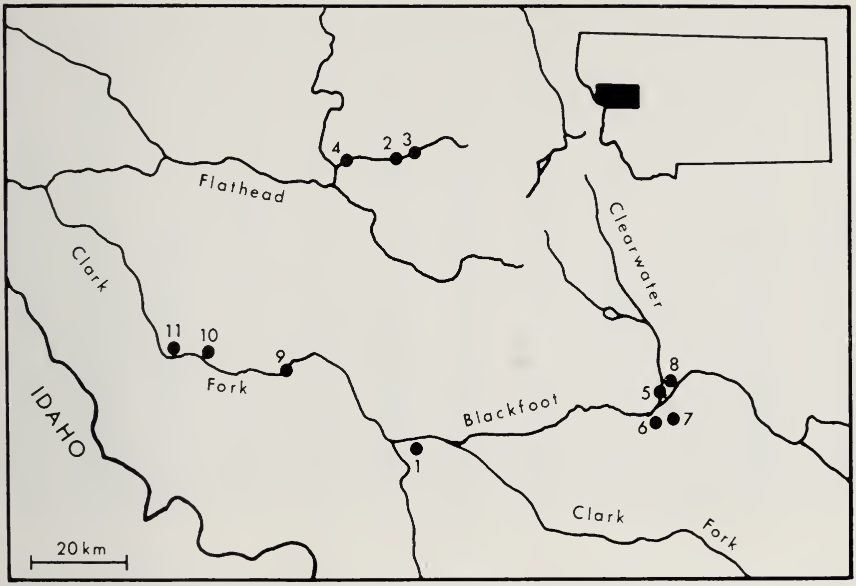


FIG. 1. Distribution of collecting sites in western Montana.

ignited at 400°C for 7 h. This procedure yielded information on water content and organic matter in the dried mud sample (Jackson 1958). These values for water content were used in the calculations of textural components.

The amount of material in each textural category, the amount of organic matter, and the water content of each sample are expressed as percentages of the total weight of the sample, while the amount of sand in each size category is expressed as a percentage of the total weight of sand in the sample.

Statistical treatment of data.—Variation between species, among sites, among nests within each site, and within individual nests in each textural and sand size category was analyzed with a mixed-model 2 factor analysis of variance (ANOVA) with 2 levels of nesting. Variation between species and among sites in water content and organic matter was analyzed with a mixed-model 2 factor ANOVA (Sokal and Rohlf 1969). Differences between samples taken from the rim and base in textural components and sand size were analyzed with *t*-tests.

All percentages were transformed to angles (arcsine transformation) prior to analysis with ANOVA or *t*-test (Sokal and Rohlf 1969).

RESULTS

Textural components.—The soil-like material in the nests of both swallows was predominantly sand, with modest amounts of silt and some clay (Fig. 2). Sand particles comprised 61.4 ± 0.8% and 56.4 ± 1.1% of the mud samples from Cliff and Barn swallow nests, respectively, while silt particles accounted

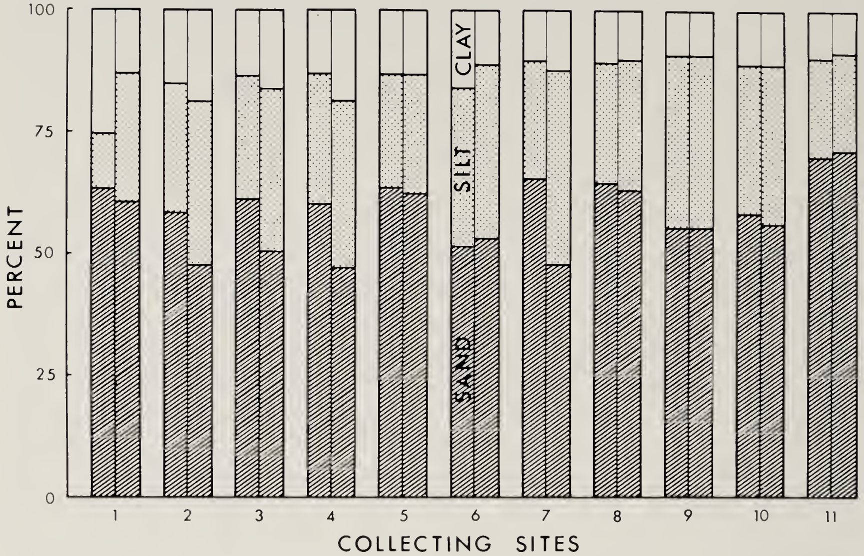


FIG. 2. Textural components of mud samples from Cliff (left half) and Barn swallow (right half) nests at all 11 collecting sites. Values are mean percentages for each component.

for 25.7 ± 0.9% and 31.5 ± 0.9% (values are means ± SE). The mean amount of clay in the mud samples was similar for both species, 12.7 ± 0.7% and 11.9 ± 0.6%, respectively.

At most localities (8 of 11), the mud in Cliff Swallow nests contained more sand and fewer silt particles than that from Barn Swallow nests (Fig. 2). These species differences in sand and silt content are statistically significant ($P < .05$), as are the differences in clay content ($P < .05$). However, the interspecific differences in clay content are more dependent on the locality, yet there is no recognizable trend among sites (Fig. 2). Cliff Swallows at 4 sites used mud with a greater clay content than that selected by Barn Swallows, while at 4 other localities the reverse was true. The variations in texture among nests within a site and among collecting sites are likewise statistically significant ($P < .05$). Intra-site variation accounts for 21%, 15.9%, and 17.8% of the total variation in percent sand, silt, and clay, respectively, while the variation among sites accounts for 47.3%, 49.9%, and 46%.

Sand size.—The sand particles in the mud samples from the nests of both species was mostly of a small size (Fig. 3). In Cliff Swallow nests, 41.0 ± 2.2% of the sand was fine, 27.8 ± 1.3% was of medium size, 9.3 ± 0.6% was coarse, and 21.9 ± 2.0% was of very coarse size (values are means ± SE).

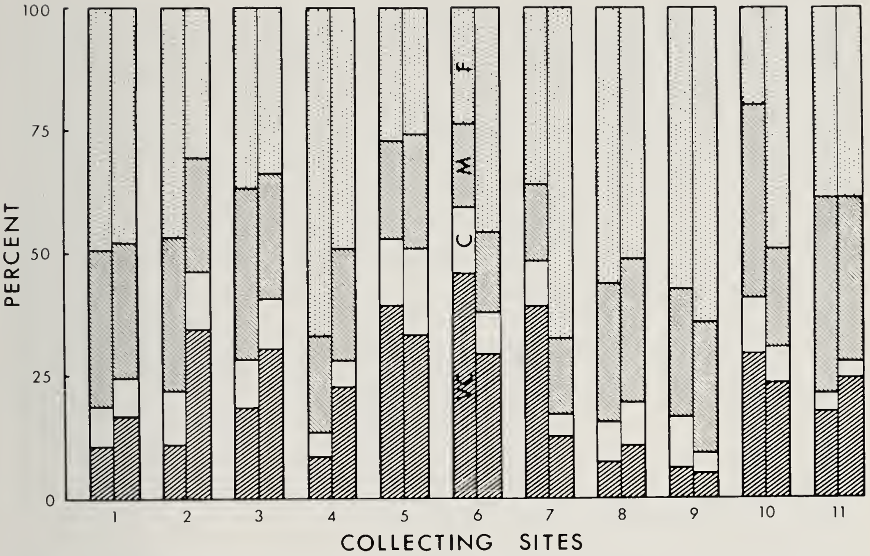


FIG. 3. Distribution of sand sizes in mud samples from Cliff (left half) and Barn swallow (right half) nests at all 11 collecting sites. VC represents the proportion of very coarse sand, C the percentage of coarse sand, M the proportion of medium sand, and F the percentage of fine sand. Values are mean percentages for each component.

The corresponding values in Barn Swallow nests were 44.9 ± 2.5%, 23.8 ± 0.9%, 8.0 ± 0.6%, and 21.7 ± 1.9%, respectively.

The amount of sand in each of these size categories varied widely among collecting sites and nests at a particular site and between species (Fig. 3). The 2 species appeared to be selecting mud with different amounts of sand in each of these categories, but these species differences were not the same at most sites (Fig. 3). The amount of sand of a specific size occurring in the mud samples was primarily dependent on the locality. Variation in the amount of sand in these size categories among nests within a site and among sites is statistically significant ($P < .05$). Variation within a site accounts for 25.7 to 36% of the total variation in all size categories, while variation among localities accounts for 35.6 to 47.7%.

Organic matter.—There was a moderate amount of organic matter in the mud of all Cliff and Barn swallow nests, although the actual amount and form of the organic matter varied with the species (Table 1). Organic matter accounted for a mean of 6.6 ± 0.5% of the samples from Barn Swallow nests, but only 4.5 ± 0.4% of samples from the nests of Cliff Swallows. This difference is statistically significant, as are the differences among collecting

TABLE 1

ORGANIC MATTER AND MOISTURE CONTENT IN MUD SAMPLES FROM CLIFF AND BARN SWALLOW NESTS

Collecting sites	Organic matter		Moisture content	
	Cliff	Barn	Cliff	Barn
1	3.2 ± 0.2[a]	7.5 ± 1.7	1.8 ± 0.1	1.9 ± 0.3
2	6.7 ± 0.7	8.5 ± 1.1	2.5 ± 0.2	3.5 ± 0.9
3	4.3 ± 0.7	8.0 ± 0.8	1.4 ± 0.1	2.0 ± 0.2
4	1.1 ± 0.2	5.2 ± 0.5	3.4 ± 1.6	1.3 ± 0.1
5	6.2 ± 1.1	5.6 ± 1.2	1.7 ± 0.4	1.8 ± 0.3
6	9.5 ± 1.3	5.2 ± 1.8	3.5 ± 0.6	1.6 ± 0.4
7	2.7 ± 0.2	4.8 ± 0.9	1.2 ± 0.1	1.9 ± 0.3
8	4.3 ± 0.3	6.3 ± 2.0	1.1 ± 0.1	1.7 ± 0.3
9	1.9 ± 0.4	4.7 ± 0.5	1.0 ± 0.2	0.9 ± 0.1
10	3.0 ± 0.6	5.5 ± 3.4	1.1 ± 0.1	1.9 ± 0.3
11	5.8 ± 1.2	12.3 ± 2.3	1.3 ± 0.2	2.2 ± 0.5

[a] Values are mean percentages ± the standard error of the mean.

sites ($P < .05$). At most localities (9 of 11), mud from Barn Swallow nests contained more organic matter than samples from Cliff Swallow nests (Table 1).

The organic matter in Cliff Swallow nests was primarily seeds and other fine particulate matter, while that in the nests of Barn Swallows consisted of coarse items, such as grass stems, horse hair, and feathers.

TABLE 2

TEXTURAL COMPONENTS AND SAND SIZES IN MUD SAMPLES SELECTED FROM THE BASE AND RIM OF 5 CLIFF AND 7 BARN SWALLOW NESTS

	Cliff		Barn	
	Rim	Base	Rim	Base
Textural component				
Sand	61.4 ± 2.8[a]	62.4 ± 2.6	50.3 ± 1.7	48.7 ± 1.8
Silt	25.0 ± 1.2	25.9 ± 1.5	33.7 ± 1.4	35.4 ± 1.4[b]
Clay	13.6 ± 1.8	11.6 ± 1.1	16.1 ± 1.3	16.0 ± 0.8
Sand size				
Very coarse	18.5 ± 7.1	20.3 ± 5.8	31.0 ± 5.7	26.7 ± 4.5
Coarse	9.8 ± 2.4	10.4 ± 1.5	8.8 ± 1.4	8.9 ± 1.4
Medium	28.8 ± 2.7	30.3 ± 2.6	23.4 ± 1.4	24.1 ± 1.4
Fine	42.9 ± 8.7	39.0 ± 5.4	36.9 ± 5.3	40.3 ± 5.4[b]

[a] Values are mean percentages ± the standard error of the mean.
[b] Difference between rim and base samples is statistically significant at the 95% probability level.

Moisture content.—The mud samples from nests of both species contained very little water. The mean moisture content of the mud in Cliff Swallow nests was 1.9 ± 0.2%, while that in Barn Swallow nests was 1.8 ± 0.1% (Table 1). These interspecific differences are slight and are not statistically significant ($P > .05$), but the differences among sites are ($P < .05$). Locality differences were not correlated with nest placement, ambient humidity conditions, or the type of structure on which the nest was located.

Intra-nest differences.—Samples taken from specific regions of the nest (i.e., base and rim) were very similar in their textural components and in sand size (Table 2). Intra-nest differences in the percentage of silt and fine sand in Barn Swallow nests are statistically significant at the 95% probability level; all other intra-nest differences are not statistically significant ($P > .05$). Hence, for all practical purposes the mud in these nests can be considered to be homogeneous.

DISCUSSION

It is clear from the preceding analyses that the 2 species of swallows select different materials for the construction of their nests. The primary differences among the variables measured are in the texture of mud and the amount of organic matter used in the nest.

Cliff Swallows selected mud with a higher sand and lower silt content than that selected by Barn Swallows (Fig. 2). These differences are especially meaningful when one considers that both species presumably had access to the same mud source at each of the collecting sites. Emlen (1954) observed that Cliff Swallows may gather mud from sources 0.8 km or more from the nesting colony, that is, from distances twice the maximum distance separating nests of the 2 species at any of our collecting sites. Buss (1942) also found that Cliff Swallows would carry mud for nest building as far as 1.2 km.

Despite these interspecific differences, both species appeared to be using mud within a restricted range of texture. Ninety-five percent of the textural observations are within the bounds of 41–77% sand, 17–43% silt, and 4–28% clay. These textural ranges include sandy loam, sandy clay loam, and loam soil types. Interestingly, Buss (1942) suggested that loam, silt loam, and clay loam might make the best mud for nest-building.

The organic matter in the nests of the 2 species differed both in form and in quantity, the former being the more conspicuous difference. Less obvious were the differences in the amount of organic matter incorporated into the nest, which while seemingly slight are statistically significant.

Emlen (1954) noted that the quality of mud used by Cliff Swallows varied considerably from locality to locality. Such variation among sites is apparent in the specific parameters of texture, sand size, moisture content, and organic matter measured in this study. These differences might be expected to reflect differences in the temporal and geographic availability of particular mud (soil) types. However, the site differences described above cannot be correlated with any major geographic or geologic features that affect the distribution or abundance of soil types in western Montana. Based on analyses of differences among sites, there is no relationship between the major geographic area of the site and the values of any of the variables. For example, the mean sand content of mud samples from Cliff Swallow nests along the Blackfoot River (sites 5, 6, 7, 8) range from 52% to 66.2%, the lowest and next to the highest values for all localities.

The texture of the mud selected for nest-building by these species is undoubtedly influenced by many factors which are important in the design and construction of a mud nest. The most obvious of these are (1) how well the mud adheres to the supporting substrate (adhesion), (2) how well the particles in the mud hold together (cohesion), (3) how well the dried mud withstands compressive and tensile stresses (strength), (4) how easily the mud is manipulated during construction (workability), and (5) how resistant the mud is to changes in volume (shrinkage and swelling).

Interspecific differences in the texture of mud incorporated in the nest, especially where there are also obvious differences in nest shape, would suggest that some of the above factors may be more important than others in the construction of a nest with a particular design. To assess the importance of each of these factors and their relationship to nest design would require a detailed knowledge of the physical properties of the mud both in a plastic and nonplastic stage. Such information is currently unavailable. However, some insight into the importance of these factors in the selection of mud can be derived from the physical properties of adobe, other aggregate building materials (e.g., concrete and stucco), and soils.

In soils, the properties of adhesion and cohesion are most affected by moisture content, although texture is also of some importance (Baver et al. 1972). Cohesion increases with decreasing moisture content and is greater for clays (soils which are largely composed of small particles) than for other soils, while adhesion decreases with declining moisture content. At very low moisture contents, like those measured in the dried mud samples (1 to 6%), the increased cohesion is primarily due to a cementation effect between the dried particles (Baver et al. 1972). In view of the lack of significant interspecific differences in the moisture content of the mud samples and since the interspecific textural differences, although statistically significant, are rather minor compared with those differences in soils which substantially affect cohesion and adhesion, it would appear that the adhesiveness and cohesiveness of the muds selected by both species are similar.

The compressive and tensile breaking strengths of adobe and aggregate building materials are greatly affected by a number of factors, but most important are differences in texture and the inclusion of impurities (Eyre 1935, Mielenz 1965, Turneaure and Maurer 1908). Addition of sand to adobe reduces its compressive and tensile strength; the degree of reduction is directly proportional to the amount of sand added. When compared with "pure" adobe, adobe containing 75% sand (by weight) shows a 56% decline in compressive and a 50% decline in tensile strength, while addition of 25% sand only results in a 20% decline in compression and has no effect on tensile strength. Inclusion of organic matter (straw and manure) in adobe also decreases its strength, both in tension and compression (Eyre 1935). The actual reduction in strength resulting from inclusion of organic matter is largely dependent on the form of the organic matter and the amount added. However, the quantitative relationships between reduction in strength and form and the amount of organic matter is not clear (Eyre 1935). The increased sand content in the mud of Cliff Swallow nests effectively reduces its strength relative to that in Barn Swallow nests. Perhaps this reduction in strength accounts for the apparent "fragileness" of Cliff Swallow nests observed by Samuel (1971) and others.

Workability of aggregate mixtures (those containing sand or gravel) is a difficult factor to quantify, primarily because it is dependent on many factors. However, the texture or proportion of the mixture is very important (Mielenz 1965). In concrete and stucco an increased sand content improves the workability. Such "lean" mixtures are often used where strength and durability are not of major importance (Mielenz 1965). The higher sand content in the mud of Cliff Swallow nests would undoubtedly improve its workability, therefore facilitating the construction of a nest with a complex shape.

Volume changes in the dried mud may be brought about by changes in moisture content (during drying and afterwards) and temperature and are affected by texture (Eyre 1935). Adobe mixed with 50% sand (by weight) has coefficients of expansion and contraction that are ½ those of pure adobe (Eyre 1935). Addition of straw to adobe also reduces the coefficients of expansion and contraction, but only by about 15%. Because of their relatively high contents of organic matter and sand, and since most nests are sheltered from direct rain, volume changes in the mud are probably not great.

The differences in materials (texture of the mud and organic matter) used by the 2 species appear not to be fortuitous, but instead to be related to the factors important in the construction of mud nests and to the differences in the complexity of design. The mud selected by Cliff Swallows, with its high sand content, is more easily manipulated mechanically which assists in the building of a more complex nest. Improved workability of the mud, however, occurs at the expense of strength and perhaps cohesion, which may explain why Cliff Swallow nests are noticeably more "fragile."

The inclusion of conspicuous amounts of organic matter (grass, feathers, and hair) in the nest of Barn Swallows may improve its cohesive nature, in that pieces of mud are bound together, which may further explain why these nests appear more durable in comparison to those of Cliff Swallows. The retort-shaped design of Cliff Swallow nests probably prohibits the use of such large pieces of organic matter.

SUMMARY

There are statistically significant differences in the composition of the mud selected by Barn and Cliff swallows for nest building. Furthermore, these differences appear to be related to the complexity of nest design. Cliff Swallows select mud with a higher sand and lower silt content than that used by Barn Swallows. A high sand content, based on the physical properties of other composite mixtures, probably improves the ease with which the mud may be manipulated and shaped into a retort-shaped nest. However, this increased workability of the mud is accompanied by a reduction in strength.

There are also statistically significant differences in the amount and form of organic matter incorporated in the mud of these nests. Mud from Cliff Swallow nests contains small amounts of seeds and other fine particulate matter, while that from the nests of Barn Swallows contains large amounts of coarse items, such as grass stems, horse hair, and feathers. The design of Cliff Swallow nests probably precludes the inclusion of such bulky materials, which in Barn Swallow nests probably serve to bind together pieces of mud.

The type and character of the mud used by these species varied from locality to locality, but within relatively narrow limits. The factors affecting the construction and design of mud nests (e.g., adhesion, cohesion, etc.) may well place constraints on the type of mud which can be used.

ACKNOWLEDGMENTS

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REQUESTS FOR ASSISTANCE

Mexican locality records.—A comprehensive bibliography and gazetter of localities concerning birds in Mexico is being prepared. We will include all papers dealing with Mexican birds and birds recorded in Mexico. Authors wishing to have material included should send reprints of their materials to Mario and Isabel Ramos, Bell Museum of Natural History, University of Minnesota, 10 Church St. SE, Minneapolis, MN 55455.

Artificial nest structure literature.—An international bibliography on the use of artificial nest structures for bird research and management is being compiled. All contributions will be acknowledged in publication. Please send reprints and title lists to Jeffrey B. Froke, National Audubon Society, Box 157, San Juan Capistrano, CA 92675.

PRODUCTION AND SURVIVAL OF THE VERDIN

George T. Austin

A review of avian demography (Ricklefs 1973) demonstrates the dearth of knowledge on this subject. Although certain demographic parameters are relatively well known for a wide variety of species, data are generally lacking for their seasonal, annual, and geographic variability. These, including population densities, nesting season, clutch size, and nesting success, are straight forward and can be obtained with relative ease. Survival and annual recruitment are also of interest, but are difficult to determine under field conditions.

If first year individuals (*I*) can be distinguished from adults (*A*), the ratio of the 2 can be used to calculate annual mortality and recruitment of first year birds into the breeding population given the assumptions of constant population size and no collecting bias. In many species, the first prebasic molt is incomplete (e.g., Dwight 1900), providing a basis of distinguishing first year birds from adults. Although it has long been recognized that I/A ratios can be used to determine annual survival (Emlen 1940, Snow 1956), this method has not been widely used.

The Verdin (*Auriparus flaviceps*) is an ideal species for a demographic study as first year birds can be distinguished from adults through at least March (Austin and Rea 1971), the species is nonmigratory and relatively sedentary, and general aspects of its life history are known (Moore 1965, Taylor 1967, 1971, Austin 1976). In this paper, I will analyze the demographic data available for the Verdin from the literature and my own studies in Arizona and Nevada. Geographical and/or seasonal trends will be examined and estimates of mortality and annual recruitment will be presented.

METHODS

Clutch size was determined for 144 nests in Pima County, Arizona (1970–71), and 87 nests in Clark County, Nevada (1959–70, 1976). Additional data were obtained through the North American Nest Record Card Program, Cornell University (NANRCP). The clutch was considered complete when the number of eggs remained constant for 2 or more successive days. Verdins lay 1 egg per day on successive days until the clutch is complete (Moore 1965, Taylor 1971, this study). Nesting success was obtained by periodically (1–3 day intervals) inspecting active nests. Hatching success is percent of eggs to hatch, fledging success is percent of eggs to produce young which fledge, nestling success is percent of hatchlings to fledge, and nest success is percent of breeding nests built to fledge at least one young.

I aged museum specimens of Verdins according to the methods of Austin and Rea (1971). Briefly, at fledging, Verdins are grayish-headed and lack the rich chestnut lesser primary coverts characteristic of adults. During the first prebasic molt, the upper greater primary coverts and the proximal 2–5 primaries are retained. These feathers appear more faded and worn than the newer distal primaries. This difference was reliable through at least late March or April of the following spring after which feather wear was too great for reliable determinations. A bird was considered a first year bird if (1) it was gray-headed (before first prebasic molt), (2) it was undergoing first prebasic molt, or (3) it had retained upper greater primary coverts and proximal primaries after molting. After April, yellow-headed birds which had not begun prebasic molt were considered adult. The latter included some birds which were not as yet one year of age but had entered one breeding season since the first prebasic molt.

RESULTS

Relative abundance.—The population density of the Verdin in the United States in winter is greatest in the Big Bend region of Texas, southern Arizona (excluding eastern Arizona), and adjacent southeastern California (Fig. 1). Distribution and relative abundance appears similar during summer (data from U.S. Fish and Wildlife Service breeding bird survey courtesy C. S. Robbins). Population densities during the breeding season in suitable habitat averaged about 8 pairs/40 ha in the San Antonio region of Texas (American Birds breeding bird censuses 1968–1972, 1974), 2–3 pairs/40 ha in the Chihuahuan Desert of western Texas and New Mexico (Dixon 1959, Raitt and Maze 1968), about 8 pairs/40 ha in southern Arizona and southeastern California (range 3–16; American Birds breeding bird censuses 1941, 1942, 1965, 1969–1971, Hensley 1954, Taylor 1967, Anderson and Anderson 1973, Tomoff 1974, this study), and about 4 pairs/40 ha in southern Nevada (Austin 1970, Miller 1974).

Clutch size.—In southern Nevada, modal clutch size remained at 4 throughout the season although mean clutch size decreased (Table 1). In southern Arizona, mean clutch size decreased through the breeding season with a modal size of 4 in March and April and 3 for the remainder of the season. Similarly, Moore (1965) and Taylor (1971) reported a decrease in clutch size through the breeding season in New Mexico and central Arizona, respectively.

There also appears to be an east to west and north to south decrease in clutch size (Table 1). Two sets of eggs from Texas contained 6 eggs each (collection at Oregon State Univ., *in* Taylor 1967), although the usual size in Texas was reported as being 4 (Attwater 1892) or 3 to 6 (Oberholser 1974, NANRCP). The average clutch in Texas and New Mexico contained 3.75 eggs, in Arizona 3.41, and in central Baja California, Mexico, 2.41. Only 1 clutch of 100 examined in the latter location contained 4 eggs (Bancroft 1930). The average southern Nevada and central Arizona clutch was nearly 0.5 egg larger than those in southern Arizona.

Breeding season.—The breeding season extends generally from mid-March

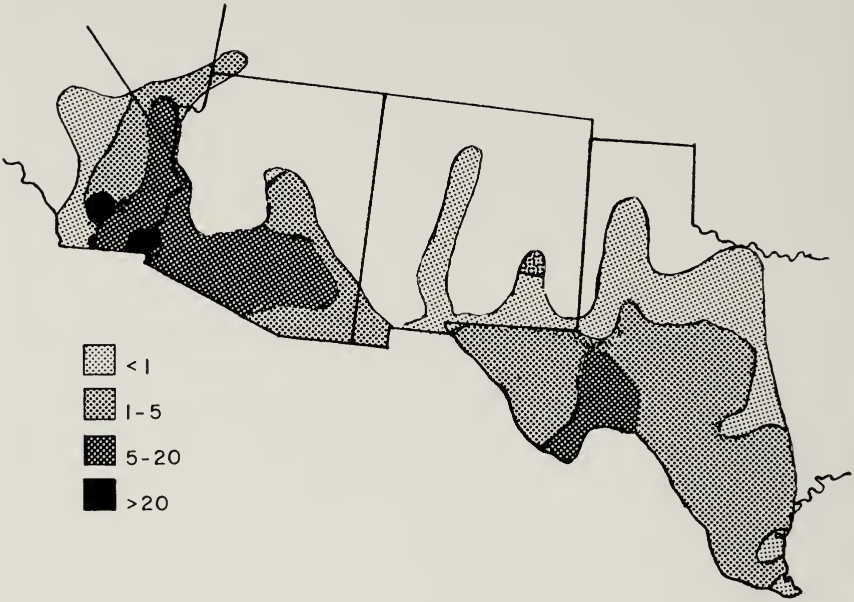

FIG. 1. Relative density of Verdin populations during winter (values are numbers/10 party hours averaged for the years 1965–1974 from American Birds Christmas bird count).

through mid-June over much of the Verdin's range (Bent 1946, Hensley 1959, Moore 1965, Taylor 1971, this study) with the earliest egg date of 4 March (Bent 1946). In desert grassland in southern Arizona, I have found fresh clutches as late as 23 July with young fledging after mid-August. Near Tucson, a fresh clutch was found in early August (P. Gould, pers. comm.).

TABLE 1

CLUTCH SIZE OF THE VERDIN

Locality	Mean clutch size (N)			Source
	Early nests	Late nests	Total	
Texas	–	–	4.06 (16)	Taylor 1967, NANRCP
New Mexico	3.71 (14)	3.00 (6)	3.50 (20)	Moore 1965
Southern Arizona	–	–	4.00 (16)	Hensley 1959
Southern Arizona	3.77 (48)	3.02 (96)	3.27 (144)	this study
Central Arizona	4.13 (16)	3.42 (12)	3.82 (28)	Taylor 1971
Southern Nevada	3.83 (53)	3.68 (34)	3.77 (87)	this study
Baja California	–	–	2.41 (est.)	Bancroft 1930

TABLE 2

LENGTH OF BREEDING SEASON IN THE VERDIN

Location	Number of clutches laid during						Index of season length (months)	Source
	March	April	May	June	July	Aug.		
Texas	1	5	6	7	1	0	3.95	NANRCP
Southern Arizona	1	3	5	5	0	0	3.50	NANRCP
Saguaro-Palo Verde	22	86	80	23	0	1	3.44	this study
Mesquite grassland	0	11	14	18	7	0	3.79	this study
Central Arizona	6	10	8	4	0	0	3.80	Taylor 1971
Southern Nevada	4	102	65	11	0	0	2.58	this study

Texas birds may occasionally breed into September (Oberholser 1974). Further south in Mexico the breeding season was apparently well underway by late March (Short and Crossin 1967) and extended into August (Amadon and Phillips 1947, Short 1974) or later (Brewster 1902, but see Banks 1963). This longer breeding season in Mexico was further suggested by Bancroft (1930) who found many fresh clutches in mid-June.

An estimate of season length adjusted for peaks in breeding activity is derived from the index of "equally probable months for nesting" (MacArthur 1964):

$$\text{months} = e - \Sigma p_i \log p_i$$

where p_i = the number of clutches initiated in each month. These data for the Verdin are presented in Table 2. Season length in southern Nevada was nearly a month shorter than in Arizona. This may be due to the lack of a distinct summer rainy season in the Mojave Desert. Here the peak of the breeding season is in April compared to a peak extending over a 2-month period in southern Arizona (Table 2).

Number of broods.—In Arizona, most pairs had no more than one successful brood per year although some with successful first nests attempted a second nesting. On the average, ½ of the pairs built 2 nests. As many as 4 breeding attempts were made in a season and as many as 2 were successful (Taylor 1967, this study).

The length of one successful cycle was approximately 43 days (6 days building, 3 days laying, 16 days incubation, 18 days nestling period). Second and successive cycles were shorter as the male constructs succeeding nests during the previous nest period. After a successful nesting, an average of 2 days elapsed between fledging and the first egg of the next clutch (r_s); after a failure, an average of 4 days elapsed (r_f) (Taylor 1967, this study).

TABLE 3

SEASONAL CHANGES IN NESTING SUCCESS OF THE VERDIN DURING 1970 AND 1971 IN PIMA COUNTY, ARIZONA

Month	Hatching (%)	Fledging (%)	Nestling (%)	Nest (%)	N eggs	N nests
March	77.8	72.2	92.8	88.8	36	9
April	85.6	71.2	83.2	82.9	146	41
May	80.0	70.5	88.2	80.0	95	30
June	48.5	29.4	60.6	36.0	68	25
July	35.3	35.3	100.0	42.9	17	7

Length of an unsuccessful cycle can be calculated (assuming a constant probability of nest loss during the nest period) with Ricklefs' (1973) equation

$$T_f = \frac{Q - mPT}{mQ}$$

where P is the proportion of successful nests, Q is $1 - P$, T is length of egg laying, incubation, and nestling periods and m is the average daily mortality rate (see below). Length of an unsuccessful attempt averaged 19.3 days in southern Arizona (all data combined) and 17.2 in southern Nevada. With these an average nesting attempt can be calculated by

$$\overset{*}{T} = P(T + r_s) + Q(T_f + r_f)$$

(Ricklefs 1970). This value was 36.9 days in southern Arizona and 31.5 days in Nevada. Thus about 3.7 and 2.1 broods could be attempted, on the average, in the 2 localities given the breeding season length in Table 2.

Nesting success.—Several factors affect nesting success in the Verdin. Nest orientation was shown to be an important variable (Austin 1976) as was found for the Cactus Wren (*Campylorhynchus brunneicapillus*) (Austin 1974). Success also tended to decrease from beginning to end of the breeding season (Table 3). Considerable variation existed in nesting success among the several localities for which data were available (Table 4), possibly a reflection of annual differences, although 2 successive years in southern Arizona were very similar. Overall fledging success for all studies reported in Table 4 was 59% which is within the range given for enclosed nesting species (Nice 1957).

Daily mortality rates calculated by

$$m = \frac{-(\log_e P)}{T}$$

TABLE 4
NESTING SUCCESS OF THE VERDIN

Location	Success (%)				N eggs	N nests	Source
	Hatching	Fledging	Nestling	Nest			
Texas	56.3	34.4	61.1	33.3	32	12	NANRCP
New Mexico	–	56.9	–	–	48	18	Moore 1965
Southern Arizona	96.4	82.1	85.5	80.0	56	15	Hensley 1954
Southern Arizona							
Saguaro-Palo Verde	73.5	65.5	89.2	76.4	264	72	this study
Mesquite grassland	61.5	44.1	71.6	54.2	143	48	this study
Central Arizona	48.8	29.1	59.5	36.0	86	25	Taylor 1971
Southern Nevada	85.9	72.4	84.2	86.5	199	52	this study
Total	72.7	59.1	81.5	67.4	780	224	
Average daily mortality rate (%)	1.67	1.42	1.13	1.06			

(Ricklefs 1969), averaged 1.42% (0.53–3.33) from laying to fledging for eggs and 1.06% (0.39–2.97) for nests. This indicates that within-nest loss exceeded total losses and was true for all samples except for the Texas sample (Table 4) and Hensley's (1954) sample. Within-nest losses exceeded whole nest losses during both the egg (0.57%) and nestling (0.26%) stages for all samples combined. Individual losses during the incubation period averaged greater (by 0.54%) than during the nestling period although 2 of the 6 samples (Hensley, southern Nevada) showed the opposite trend (Table 4). Similarly, whole nest losses averaged greater during incubation (0.23%).

These low values are typical of enclosed nesting species, and the resultant vectors indicate that hatching failure and possibly desertion are major factors of mortality (Ricklefs 1969). I was able to assign probable factors responsible for mortality of 105 individuals (65 eggs, 40 nestlings). Hatching failure accounted for 24.8% and desertion for 21.9% of all mortality. These factors accounted for only 8.2% and 5.2% of total mortality in 6 species summarized by Ricklefs (1969). Predation accounted for 58.4% of nest mortality in these species compared to 19.0% in the Verdin.

Success and productivity comparisons between 3 and 4 egg clutches are presented in Table 5. Four egg clutches produced more young per nest than 3 egg clutches. The difference is greater in early nests than in late nests. In early nests, 4 egg clutches were more efficient in fledging young from eggs which hatched than were 3 egg clutches. In late nests, however, 3 egg clutches were somewhat more efficient in fledging young. The relatively high pro-

TABLE 5

COMPARISON OF PRODUCTION AND NESTING SUCCESS BETWEEN 3 AND 4 EGG CLUTCHES OF THE VERDIN

	Early nests clutch size		Late nests clutch size	
	3	4	3	4
Number of nests	13	69	81	38
% Nests with hatched eggs	85	94	77	87
% Nests with fledged young	69	88	65	74
% Nests hatch. young/fledg. young	82	94	85	85
% Eggs hatching	85	85	68	74
% Eggs producing young which fledged	62	74	55	56
% Eggs hatch./producing yg. which fledged	73	87	81	76
Mean no. of fledglings per nest in which eggs hatched	2.2	3.1	2.2	2.6
Mean no. of fledglings per nest	1.9	3.0	1.7	2.2

portion of 4 egg clutches among late nests may be of value during favorable years.

Post-fledging mortality.—Fledgling Verdins remained dependent on the parents for 2 or more weeks post-fledging. In southern Arizona, I was able to follow 21 fledglings of which 17 survived this period. Mortality rates averaged 0.87% per day (1.05% per day during the first 15 days). The immediate post-fledging period has previously been shown to be the time of heaviest mortality of birds out of the nest (Lack 1966, Ricklefs 1973).

Immature adult ratios.—Immature to adult ratios for 286 specimens from southwestern United States are presented in Table 6. These were high during and immediately after the breeding season, decreased rapidly thereafter and leveled off in November at a value averaging about 0.67. The change reflected a greater mortality rate of first year birds than adults until mid-winter. Thus, the breeding population of Verdins was composed approximately of 60% birds in at least their second season.

TABLE 6

NUMBERS OF IMMATURES (I) AND ADULTS (A) AMONG SPECIMENS EXAMINED AND RATIO OF IMMATURES TO ADULTS

	May–June	July–Aug.	Sept.–Oct.	Nov.–Dec.	Jan.–Feb.	March
I	32	40	31	24	17	4
A	18	22	29	39	24	6
I/A	1.78	1.82	1.07	0.62	0.71	0.67

TABLE 7

NUMBER OF YOUNG FLEDGED BY VERDINS

Location	Number of pairs	x̄ no. young fledged per nest	x̄ no. young fledged per individual	Source
Nevada-Arizona[1]	–	3.61	1.81	this study
Nevada[2]	9	3.44	1.72	this study
Arizona[2]	20	3.40	1.70	this study
Arizona[3]	8	2.88	1.44	Taylor 1967
New Mexico[4]	14	3.78	1.89	Moore 1965

[1] Data for Clark County, Nevada and Pima County, Arizona (1969–1971) assuming 50% of pairs build late nests (Moore 1965, this study) and means of 2.74 and 1.73 young fledged per early and late nest, respectively (this study).

[2] Known pairs followed throughout season.

[3] Data for 1965 excluding 4 pairs which left study area shortly after laying.

[4] Data for 1965 assuming as stated that 50% of pairs renest and mean of 2.64 young fledged per nest from first nests and 2.27 young fledged per nest from second nests (Moore 1965).

Because first year Verdins before the first prebasic molt are distinguishable from adults in the field, a bias by collectors may result. As a check on the accuracy of the I/A ratio during and just after the breeding season, I compiled data on average production per pair (Table 7). This averaged 1.71 young fledged per adult and was very similar to the I/A ratio (Table 6). Another check was made by multiplying mean clutch size (3.55) by mean fledging success (0.591) and number of broods attempted (1.5) which gave a similar value of 1.57 nestlings per individual (3.15 per pair). Thus, for the Verdin, the I/A ratio (in May–August) appears to be a good indicator of successful production.

For a sample of 54 specimens for October to March from Baja California, Mexico, the I/A ratio was 1.16 (29/25) and for 23 specimens from the main part of Mexico a ratio of 0.92 (11/12). These ratios were considerably higher than for southwestern U.S. populations.

First year and adult mortality.—From the I/A ratio data, mortality and survival rates can be calculated. Assuming breeding populations are stable and adult mortality rates are constant throughout the year, mortality rates of first year birds can be calculated on a seasonal basis. Because I assumed stable populations and that the proportion of first year birds in the breeding population equaled adult losses, annual adult mortality was 40%. Annual mortality for first year birds was 75%. This complements the 24% first year survival predicated from known production (1.7 fledglings per adult) and adult mortality (40%).

Mortality rates of first year birds from 1 July to 1 December averaged 0.81% per day. From 1 December to 1 May, mortality averaged 0.13% per day similar to the adult rate of 0.14% per day. The mortality differential between first year birds and adults can be calculated by:

$$m_A - m_I = \frac{\log_e R(t)/R(o)}{T}$$

(Ricklefs 1973) where $R(o)$ is the I/A ratio at some time o and $R(t)$ is the I/A ratio after some period of time (T). This value for the Verdin was nearly 20% per month until 1 December. The mortality differential from 1 July to 1 May was 9.7% per month.

The samples from Mexico indicated a greater annual adult mortality (approaching or exceeding 50%) than further north.

DISCUSSION

Among passerine birds, mortality rate generally decreases at each stage of the life cycle from egg to adult (e.g., Lack 1966, Ricklefs 1969, 1973). These data for the Verdin are summarized in Table 8. As noted by Ricklefs (1973) post-fledging survival rate appears higher in species with long nestling periods reflecting their greater maturity at fledging. In many species post-fledging mortality rate is lower or about equal to nestling mortality rate. Most species in which post-fledging mortality rate approached or exceeded nestling mortality rate, nest in enclosed nests or cavities. Such species are well-known for their high nesting success (Nice 1957). The first week out of the nest may be the most critical for some species (Snow 1958) and newly fledged young may be especially susceptible to severe weather (Smith 1967). First year survival rate is usually greater than in the nest and lower than annual adult survival rate. As was true for thrushes and tits (Lack 1946, 1966) survival rates of the Verdin approached adult levels after 6 months. The adult survival rate of 60% per year is at the upper end of the range for passerines given by Lack (1954).

In addition, first year survival was about 42% of adult annual survival and considerably higher than the 25% of adult survival suggested for first

TABLE 8

MORTALITY AND SURVIVAL RATE OF THE VERDIN

	Egg stage[1]	Nestling stage	Post-fledging stage	First 6 months[2]	Second 6 months	Adult
Mortality (% per day)	1.69	1.05	0.87	0.81	0.13	0.14
% Eggs to survive to the end of this period	72.5	59.9	46.9	13.9	11.0	—
Number of days	19	18	28	180	180	—

[1] Including laying period.
[2] Including post-fledging stage.

year small land birds (Ricklefs 1973) and may reflect the lower level of productivity in arid temperate regions (Ricklefs 1973).

The increase in I/A ratio with decreasing latitude and clutch size was counter to the trend for Blue Tits (*Parus caeruleus*) (Snow 1956) and Rough-winged Swallows (*Stelgidopteryx ruficollis*) (Ricklefs 1972). The data for the Verdin from Mexico suggest that nesting success or first year survival is greater in Mexico or that the nesting season is substantially longer (as indicated above) and productivity is greater to offset a higher rate of adult mortality.

SUMMARY

Demographic parameters of the Verdin are discussed. Clutch size displayed a decreasing gradient from east to west and north to south. Breeding season length decreased from south to north. Nesting success was greatest during the first 2 months of the breeding season and varied with locality and year. Based on immature/adult ratios, annual adult survival was 60% in southwestern U.S. and 50% in Mexico. Survival increased during the first year of life and approached adult levels at about 6 months.

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MALE BEHAVIOR AND FEMALE RECRUITMENT IN THE RED-WINGED BLACKBIRD

Patrick J. Weatherhead and Raleigh J. Robertson

In most species of birds females devote more energy to reproduction than do males. Consequently natural selection has favored increased discrimination on the part of the females when seeking a mate and thus, in such species, selection of mates is expected to be determined by female choice (Trivers 1972). This would be particularly true in highly polygynous species where the male role in reproduction is very limited. The factors on which female choice can be based are individual differences among males and differences among the territories of males (Orians 1969). When the male contribution to reproduction is restricted to supplying genetic information, or when pair bonds are made away from breeding grounds, female choice must rely solely on differences in individual characteristics (Verner 1964). However, as the male contribution increases to include the maintenance of a territory which influences reproductive success through provision of food or nest sites, then female choice should also be influenced by territory quality (Orians 1969). This latter point has formed the basis for the Orians-Verner model for the evolution of polygynous mating systems (Selander 1972, Wilson 1975).

The Orians-Verner model attributes polygynous mating to the existence of major differences in territory qualities. When these differences are great enough, a female will improve her chances of successfully reproducing by choosing to share a high quality territory with another female rather than by choosing to be the sole female in a poor quality territory. Implicit in this model is that the differences in males' individual characteristics will be reflected by differences in the qualities of their territories, since the fittest males should be best able to defend superior territories. It follows then that female choice will be meditated by territory quality and therefore behavioral differences in males should not influence female recruitment. One might further predict that selection would favor a reduction in recruitment and courtship behavior since it should lack any advantage in attracting mates while making the male more vulnerable to predators.

From a study of Red-winged Blackbirds (*Agelaius phoeniceus*) we have shown that female choice as reflected by harem size, did not correlate with territory quality (Weatherhead and Robertson 1977). Some females therefore appeared to be making poor choices in terms of territory quality. We concluded that these choices must result from behavioral influences of territorial males not associated with the quality of their territories. Although such choices lower reproductive success in the F_1 generation, we developed a model which showed that as long as those losses did not exceed a critical maximum, the females would ultimately benefit through their male offsprings' superior ability to recruit a harem (Weatherhead and Robertson, in press). The purpose of the present study was to determine to what extent territorial males differ in their behavior towards females and to establish whether or not such differences reflect success at recruiting females independent of territory quality. We previously reported (Weatherhead and Robertson 1977) that female reproductive success was negatively correlated with the density of females within male territories and positively correlated with territory quality with respect to nest site suitability. We predicted, therefore, that if territory quality could be held relatively constant then the density of females in a male's territory would be an indication of his recruitment ability. This technique is useful in that it allows one to compare recruitment ability relative to territory size. It is also necessary if one is to be able to distinguish between behavioral characteristics related to recruitment and those related to territory acquisition.

METHODS

The area chosen for this study was Cow Island Marsh located near the Queen's University Biology Station, 40 km north of Kingston, Ontario. The vegetation of the marsh is predominantly cattail (*Typha latifolia*), bordered by sweet gale (*Myrica gale*) and alder (*Alnus rugosa*). The marsh is approximately 1 ha in area.

In order to quantify differences between males, behavioral tests were conducted from the onset of breeding in early May until nesting terminated in late June. Tests were performed between 0900 and 1130 two days a week. A single test consisted of a 5 min presentation of a normally postured, freeze-dried female Red-winged Blackbird to a territorial male. The model was attached to the top of a wooden pole positioned so the model was just above the vegetation, close to the center of a territory to ensure that the behavior recorded was that of the territory holder. To avoid behavior associated with nest defense the model was never placed within 5 m of an active nest.

The observer was positioned outside the territory in which the test was conducted, using a portable burlap blind for concealment early in the season and relying on the new growth of vegetation when it became available. The events of the trial were recorded on a portable tape recorder. No male was tested more than once on any given day and the order in which males were tested was varied each day.

The scoring system used was similar to that used by Robertson and Norman (1976) in ranking host aggression to cowbirds (*Molothrus ater*). It was first necessary to rank the behavioral acts in order of increasing intensity of courtship. The basis for the ranking came primarily from the work of Nero (1956a, b) although some intuitive judgments based on field observations had to be made. Such was the case when a departure from strict ordinal ranking was made in scoring an act thought to be of much higher intensity than the act ranked below it. The list of acts and their respective scores is presented in Table 1. The distinction between close and distant acts is that the latter occur further than 3 m from the model.

TABLE 1

SCORING SYSTEM FOR BEHAVIORAL TRIALS

Score	Act.
1	distant silent observation
2	close silent observation
3	distant observation with "check"
4	close observation with "check"
5	distant display flight (6 sec)
6	distant "song-spread" (3 sec)
7	distant crouch or strutting
8	close display flight (6 sec)
9	close "song-spread" (3 sec)
10	close crouch or strutting
15	aggression to other females*
17	pecking at model
20	attempted copulation

* This was considered a recruitment act since it discouraged aggression toward a potential mate by those females already recruited.

The intensity of courtship is also a function of the length of time various acts were elicited during the 5 min trial. Thus, a duration score was also assigned to acts as follows: 1 for acts elicited for less than 5 sec; 2 for acts lasting between 5 sec and 1 min; 3 for acts lasting between 1 and 3 min; 4 for acts lasting greater than 3 min. For discrete acts which were recorded on the basis of how often they were elicited rather than for how long, their duration score in a trial was the mean time required for that act (given in brackets in Table 1) times the number of elicitations. The score for each test was then computed by multiplying each act score by its duration score and then summing these values.

In addition to the model testing, general reproductive information was collected throughout the breeding season. Twice weekly the marsh was thoroughly searched for new nests while the progress of nests found previously was recorded. Territory boundaries were determined as soon as the males became resident. This was accomplished by observing individual movements, use of song posts, and points of conflict between males. Following the breeding season the marsh was surveyed and mapped and territory areas were computed using a polar planimeter. Harem sizes were then determined from nest records as the maximum number of active nests in a territory at any given time during the breeding season.

RESULTS

Figure 1 is a map of Cow Island Marsh indicating the territorial boundaries of the 11 resident males involved in the study. The range of harem sizes and territory areas (see Table 2) are similar to those found in other Red-wing studies (Holm 1973, Goddard and Board 1967, Case and Hewitt 1963, Orians 1961). We conducted 61 tests, with the number of tests per individual

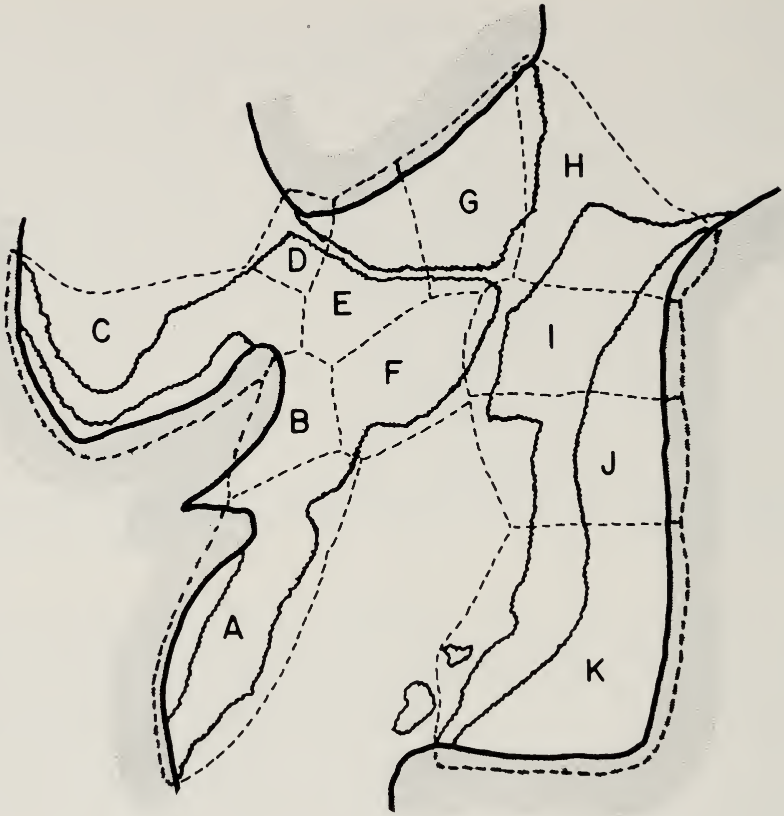

FIG. 1. Territorial males in the study of area. Solid lines indicate dry land (shaded), wavy lines separate cattail from open water and shrub vegetation. Broken lines indicate territory boundaries.

ranging from 4 to 9. Each male was not tested an equal number of times because some males were off their territories on several occasions when they were to be tested. No score was assigned to such trials although a score of zero was given if the male was present at the initiation of a trial and left without eliciting any courtship behavior. Whether such zero scores actually indicated a complete lack of motivation by the male or only a failure to see the model is uncertain. Therefore, the use of such scores in the analysis has been minimized as will be indicated.

Before comparisons could be made between the trial scores of individual males and their respective recruitment success, it was first necessary to test the validity of the scoring system. We felt that if the scores obtained in the

TABLE 2

TERRITORY PARAMETERS AND TEST SCORES FOR ALL MALES TESTED

Male	Territory Area (m²)	Harem Size	Area Per Female (m²)	Score Test	Mean Song-Spread Freq.
A	1298	3	433	11.5	4.3
B	213	1	213	20.0	2.7
C	833	4	208	42.4	7.3
D	153	2	77	47.5	10.0
E	475	3	158	20.3	13.0
F	453	3	151	35.5	5.3
G	620	4	155	17.5	2.6
H	1013	4	253	8.0	3.0
I	550	1	550	0.0	2.0
J	863	2	432	13.8	3.8
K	2078	2	1039	4.5	0.7

behavior tests were representative of courtship intensity, then the scores should be highest when the receptive females were most abundant. Nero (1956a) found that female Red-wings are generally receptive around the time of clutch initiation. Thus, by comparing the distribution of dates of clutch initiation with the mean trial score of all males combined over the breeding season, it is possible to determine if the predicted correlation exists. Figure 2 illustrates the results of this comparison. A highly significant correlation (Spearman rank correlation, $r_s = 0.85$, $p < 0.01$) was found between the abundance of receptive females and the mean test scores over the breeding season. Only non-zero test scores were included.

The results of the model tests for individual males are presented in Table 2. Because of the uncertain meaning of zero test scores, the lowest score was discarded for each male. To prevent any possible biasing due to this dropping of the lowest score, the highest score for each male was also dropped. The mean of the remaining scores was then used to determine the overall test score. If males were able to influence female choice by this behavior, we predicted that those males with the highest overall test scores should also be those that were most successful in recruiting females relative to the qualities of their respective territories. The study area was chosen for its consistent nest site quality and therefore the major differences in overall quality among the territories were due to significant differences in area. Thus, the highest scoring males were predicted to be those with the lowest area per female. Using a Spearman rank correlation, a coefficient of –0.87 ($p < 0.01$) was found for the correlation of female model test score with

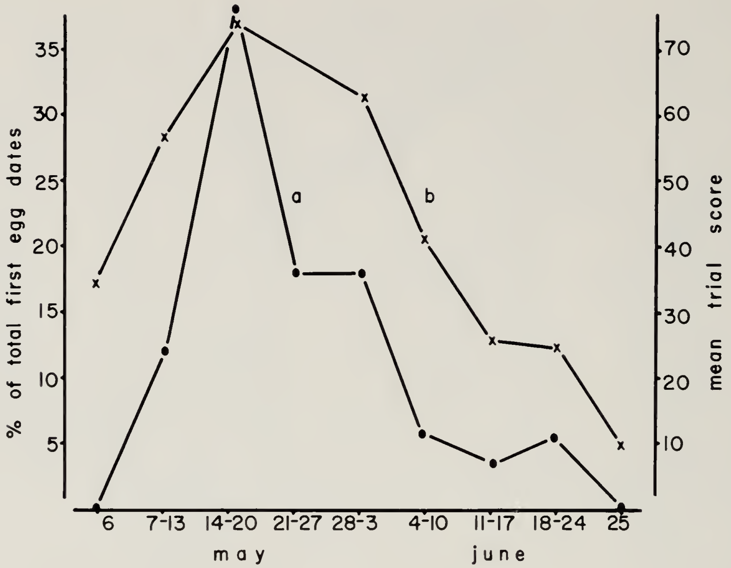

FIG. 2. Distribution of clutch initiation dates (a) and mean trial scores (b) for all males over the breeding season.

area per female. Thus, the males that maintained the highest intensity of courtship to the female model are those that were able to achieve the highest nesting density of females. Since high nesting density is disadvantageous to females, those which chose such a situation must have been influenced to do so by the behavior of the territorial male. Figure 3 clearly demonstrates this finding. As the area per female drops below 300 m^2 the intensity of courtship required by males to increase density further rises sharply.

There is also a significant negative correlation (Spearman rank correlation, $r = -0.65$, $p < 0.05$) between the model test score and territory area (Table 2). This indicates that male behavior associated with recruitment ability is not synonymous with the ability to establish a large territory. In fact, it appears that the 2 are in some way mutually exclusive since the males with the best territories scored the lowest in the behavioral tests.

Of the 13 acts that were recorded in the model tests, the song-spread display was most frequently observed and is perhaps the behavior most commonly associated with male Red-winged Blackbirds. Nero (1956a) considers the song-spread to be a warning display to other males although he does state that it is given more frequently in the presence of females. The mean frequency of song-spread displays per trial where the male was present for the

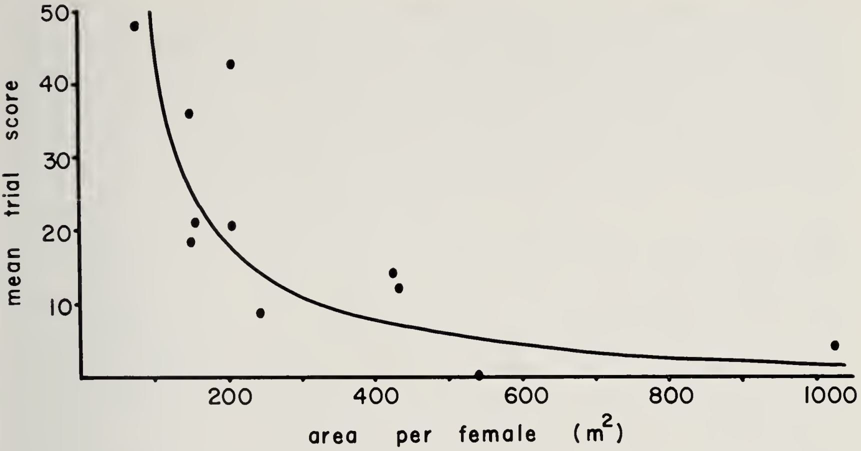

FIG. 3. Individual males' model test scores vs. area per female.

full 5 min was determined for each male. The results of this investigation are included in Table 2. Using Spearman rank correlation, a significant positive correlation ($p < 0.05$) was found between song-spread frequency and mean trial score, and a significant negative correlation ($p < 0.05$) between song-spread frequency and area per female. Thus, it appears that during the time of model testing, this display was of significant importance in female recruitment and did not function solely as a warning display.

DISCUSSION

The notion that males are able to influence the choice of mates by females is not a new one. In his treatment of the topic of sexual selection, Darwin (1871) considered this ability of males to be a major driving force in the evolution of secondary sexual characteristics. The importance of individual differences between males has not been ignored in the Orians-Verner model of polygyny. However, in defining the polygyny threshold in terms of territory quality, the assumption has been made that the difference in qualities of males is reflected in the difference in the qualities of their respective territories. This assumption has not allowed for the possibility that the ability to maintain a good quality territory may be derived from attributes unrelated to those involved in female recruitment. The results of this study suggest that this is in fact the case since recruitment success, as measured by female density, was generally higher for those males with the smaller territories.

Results of other studies of the Red-winged Blackbird support the conclusions drawn above. Smith (1972) investigated the role of the male's red epaulets and found them to be important in territory maintenance but not female recruitment. This indicated that if males were actively recruiting females the epaulets are not important. However, it did not, as Smith suggests, prove that males exert no influence over female choice. Peek (1972) performed similar experiments to those of Smith in which male epaulets were blackened. His results supported Smith's in that the loss of red epaulets resulted in a reduced ability to maintain a territory. However, Peek also performed experiments in which male Red-wings were muted and his results suggest that muted males were unable to obtain mates. In a study of 97 territorial male Red-wings, Weatherhead (1976) reported that only one male remained unmated. This male was also unique in its inability to perform the normal vocalization accompanying the song-spread display, uttering only a high-pitched squeak in its place. The results of the studies cited above suggest that the ability to maintain a territory is related more to visually directed displays while the ability to recruit females has its basis in vocalizations. However, a more recent study by Smith (1976) produced contradictory results. Males that were vocally altered (= muting by Peek) did not appear to suffer any loss of ability to maintain a territory or attract females. Smith interprets the contradictory results as a possible consequence of habitat differences where the 2 studies were conducted. He suggests that only in the best habitats where competition between males is most intense would a male perform poorly if his vocal or visual displays were altered.

It has been demonstrated that males differ behaviorally and that these differences affect recruitment success. However, what remains to be explained is why those males most successful at recruitment are least successful at the establishment of good quality territories. A possible explanation might be that, given a fixed amount of energy available for reproduction there are 2 strategies available. One would be to expend a great deal of energy in establishing a large, good quality territory. In addition to the high energetic costs of the acquisition of such a territory would be the accompanying high maintenance costs throughout the breeding season. This would leave only limited time and energy available for recruitment. The consequence of this strategy would be that fewer females would nest in the territory than would be expected, but because of low nesting density, individual success should be high.

The alternative strategy would be to use very little energy in territory establishment, thereby securing a small territory with low maintenance costs. This would allow much more energy to be devoted to attracting females. The consequence here would be that more females would nest in the territory than would be predicted from its quality. Although female success would be reduced, the male would still benefit by virtue of the number of females recruited.

As a consequence of the 2 male strategies, females could choose either a high quality territory with low female density and therefore higher chances of nest success or a low quality, high density territory in which the chances of success were reduced but any male offspring produced would be expected to have superior ability to recruit mates.

It is not expected that only 2 "pure" strategies would be observed in nature since males should differ with respect to their total energy available for reproduction. Differences in past experience may also affect how effectively this energy is partitioned. The consequence therefore would be that a range of males might exist such that the most fit obtained many females and high quality territories while the least fit obtained few females and poor quality territories. Between the 2 extremes would be a range of combinations of harem sizes and territory qualities. This would account for the consistent finding of many Red-winged Blackbird studies that harem size and territory area are not correlated (Holm 1973, Case and Hewitt 1963, Orians 1961, Nero 1956b).

SUMMARY

Behavioral tests using freeze-dried female Red-winged Blackbird models were conducted on 11 territorial males through one breeding season. The intensity of courtship in the tests reflected recruitment success but not territory quality, indicating that those male attributes associated with territory establishment differ from those related to female recruitment. A negative correlation was found between recruitment success and territory quality and a possible explanation is presented.

ACKNOWLEDGMENTS

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REDUCTION OF COURTSHIP BEHAVIOR INDUCED BY DDE IN MALE RINGED TURTLE DOVES

M. A. Haegele and Rick H. Hudson

Some wildlife investigators who have studied declining bird populations have reported what they consider to be aberrant reproductive behavior. For instance, Gress (1970) reported abnormal behavior in the California Brown Pelicans (*Pelecanus occidentalis*) nesting on Anacapa Island, and Snyder et al. (1973) observed abnormal reproductive behavior in Cooper's Hawks (*Accipiter cooperii*). These investigators suggested that the behavior problems were caused by DDE residues. Effects of DDE on behavior have been observed in laboratory studies concerned with reproduction of birds. Lincer (1972) observed possible abnormal parental behavior in American Kestrels (*Falco sparverius*) treated with dietary DDE and polychlorinated biphenyls (PCB's). In our own studies with Ringed Turtle Doves (*Streptopelia risoria*) we found that DDE-treated birds in undisturbed reproductive cycles took an average of 2.5 times longer to renest than did control birds (Haegele and Hudson 1973).

In the laboratory and field studies cited, few quantitative data were available to test if DDE does affect reproductive behavior of birds. The purpose of the present study was to measure the quantitative effects of dietary DDE on the initial courtship behavior of male Ringed Turtle Doves.

METHODS

The 18 pairs of Ringed Turtle Doves used in this study were hatched and raised at the Denver Wildlife Research Center. Each pair had raised at least 1 young to 21 days of age prior to use in this study. After all 18 pairs of birds had successfully completed 1 breeding experience, each bird was isolated from viewing others (sight isolation) for 18 days. At the start of isolation, the outside of each wing of all males was marked with red ink so that we could easily distinguish the male birds when paired for courtship observations. Lights were clock-controlled, turned on at 06:30 and off at 20:00 MST and temperature in all rooms was maintained between 22° and 24°C. Water, food, and mineralized grit were provided *ad libitum.*

After the 18th day of isolation, each male dove was randomly paired with a female dove with which he had never previously mated, and the pairs were placed in observation cages for 12.5 min each day for 5 consecutive days. Courtship behavior displayed during this period was recorded on video tape. This procedure provided a base line for normal courtship behavior. In order to keep assigned pairs separate until the video tape equipment was in operation, each observation cage was divided by an opaque partition. These partitions were removed after our recording equipment was started.

To quantify courtship behavior, the video tapes were later played back and the number of bow-coos performed by each male bird was counted for each observation period. A stopwatch was used to measure total time each male bird spent in performing sexual behavior. The types of behavior which we timed included driving, bow-coo, wing-flip, hetero-preening, billing, sex-mount, and stick-nest building (Miller and Miller 1958). The first 30 sec of video-taped behavior for all 12.5-min observation periods were not used. This allowed the investigator to leave the room and gave the doves time to adjust to the experimental conditions and their assigned mates. The video tape recorder and TV monitor were kept in an adjacent room so that no one was present in the room with the doves during a taping session. At the end of each observation period, all birds were returned to sight isolation until the next period. During all recording periods, each male dove was always paired with the same female.

After the pretreatment data were gathered, the 18 pairs of doves were randomly assigned to 3 treatment groups each consisting of 6 pairs. One group was given a 10-ppm p,p′-DDE diet and one a 50-ppm diet dry weight basis. The remaining group served as a control and received an uncontaminated pigeon checkers diet. Initiation of treated diets was designated as day 0. Treated diets were made by adding proper amounts of DDE to ground Purina pigeon checkers. (Trade names are provided for identification only. Their mention does not imply endorsement of commercial products by the Federal Government.) All birds were fed *ad libitum* for 63 days at which time the study was terminated.

The 10-ppm dietary treatment was chosen to simulate what was considered a possible field exposure level and the 50-ppm dietary treatment was selected to approximate the exposure level which adversely affected reproduction in our earlier study (Haegele and Hudson 1973). To minimize possible intoxication effects, both treatment levels were selected to be sufficiently below the 20-day LC50 value of 250–300 ppm p.p′-DDE for Ringed Turtle Doves, which we determined before initiating this study.

On days 31–35 and days 59–63, all birds were again paired with the same female and put into observation cages for video taping of courtship behavior. All doves were kept in sight isolation between observation periods. After completion of the observations, on day 63, all birds were sacrificed and the males plucked, eviscerated, and analyzed for residues. All birds were examined internally to confirm that they had been correctly sexed. One pair on the 50-ppm diet consisted of 2 males; therefore, all results for the 50-ppm dietary treatment are based on a sample size of 5 pairs rather than 6.

A 3-factor analysis of variance with repeated measures on the last 2 factors (Winer 1971) was used to determine significant differences in bow-coo frequency and total activity time. Factor 1 was the 3 treatments, factor 2 was the 2 time periods (days 31–35 and 59–63), and factor 3 was the 10 1-day periods. Analysis of variance and Duncan's new multiple range test were used to determine significant differences between percent lipids found in whole body carcasses. Residue values were determined by the method of Peterson et al. (1976).

RESULTS

The mean number of seconds of total courtship activity time displayed by male Ringed Turtle Doves was reduced by the DDE treatment (Fig. 1). Control birds increased their average courtship activity by 25% and 23%, respectively, for the 31–35 and 59–63 day posttreatment observation periods. The 10-ppm-treated birds showed no courtship activity time behavior effects at 31–35 days, but activity time decreased 55% from pretreatment values at 59–63 days. The birds on the 50-ppm DDE-contaminated diet had a 30%

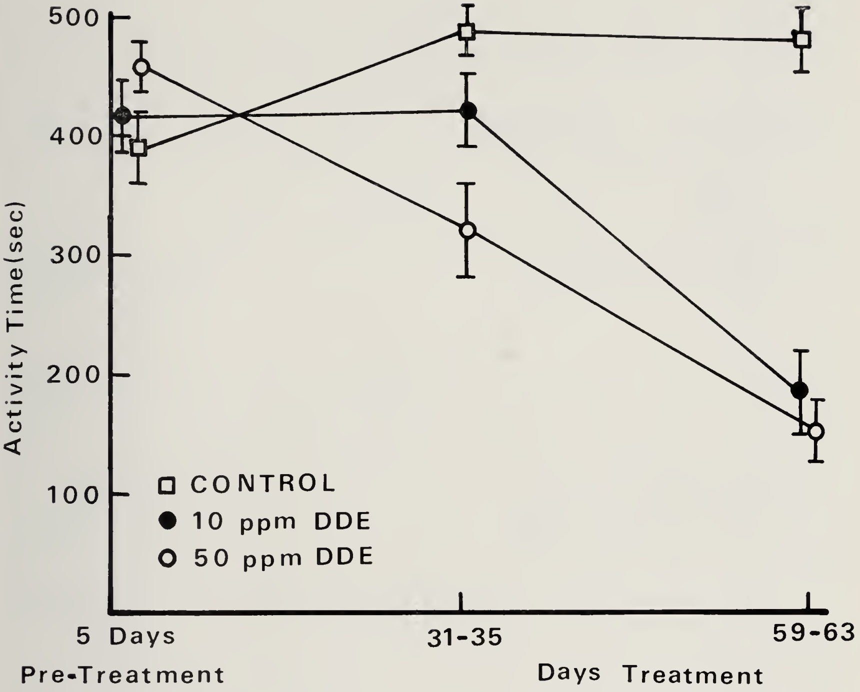

FIG. 1. Mean total courtship activity time displayed by male Ringed Turtle Doves per 12.5-min observation period. The vertical lines indicate ± S.E. of the mean.

reduction in activity time at 31–35 days, and a 67% reduction at days 59–63, when compared to pretreatment activity. The analysis of variance showed: (1) a significant difference among the 3 treatments ($F_{[2,14]} = 6.58$, $p < 0.01$), (2) a significant difference between the 2 time periods ($F_{[1,14]} = 16.51$, $p < 0.005$), (3) a significant difference among the 6 treatment × time period interaction means ($F_{[2,14]} = 4.08$, $p < 0.05$), (4) a significant difference among the five 1-day periods ($F_{[4,56]} = 2.72$, $p < 0.05$), and (5) a significant difference among the 10 time period × 1-day period interaction means ($F_{[4,56]} = 3.81$, $p < 0.01$). In summary, Figure 1 shows that the controls maintained a high level of activity time for both observation periods while the treated birds showed a marked reduction in activity time at the 59–63-day period. These results indicate that the difference in activity time between the 2 observation periods was due to the DDE treatment over time.

The mean bow-coo frequency by male Ringed Turtle Doves treated with the DDE diet was also reduced (Fig. 2). When compared with their pretreatment values, the bow-coo frequency of control males increased 19% at

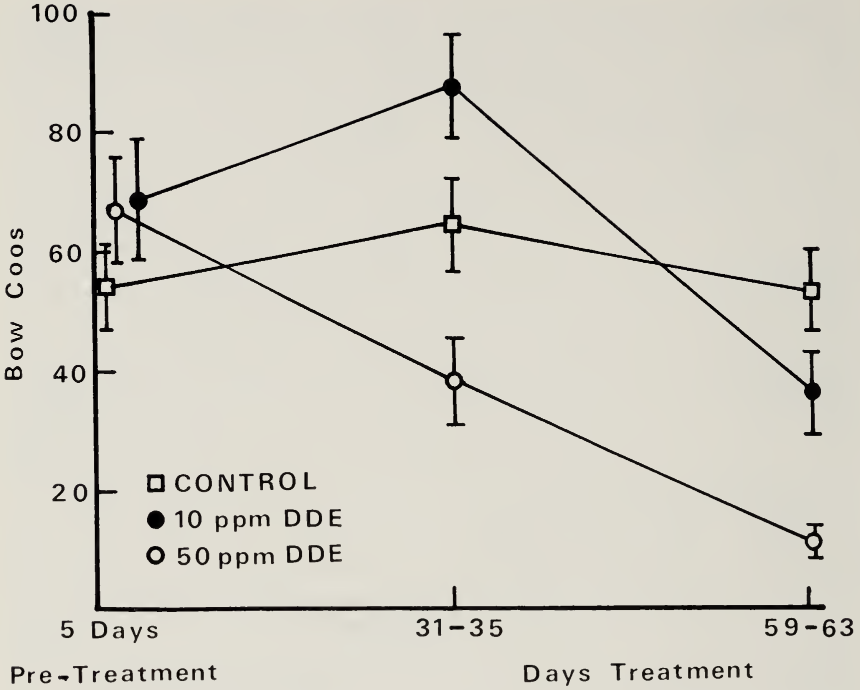

FIG. 2. Mean number of bow-coos performed by male Ringed Turtle Doves per 12.5-min observation period. The vertical lines indicate ± S.E. of the mean.

31–35 days and then decreased 1% at 59–63 days. The 10-ppm group also increased (26%) at 31–35 days; however, after 59–63 days, the 10-ppm treatment had begun to affect bow-coo frequency causing a reduction to 53% fewer bow-coos than were observed during pretreatment observations. The 50-ppm group had a reduced bow-coo frequency of approximately 43% during the first observation period and 84% during the second. The analysis of variance showed a significant difference among the 3 treatments ($F_{[2,14]} = 3.58$, $p < 0.06$) and a significant difference between the 2 time periods ($F_{[1,14]} = 11.05$, $p < 0.01$). The difference between the 2 observation periods indicates that, as DDE residues were increasing in treated birds, bow-coo frequency was decreasing. Figure 2 shows that all groups performed fewer bow-coos at 59–63 days than they did at 31–35 days, but the greatest changes in bow-coo frequency were shown by the DDE-treated groups.

For this study, total activity time, rather than the frequency of bow-coos, was probably a more sensitive index to the effects of the treated diet. Whereas bow-coos are only an early segment of courtship behavior displayed by male

TABLE 1

PERCENT BODY WEIGHT LOSS OF RINGED TURTLE DOVES DURING THE STUDY (0–63 DAYS)

Dietary DDE treatment	N	Males Mean percent body weight loss (S.E.)	Females Mean percent body weight loss (S.E.)
0 ppm	6	6.0 (3.4)	5.3 (3.7)
10 ppm	6	7.7 (2.7)	11.7 (6.2)
50 ppm	5	12.5 (10.6)	14.1 (7.9)

Ringed Turtle Doves, total activity time took into account all types of courtship behavior occurring during the observation period, such as nest site selection, wing-flipping, hetero-preening, billing, driving, bow-cooing, and copulation. The fact that male Ringed Turtle Doves could bow-coo infrequently during the observation period but still score very high in total time spent in courtship activity explains why our control birds showed a 1% decrease in bow-coo frequency at 59–63 days and yet had an increase of 23% in activity time during the same period (Figs. 1 and 2).

Body weight losses for both the male and female Ringed Turtle Doves are given in Table 1. All birds tended to lose weight during the study. A small amount of weight loss during isolation seems to be normal. We have usually observed this effect in our laboratory when we have isolated doves for any extended period of time. Although the doves fed 50 ppm DDE weighed somewhat less than others at the termination of the experiment, group differences were not statistically significant.

Brain and whole-body DDE residues, along with lipid values, are given in Table 2. Small amounts of Aroclor 1254-like residues, which could have accumulated from small amounts of background contamination in the feed, were also found in all birds. Although there may be a possibility of PCB's acting synergistically with DDE, the levels found in the different treatment groups, including controls, were probably too low (0.80 to 0.86 ppm wet weight) to affect the results. The percentage whole-body lipid in the male Ringed Turtle Doves was significantly ($p \leqslant 0.05$) reduced by the diets contaminated with DDE. The standard errors for whole-body lipids were 0.5, 1.2, and 1.3 for the controls, 10-ppm DDE and 50-ppm treatment groups, respectively. Thus, DDE treatment not only reduced the percentage whole-body lipid found in male Ringed Turtle Doves, but it also increased the within-treatment variance of percentage whole-body lipids. The percentage lipid in brain tissue, not included in the whole-body lipid determination, was constant regardless of treatment (Table 2).

TABLE 2

DDE RESIDUES FOUND IN MALE RINGED TURTLE DOVES AFTER 63 DAYS OF DIETARY TREATMENT

Dietary DDE treatment	N	Brain ppm wet weight (S.E.)	Brain ppm lipid weight (S.E.)	Brain Percent lipid (S.E.)
0 ppm	6	0.09 (0.02)	1.6 (0.3)	6.7 (0.2)
10 ppm	6	2.9 (0.5)	40.9 (7.1)	7.0 (0.0)
50 ppm	5	7.6 (0.9)	116 (14.6)	6.6 (0.2)

Dietary DDE treatment	N	Whole body ppm wet weight (S.E.)	Whole body ppm lipid weight (S.E.)	Whole body Percent lipid* (S.E.)
0 ppm	6	0.39 (0.16)	1.8 (1.8)	13.4^a (0.5)
10 ppm	6	37.8 (4.4)	446 (108)	9.9^b (1.2)
50 ppm	5	153 (25.2)	2477 (1107)	8.4^b (1.3)

* Those % lipid values with different letters as superscripts are significantly different from each other ($p \leqslant 0.05$)—Duncan's New Multiple Range Test.

DISCUSSION

Throughout this study, we continued the exposure to the DDE-treated diet and did not assess whether or not or how long it would take for the birds to recover from the treatment. It is not common for a population of wild birds to be continually exposed to levels of DDE of the same magnitude as were used in our experiment. Yet, it is not unusual for wild birds to be exposed to levels of DDE equal to our 10-ppm (dry weight) contaminated diet for fairly long periods of time during some part of the year and build up body residues equal to or greater than those found in our 10-ppm birds (Table 2). Some examples are Brown Pelicans (Keith et al. 1970), Prairie Falcons (*Falco mexicanus*) (Enderson and Berger 1970), and Peregrines (*Falco peregrinus*) (Lincer et al. 1970, Cade et al. 1968, Enderson and Berger 1968).

This study supplements our earlier work (Haegele and Hudson 1973) by showing that dietary DDE at low levels can adversely affect sexual behavior and performance in Ringed Turtle Doves. The 40-ppm DDE-contaminated diet in our earlier study caused a significant delay in renesting and an abundance of single-egg clutches. This delay in renesting could have been caused by a reduction in courtship behavior displayed by the male Ringed Turtle Doves treated with DDE.

The 1-egg clutches observed in our 1973 study could also have been caused by behavioral effects of DDE. Courtship and nest building behavior are very important in stimulating the female Ringed Turtle Dove to ovulate and lay eggs (Lehrman et al. 1961, Lehrman 1965). The DDE diet could have reduced male and female Ringed Turtle Dove courtship behavior to a level that was insufficient to cause normal egg laying. Embryo development was absent in the eggs from single-egg clutches after 18 days of incubation (14 days is the normal incubation period); this suggests that the pairs of doves with infertile single-egg clutches never copulated before egg laying. The fact that these birds may not have copulated could be related to DDE effects on reproductive behavior.

The reduced intensity of male Ringed Turtle Dove courtship behavior observed in this study supports the suggestion that DDE accumulation in wild birds is causing aberrant reproductive behavior and thereby reducing fecundity. Gress (1970) reported what he felt was aberrant reproductive behavior in Brown Pelicans, and he believed that the presence of large amounts of chlorinated hydrocarbon residues found in pelican tissue should be considered as a potential cause of this erratic behavior. Snyder et al. (1973) suggested that the disturbed behavior they observed in Cooper's Hawks might also have been linked to DDE residues present. Switzer et al. (1971) felt that the cause for the low reproductive success of their study population of Common Terns (*Sterna hirundo*) was attributable to aberrant reproductive behavior caused by DDE residues. Koeman et al. (1972) state that in their study 60% and probably 80% of the reproductive failures were caused by some intrinsic derailing factor in the Sparrow Hawk's (*Accipiter nisus*) breeding process. They felt this might be caused by DDE residues the birds were carrying.

All of the above examples suggest that some wild populations of birds contaminated with DDE are showing altered reproductive behavior and consequent reproductive failure. Judging from the effects dietary DDE had on courtship behavior of male Ringed Turtle Doves in our study, it is likely that DDE is affecting behavior in wild birds such as those mentioned above. The subsequent degree of reproductive inhibition may depend on the importance and complexity of courtship behavior for different species. Whether other pollutants may contribute to these reproductive failures cannot be answered without further study, but DDE may be the most important factor.

A possible mechanism for DDE effects on reproductive behavior has been suggested by Peakall (1970). He found that Ringed Turtle Doves treated daily with DDT had significantly lower estradiol levels in the blood associated with increased hepatic enzyme activities. Since DDE is also a microsomal enzyme inducer (Conney et al. 1967), it could be influencing reproductive behavior in the same manner as DDT. However, no study to date has demonstrated a sequential occurrence of elevated hepatic microsomal enzyme activity, reduced circulating levels of sex hormones, and altered reproductive behavior in the same birds.

The results of this study demonstrated that environmental levels of dietary DDE can lower the intensity of courtship behavior in male Ringed Turtle Doves. Therefore, we feel that DDE might indeed be a significant factor contributing to reproductive failure in wild birds.

SUMMARY

The effects of p,p′-DDE on the intensity of male Ringed Turtle Doves' courtship behavior were determined for dietary levels of 10 ppm and 50 ppm (dry weight). Pairs of doves were placed in cages for 12.5 min on 5 consecutive days for behavioral observation before dietary treatment and for periods 31–35 and 59–63 days after initiation of the treated diet. Total amount of time spent displaying courtship behavior and bow-coo frequency were analyzed through video tape recording.

The 50-ppm diet caused a reduction in total courtship activity time and in bow-coo frequency for both posttreatment observation periods. The 10-ppm diet did not affect bow-coo frequency and total activity time at 31–35 days but did cause a significant reduction in courtship behavior during the 59–63-day observation period. The DDE residues found in the male Ringed Turtle Doves showing reduced courtship behavior were lower than residues found in many species of birds that have shown reproductive failures in the wild.

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MOVEMENTS OF THE GREAT-TAILED GRACKLE IN TEXAS

KEITH A. ARNOLD AND LEON J. FOLSE, JR.

The Great-tailed Grackle (*Quiscalus mexicanus*) is an interesting species in that it has expanded its distribution rather dramatically in the 20th century (Selander and Giller 1961, Oberholser 1974). The species has received much attention, including systematics (Selander and Giller 1961), vocal behavior (Kok 1971), food habits (Davis and Arnold 1972), and growth rate and thermoregulation (Gotie and Kroll 1973). Little information is available on the movements of this grackle, especially in the area of its range expansion. This paper is intended to present such information for the Great-tail in the central parts of Texas.

METHODS AND STUDY AREA

Arnold initiated a banding and color-marking program in April 1967, as part of a study on the population dynamics and social structure of the Great-tailed Grackle. Except for minor interruptions, this banding program has been continued by Arnold and his graduate students to the present. Emphasis in mode of capture has varied from one year to the next. Thus most bandings of nestlings took place in the breeding seasons of 1967, 1968, 1971, and 1972, while mass banding at roosts with a light trap was limited to 1969, 1970, and 1971. Decoy traps were used every year, generally from September through March since 1969, but were used through July in 1973 and used continuously since September 1973. This latter method caught relatively few Great-tails until November 1973, when the permanent trap began to catch this species almost exclusively.

We banded most birds in the area of Bryan-College Station, Texas. However decoy traps have been operated up to 15 km from these cities, and a light trap was used at a roost approximately 17 km west of Bryan.

The area encompassed by our banding operations included the Bryan-College Station metropolitan area, flood plains of the Brazos and Navasota rivers, plus many hectares that were originally post oak (*Quercus stellata*) savannah and blackland prairie (see Coon 1974, for detailed description of the study area). The Brazos River lowlands were used primarily for production of cotton (*Gossypium hirsutum*), grain sorghum (*Sorghum bicolor*), and soybeans (*Glycine max*), while much of the uplands and the Navasota River lowlands was used for pasturing livestock (Coon 1974).

We grouped our recoveries for analyses by location of recovery, sex, and age at banding. The age groups differ between males and females, but these differences reflect breeding characteristics of the birds. For males in the spring, second year birds can be distinguished from older birds by plumage characteristics, and these second year males do not breed. Among females in the spring, second year birds are difficult to distinguish from older birds. However, these second year females do nest along with the older females. Consequently, we class second year males as immatures, but second year females as adults.

Kruskal-Wallis statistical tests were from Conover (1971) and are based on ungrouped

TABLE 1

NUMBER OF BIRDS BANDED BY YEAR IN EACH SEX-AGE CATEGORY

	1967	1968	1969	1970	1971	1972	1973	1974	Total
Males									
Adults	97	78	114	288	131	8	71	239	1026
Immatures	30	19	37	25	76	1	28	894	1110
Nestlings	42	51	18	6	61	26	–	–	204
Females									
Adults	109	58	106	286	542*	113	121	507	1842
Immatures	122	23	22	49	–*	2	249	1207	1674
Nestlings	50	34	12	2	53	32	–	–	183
Totals	450	263	309	656	863	182	469	2847	6039

* No attempt made this year to age females in roost-trapping.

data, and other statistical tests were from Steel and Torrie (1960). We used a .05 significance level in all statistical tests.

RESULTS

Between April 1967 and December 1974, we banded over 6000 Great-tailed Grackles within the study area (Table 1). We received 117 recoveries, of which 60 were from outside the study area (Fig. 1). All recoveries but one are from Texas. The exception is a winter-banded adult male recovered the second spring after banding in Oklahoma City, Oklahoma. These recoveries may be roughly grouped into 3 categories: (1) those recovered south (S) of the study area in the drainage of the Brazos River and adjacent portions of the coastal plain; (2) those recovered to the west and northwest (WNW) of the study area, generally within the drainage of the Brazos River; and (3) those recovered to the north (N) of the study area and outside the drainage area of the Brazos River. The remaining 57 recoveries were within the Bryan-College Station area (BCS).

The recoveries from the different areas did not occur at the same times of year (Fig. 2; Kruskal-Wallis test, based on days to recovery after 1 December). Basically, those recoveries from the south (S) occurred in late winter or spring migration, while those from the remaining areas were made at other times of the year.

There were no significant differences among areas, between the sexes or between birds banded as adults and fledglings in mean time to recovery after banding. Mean time to recovery of birds banded as nestlings was less than

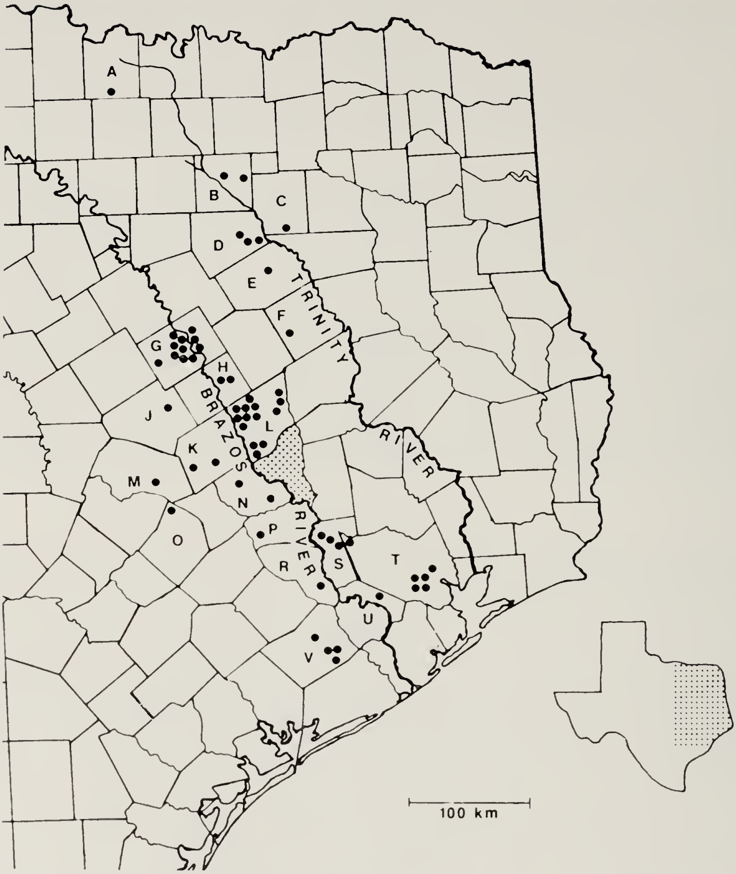

FIG. 1. Locations of Great-tailed Grackles recovered in Texas outside the study area (stippled). Counties as indicated by letters: A, Montague; B, Dallas; C, Kaufman; D, Ellis; E, Navarro; F, Freestone; G, McLennan; H, Falls; J, Bell; K, Milam; L, Robertson; M, Williamson; N, Burleson; O, Bastrop; P, Washington; R, Austin; S, Waller; T, Harris; U, Fort Bend; V, Colorado. Insert shows relative portion of Texas depicted on map.

that for birds banded when older (Kruskal-Wallis tests, based on days to recovery after banding).

Recoveries were classified by location, sex, and age at banding (Table 2). An analysis of variance with these 3 factors revealed no significant variation with respect to sex and age upon percent of banded birds recovered. There was significant variation in percent recaptures among the recovery areas. Single degrees of freedom comparisons showed that percent recoveries were

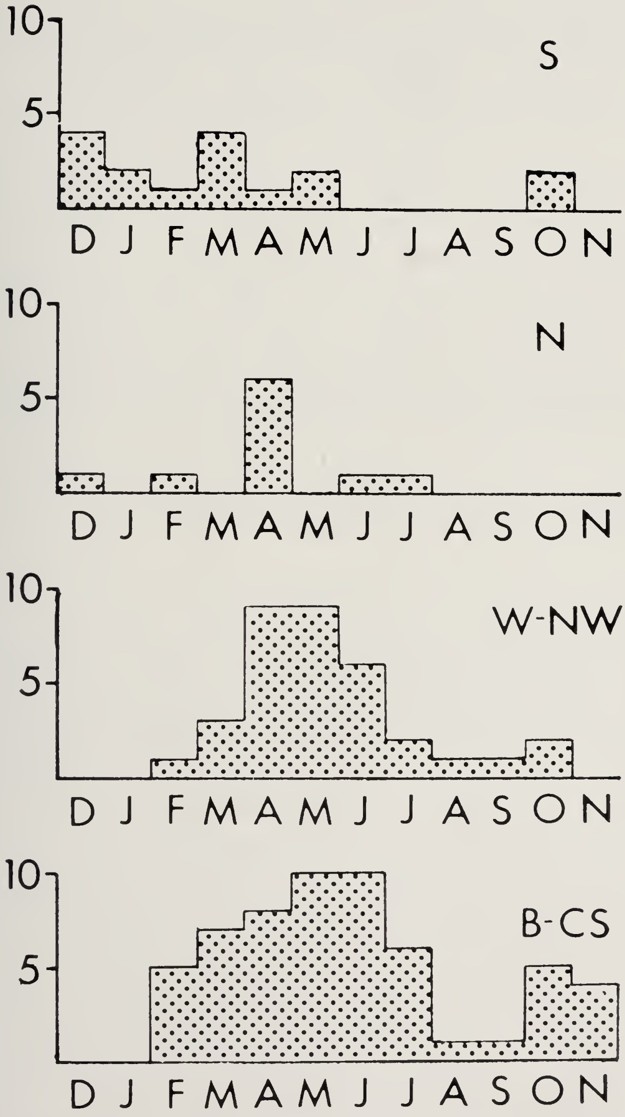

FIG. 2. Recoveries of Great-tailed Grackles by month and location. (See text for locations.)

TABLE 2

NUMBER AND PERCENT OF TEXAS RECOVERIES BY REGIONS

	North*	Northwest & West	South	Bryan-College Station	Total
Males					
Adults	3 (.29)**	6 (.58)	2 (.20)	13 (1.27)	24 (2.34)
Immatures	1 (.09)	8 (.72)	6 (.54)	12 (1.17)	28 (2.52)
Nestlings	0	1 (.49)	0	4 (1.96)	5 (2.45)
Females					
Adults	5 (.27)	13 (.71)	6 (.33)	16 (.87)	40 (2.18)
Immatures	1 (.06)	4 (.24)	2 (.12)	7 (.42)	14 (.84)
Nestlings	0	2 (1.09)	0	4 (2.19)	6 (3.28)

* Includes the Oklahoma recovery.
** Percentages are based upon numbers originally banded in each sex-age category from 1967 through 1974.

greatest in Bryan-College Station with WNW next, followed by S and N which were indistinguishable from each other.

DISCUSSION

The Great-tailed Grackle has expanded its range northward into Kansas in the past few years and has become established there as a summer resident (Schwilling 1971). In this northward expansion, the status of the species has changed dramatically in central and northern Texas (Davis 1940, Arnold 1973). These northern Texas populations are apparently partially migratory as evidenced by recoveries in this study and by the dramatic increase in numbers of this species that occur in the local fall and winter roosts.

Our banding studies demonstrate southward shifts in blackbird populations of the Bryan-College Station, Texas area in mid-winter with replacement by populations from the north; this is indirectly indicated by the lack of recaptures for Great-tails banded in the earlier part of the winter even though large numbers of this species continue to be captured. These population shifts, which generally coincide with the onset of the severe portion of our winter, do not always occur in mild winters. We know of several winter roosts in the Dallas-Ellis county area that have Great-tails associated with them, so not all Great-tailed Grackles migrate south from that area. We have a number of recaptures and sightings in the Bryan-College Station area of color-marked birds or birds marked during the breeding season or fall and early winter that were made in the severe portion of the winter. Further, at least 2 Great-tails have been recovered in the Dallas-Ellis county area during the winter months subsequent to their banding on the study area in a preceeding October. It is not clear whether these birds represent an age class with migratory patterns different from other age classes or whether this represents a failure to migrate due to mild climatic conditions; only further recoveries will resolve this point. The latter possiblility is likely since 2 winters occurred (1969–70 and 1973–74) without a mid-season population shift for Great-tailed Grackles in our study area.

We believe that the Brazos River valley serves as a natural migration route, based on recoveries south and west-northwest of our area. The grackles recovered to the north, however, are in the Trinity River drainage. Area N (Fig. 1) lies at the eastern edge of the post oak savannah and black land prairie regions and at the western edge of the East Texas pinelands. As the Great-tail is essentially a bird of the open country, it appears to us that the southward migration from the Dallas-Ellis county area represents avoidance by this grackle of unsuitable vegetation zones. Recoveries from Navarro and Freestone counties, intermediate in geographic position, support this idea. The presence of livestock operations and extensive growing of grain sorghum in the Brazos River valley may offer attractive food sources to flocks of migrating Great-tails.

Two female grackles recovered to the south of Bryan-College Station represent another problem; both were recovered in May (one each in Waller and Washington counties). The date is late for migrant grackles, but the locations are geographically intermediate between wintering areas on the coastal plain and the study area. As one of the females was banded as an adult the previous May, the possibility exists that the bird had changed breeding areas.

Many of the birds recovered from the north and west-northwest were banded in September and October as immatures. We do not know whether these birds were hatched locally or were migrants. Some of these recoveries must represent dispersal of young birds in a species that is rapidly expanding its range. This is supported by recoveries of 3 birds banded as nestlings on the study area: a male and a female recovered in Robertson County, and a female recovered in McLennan County, both northwest of our study area.

It is possible that birds entering the local roosts in late summer and early fall (August to October) may represent the coalescing of adjacent breeding populations with those of the Bryan-College Station area; however additional studies are needed to clarify this. We know that many breeding colonies of this species exist in surrounding communities, but Great-tails are difficult to observe in those areas during the winter months. Further recoveries will clarify our knowledge of the migration of Great-tailed Grackles.

SUMMARY

Between April 1967 and December 1974, over 6000 Great-tailed Grackles were banded in Brazos County, Texas. Through September 1976, 117 recoveries were reported, with 60 from outside of Brazos County. These outside recoveries were grouped into 3 geographic areas: birds recovered to the south that represent a mid-winter population shift; those recovered to the west and northwest, representing migration along the Brazos River valley; and birds from the north that may represent migration along the edge of the East Texas pine lands. These latter 2 groups probably also include young birds dispersing away from breeding colonies in the study area.

ACKNOWLEDGMENTS

This study is a part of a continuing project of the Texas Agricultural Experiment Station (TAES contribution number TA 12114). We thank the following persons for their help in banding the grackles: W. R. Davis II, D. W. Coon, R. F. Gotie, R. Klein, R. Summers, J. C. Newman, A. L. Barr, M. T. Hanson, and C. E. Grue. R. D. Slack and B. W. Cain critically reviewed the manuscript. C. S. Robbins provided many useful suggestions.

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GENERAL NOTES

Tropical Screech Owl nest defense behavior and nestling growth rate.—The Tropical Screech Owl (*Otus choliba*) is a common and wide spread resident in the Neotropics from Costa Rica to Argentina. General accounts of it are given by ffrench (A Guide to the Birds of Trinidad and Tobago, Livingston Publ. Co., Wynnewood, Pa., 1973), Haverschmidt (Birds of Surinam, Oliver and Boyd, Edinburgh, 1968) and Wetmore (The Birds of the Republic of Panama, Part 1, Smithsonian Institute Press, Washington, D.C., 1965). Although there are more than 30 owls, world wide, in the genus *Otus*, little has been published on their nestling behavior and growth, except for *Otus asio*, *O. trichopsis*, and *O. flammeolus* by Bent (U.S. Natl. Mus. Bull. 170, 1938). There is also a note on nestling screech owl behavior and growth by Sumner (Condor 30:333–338, 1928). References indicated below for soft part colors are from Smithe (Naturalist's Color Guide, The American Museum of Natural History, New York, 1975).

This note presents information on the defense behavior of adults and nestlings, and the growth rate of the latter, from observations made at a nest in a rural residential area 30 km south of Caracas, Venezuela.

The nest was located in an abandoned wooden box, a cube of about 40 cm wedged into the lowest branches of a pardillo tree (*Cordia alliodora*), 3 m from the ground. The box was in an angled position and about half of one side was open. The owl's choice of such a nest site probably reflected the lack of suitable natural cavities in the area, a region of fallow, grassy hillsides with only a few scattered trees.

On 25 February 1975 the nest contained 2 eggs (smooth, white, and nearly spherical; 33.3 × 30.5, 32.7 × 29.9 mm) which rested in the lowest corner of the box on some weathered fragments of cloth. The cloth was probably left over from the former tenant, a pet monkey. To stop tree climbing predators I fastened a 1 m wide piece of aluminum around the tree trunk.

Nestling period.—By the evening of 12 March both nestlings had hatched and their natal down was completely dry. They weighed 17.0 and 13.5 g. I believe the larger one had hatched on the previous day. They were covered with white down, sparser on the dorsal area. The legs and feet were pale pink (color 7) and the bills pearl gray (color 81) with a white egg tooth. The nestlings' eyelids were closed, but on the 6th day of observation the smaller bird's eyelids were slightly open, the larger nestling's eyelids were not fully open until the 10th day. At first the irides were cream color (color 54), they did not become nearly spectrum yellow (color 55) until about the 19th day.

The nestlings' bills had changed by the 4th day to pale neutral gray (color 86) and the egg tooth was greatly diminished; the legs and feet were now almost translucent white. Feather sheaths were clearly visible on the larger nestling on the 6th day on its spinal, alar, and ventral tracts. Rictal bristles appeared on both birds in 2 weeks. By the 16th day their white natal down (protoptile) had generally changed to pale neutral gray (color 86) and white banded down (mesoptile) and their primaries and secondaries were beginning to expand. The central rectrices started to emerge from their sheaths on the 26th day.

A pesola scale was used to weigh the nestlings daily (except days 21 and 28) at about 18:00, before their first nightly feedings. The fairly constant increase of weights is shown in Fig. 1. The decreased weights recorded on the evenings of observation days 14 and 16 might be indicative of a lesser quantity of food brought to the nestlings on the previous nights. Weight losses on days 23, 25, and 27 possibly signal the approaching end of the nestling period.

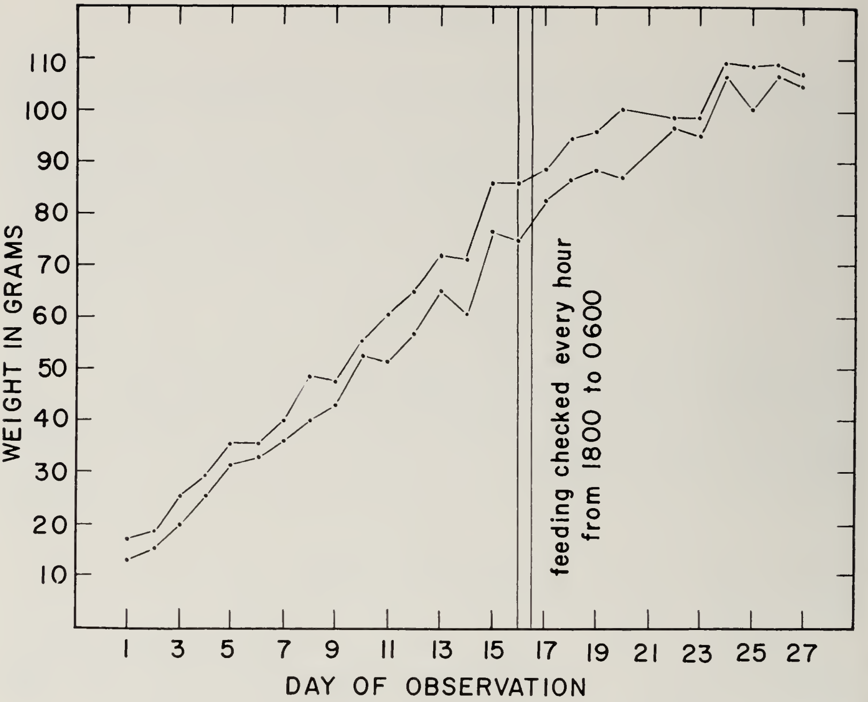

FIG. 1. Daily weights of Tropical Screech Owl nestlings.

The nestling owls never regurgitated food on being handled; therefore the only food seen was that encountered in the nest. At different times I found all or parts of 2 mice, 1 rice rat (*Oryzomys*), 2 cockroaches (*Periplaneta* and *Blaberus*), 1 locust (*Schistocerca*), 1 very small snake (*Helminthophis*) and 1 earthworm (*Lumbricus*). On the 27th day I collected the only pellet found in the nest. It was moist, measured 2 × 1.25 cm, and contained insect and bone fragments too small for identification. Nest sanitation was poor only on the first 2 days; thereafter the nest was kept clean. Ectoparasites found on the nestlings were 1 louse fly *Icosta* (= *Lynchia*) *americana* and at various times 4 maggots were found attached to the nestlings' ventral sides. One maggot has been tentatively identified as *Neomusca* (= *Philornis*) *falsificus.*

An adult owl brooded the nestlings all day through the 6th day, leaving only after dark. However after a cessation of brooding for 3 days, an adult stayed all day in the nest for a single day, the 10th. I was unable to establish whether 1 or 2 owls attended the nest. Presumably the nestlings left the nest normally during the night of 8 April at the ages of about 28 and 29 days. That night around 02:00 there was much low calling by an adult owl. The next morning the nest box was empty and I could not locate the young owls in the area.

Defense behavior by the adult.—The first time that the nest box was examined, during the day, an adult owl was incubating the eggs and it puffed up its feathers and erected its "ear tufts." Then it flew out of the box onto the lowest limb of a tree 5 m distant

FIG. 2. Tropical Screech Owl nestling on the 26th day showing black feathers on eyelids.

from where it watched the nest. On subsequent nest examinations, in addition to ruffling out its plumage and erecting its "ear tufts" the adult owl snapped its bill, swayed back and forth sideways, and raised and lowered its body by flexing its legs. During the first examination after the nestlings had hatched, the brooding owl threw itself flat on its back over the nestlings and raised its legs with claws extended toward me. Gradually, however, the attending adult owl appeared to become accustomed to the daily visits and soon I was able to easily remove and replace the nestlings from under it without causing more than a token feather ruffling.

On the 16th day I examined the nest for food every hour on the hour from 18:00 to 06:00. At 22:00 while I was at the nest, an owl struck me quite hard on the arm, leaving 3 small bloody marks from the claws' impact in a triangle roughly 3.5 to 5 cm. In no way was this a serious wound, it is mentioned only as a measure of the probable size of grasp of an adult *Otus choliba.* An owl struck me again, twice at 01:00 and once more at 03:00, as well as on another night at about 21:00. I heard no sound of the bird's approach before the strikes nor was I able to see an owl in the area before climbing to the nest.

Defense behavior of the nestlings.—Nestling defense behavior may have started on the first day of examination when they made tiny squeaking sounds or distress calls on being weighed. They both continued their vocal protests with increasing vigor as they grew. On the 6th day, the smaller nestling gripped my glove with its bill and hung on tenaciously. The larger nestling began bill snapping on the 11th day; the smaller bird 2 days later. The more active nestling, the smaller one, dug its claws into my exposed finger on the 16th day of examination. That same day, for the first time, both nestlings fluffed up their downy feathers and crouched down deeply on their tarsi at my approach. The next day they both began flapping their wings on being handled. On the 23rd day the larger nestling threw itself on its back with its legs raised and claws extended, exactly as the previously described adult behavior.

Most of the nestling owls' day was spent sleeping pressed tightly together. At 3 weeks they began sleeping facing the open entrance of the nest box. It was then that I first saw, on looking into the box, what appeared to be 2 pairs of large eyes staring at me, when, in fact, the nestlings had their eyes closed in sleep. Careful examination revealed that the eyelid skin was light pearl gray (color 81) with a tuft of sparce white feathers near the outer corner, and that centrally on the lid there was a prominent area of short black feathers. The effect of this pattern was to make the eyelids, when closed and viewed in the weak light of the nest, excellent mimic eyes (Fig. 2). This appears to be an adaptation for startling a predator who might look into the nest hole in daylight, after the nestlings are no longer brooded by an adult owl.

Summary.—This paper presents observations of the nesting of the Tropical Screech Owl (*Otus choliba*) and discusses development of the nestlings, their food, defense behavior of the adult and the nestlings, as well as a description of a probable warning color pattern development of eyelid feathers as a defense strategy.

Acknowledgments.—I wish to thank Paul Schwartz for reading the first draft of this paper and for making a number of helpful criticisms of it. I am also indebted to Dr. Francisco Fernández Yépez for identification of the insect food items, and to Dr. Andrew J. Main, Jr. and Dr. T. H. G. Aitken for identification of the ectoparasites.—BETSY TRENT THOMAS, *Apartado 80450, Caracas 108, Venezuela.* *Accepted 1 Aug. 1976.*

Three more new specimen records for Guatemala.—During continuing studies of the avifauna of the Pacific lowlands of Guatemala near La Avellana, Santa Rosa Department (Dickerman, Wilson Bull. 87:412–413, 1975), I collected 3 more species of birds not previously taken in the country. During April and May 1975 Richard R. Viet and in April 1976 Alexander Brash and Thomas Will participated in the field work. Collecting was done under permit from the Departmento de Vida Silvestre, Instituto Nacional Forestal of Guatemala and specimens are deposited at the American Museum of Natural History.

Calidris bairdii, Baird's Sandpiper.—Although Baird's Sandpiper is a regular migrant at least in interior areas of Mexico, and winters in South America, there are few specimen records from Central America, and to date none from Guatemala. On 21 April 1976 Thomas Will identified 2 Baird's Sandpipers and I collected one, on mud flats between the villages of La Avellana and Monterrico, Santa Rosa Department. The birds were found in the afternoon following a major rainstorm the night of 20–21 April that continued to mid-morning of the 21st. The specimen collected, an immature female, weighed 33.3 g and was moderately fat.

Calidris alpina, Dunlin.—An adult male Dunlin, well advanced in prealternate molt, was taken about 21:30, 6 April 1976 from nets set on the same mud flats mentioned above. This is apparently the southernmost specimen record for the species in the New World. Its wing chord measures 115 and the culmen 36.5 mm; the specimen was identified by John Farrand, Jr. as *E. a. pacifica* based both on measurements and on the deep coloration of the fresh alternate plumage.

Sterna albifrons, Least Tern.—Although the AOU Check-list (1957) records *S. a. browni*, the race that nests along the coast of California and Baja California, as probably ranging south to Guatemala in winter, Land (Birds of Guatemala, Livingston Publ. Co., Wynnewood, Pa., 1972:112) knew of no specimens of the species from Guatemala. Accordingly he placed the species name in brackets indicating a hypothetical status. He mentioned August and September sight records for both coasts. We have seen 1 to 3 Least Terns on the following dates at the mouth of the Rio Los Esclavos, Santa Rosa Department: 2 and 4 May 1974, 24 April 1975 and 29 April 1976. An adult collected 24 April 1974 was identified by John Farrand, Jr. as *S. a. antillarum*, the race of central and eastern United States and of the Caribbean region.—Robert W. Dickerman, *Dept. Microbiology, Cornell Univ. Medical College, 1300 York Avenue, New York 10021.* *Accepted 20 Oct. 1976.*

Feeding behavior of two hummingbirds in a Costa Rican montane forest.—Between the end of April and mid-June 1974, I made observations on hummingbirds feeding in primary forest between 1480 and 1680 m at Monteverde on the Pacific slope of the Cordillera de Tilaran of Costa Rica. At this level the forest is transitional between the Lower Montane Rain Forest and the Lower Montane Wet Forest (Holdridge, Life Zone Ecology, Tropical Science Center, San Jose, Costa Rica, 1967). Within the shade of this forest the 2 most abundant resident hummingbirds were the Purple-throated Mountain Gem (*Lampornis calolaema*) and the Guy's Hermit (*Phaethornis guy*). At Monteverde these 2 species largely overlap in habitat and altitudinal range, as they do elsewhere in their geographical range (Slud, Bull. Am. Mus. Nat. Hist. 128, 1964), but I observed no overlap in the flowers visited for nectar (Table 1). These hummingbirds also differ in size and proportion; the mean measurements, sexes combined, of Guy's Hermit are: weight 5.8 g (N = 3), wing 61 mm (N = 20), culmen 42.5 mm (N = 20) (Wetmore, The Birds of the Republic of Panama, Part 2, Smiths. Misc. Coll. 150, 1968). Those for the Mountain Gem, treating the sexes separately, are: female—weight 4.2 g (N = 2), wing 56 mm (N = 6), culmen 22.1 mm (N = 6); male—weight 5.6 g (N = 7), wing 63 mm (N = 7), culmen 21.4 mm (N = 6) (Feinsinger, Organization of a Tropical Guild of Nectarivorous Birds, Ph.D. thesis, Cornell Univ., Ithaca, N.Y., 1974 for weights quoted). In addition the Guy's Hermit has the typical curved bill of the hermits and the Mountain Gem a straight bill.

Except for 1 tree (*Quararibea* sp.) the feeding records were from vines, shrubs, herbaceous plants, or epiphytes (Table 1). With the exception of the epiphytes, the other plants appeared to be shade tolerant species growing and flowering under unbroken canopy or in the partial shade of mountain paths or very steep slopes. The herbaceous plants flowered at heights of 30–90 cm and the shrubs and vines at 0.6–6 m. Of the 2 epiphytes, *Columnea magnifica* grew sparsely on trees just below canopy level and continued to grow and flower in partial shade on fallen trees; whereas the epiphytic heath (Thibaudiae) grew in large clumps locally dominating its host tree and enjoying full sunlight, but was not seen flowering on fallen trees in partial or heavy shade.

Guy's Hermits were feeding at 3 levels, between 30 and 90 cm when feeding at herbaceous plants, between 1.5 and 2 m when feeding at vines, and just below the canopy at 12–18 m when feeding at the epiphyte. The Mountain Gem fed at shrubs between 60 cm and 6 m, at the epiphyte between 6 and 10.5 m, and at the *Quararibea* tree between 12 and 15 m.

I defined a feeding record as a bout of feeding by an individual hummingbird at 1 plant species. The actual number of flowers visited in a feeding bout varied greatly depending on flower size; thus a record of Guy's Hermit feeding on *Drymonia conchocalyx* would consist of probes into 2 or 3 flowers, while a record of a Mountain Gem at *Palicourea* typically consisted of probes into 20 or more flowers. To attempt to adjust the data to number of flowers visited would distort the results because some nectar

TABLE 1

FLOWER CHARACTERISTICS AND HUMMINGBIRD FEEDING RECORDS

	Plant form	Color	Corolla length[1] (mm)	Width (mm)	*Lampornis calolaema*		*Phaethornis guy*
					♂	♀	
Gesneriaceae							
Drymonia conchocalyx	vine	dark pink	56	10		1*	4
Drymonia sp.	vine	orange	38	8			1
Alloplectus tetragonus	herb	red	44	6			1
Besleria formosa	shrub	orange	16	6	2	15	
Campanaea humboldtii	vine	green	–	6		3	
Columnea magnifica	epiphyte	orange	28	4.5			1
Rubiaceae							
Cephaelis elata	shrub	white†	17	2.0	7	4	
Palicourea lasiorrhachis	shrub	yellow	14	2.5	13	9	
Lobeliaceae							
Centropogon solanifolius	herb	red	43	7.5			2
Musaceae							
Heliconia tortuosa‡	herb	yellow†	34	4.0			2
Bombacaceae							
Quararibea sp.	tree	white	23	2.0	11		
Ericaceae (Thibaudiae)	epiphyte	pink	19	3.0	3	2	
				Total	36	34	11

* Corolla pierced.
† Red bracts.
‡ Taxon H-5 (Stiles 1975).
[1] Corolla lengths measured are the distance from the opening of the corolla tube to the nectar chamber. One typical corolla measured from each species.

sources were more scattered than others and a feeding hummingbird in the forest is more quickly lost to view when feeding on scattered flowers than on the more concentrated ones.

Except for the record of the Mountain Gem piercing the corolla of *Drymonia conchocalyx*, no other hummingbirds were seen feeding at the flowers exploited by the Guy's Hermit within the 1480–1680 m altitudinal limits. Below these altitudes the Violet Sabrewing (*Campylopterus hemileucurus*) commonly fed at *Heliconia tortuosa* and the Stripe-tailed Hummingbird (*Eupherusa eximia*) occasionally did so.

There was more competition for the flowers exploited by the Mountain Gem. The larger clumps of the epiphytic heath were dominated by the Fiery-throated Hummingbird (*Panterpe insignis*), and the Slaty Flower-piercer (*Diglossa plumbea*) also fed at it. The Stripe-tailed Hummingbird was the only other hummingbird seen exploiting any of the nectar sources of the Mountain Gem listed in Table 1. I have 3 records of it feeding at *Palicourea lasiorrhachis*; 2 were below 1480 m. Feinsinger (op. cit.) frequently recorded the Mountain Gem below 1480 m where it defended high density nectar sources in more open habitats of secondary growth and forest edge and competed with several other hummingbird species. The flowers it visited were all different from those listed in Table 1.

There are several differences between the flowers exploited by Guy's Hermit and the Mountain Gem. The 6 hermit flowers are larger, with an average corolla length of 44 mm and a width at the base of the corolla of 7.2 mm. The corollas are curved and colored either orange, red, or dark pink (in *Heliconia tortuosa* the corolla is yellow but the flower is embedded in a red bract). The color of the 6 species at which the Mountain Gem fed are more varied and include pink, orange, yellow, white, and green. The corollas are all straight rather narrow tubes with an average length of 18 mm and a basal width of 3.1 mm. The vine *Campanea humboldtii* is an exception and not included in the above average; its corolla is a large open bell with a width of 30 mm at the mouth. The Mountain Gem feeds at this flower with its whole head inside the bell.

These differences in feeding niche between the Guy's Hermit and the Mountain Gem are generally similar to the differences in Trinidad between the Guy's Hermit and the Blue-chinned Sapphire (*Chlorestes notatus*), a straight-billed forest hummingbird slightly smaller than the Mountain Gem (Snow and Snow, J. Anim. Ecol. 41:471–485, 1972).

Guy's Hermits were not seen defending nectar resources and are evidently "trapline" feeders as are other hermit hummingbirds that have been studied (Stiles, Ecology 56: 285–301, 1975). Mountain Gems, on the other hand, were frequently seen defending their nectar resources against conspecifics. Since the sexual difference in plumage is apparent in this species before the young leave the nest (Skutch, Publ. Nuttall Ornithol. Club 7, 1967) it was possible to separate with certainty the feeding records of the sexes.

The differences in the feeding niches of the sexes (Table 1) reflect the male's dominant behavior over the richer resources. *Quararibea* sp., a tree reaching canopy level, was a concentrated source over which males held feeding territories; they also held territories at the smaller patches of the epiphytic heath, the larger patches being dominatd by the Fiery-throated Hummingbird, and at the shrub *Palicourea lasiorrhachis. Palicourea*, growing to 6 m with an abundance of small flowers, is the biggest of the 3 shrubs at which I recorded the Mountain Gem feeding and the one over which males most frequently held territories. *Palicourea lasiorrhachis* grows in 2 forms; both have similar yellow corollas, but 1 form, common between 1400 and 1540 m, has a red calyx and pedicel; the other form, not noted growing below 1530 m and generally a smaller plant, has a green calyx and pedicel. Nine of 13 records of male Mountain Gems feeding at *Palicourea* were from the red-calyxed form, but only 4 of 9 records of females feeding at *Palicourea* were from this form and 2 of these appeared to be permitted intrusions by a male into his territory (see below). *Besleria formosa* is a much smaller shrub than *Palicourea*, growing to only 90 to 120 cm, and is thinly scattered through deeply shaded forest; typically each shrub has between 4 and 8 open flowers at one time, but more where it grows at path edges. Exploited largely by females, individual shrubs were re-visited on an average of every 10 min. Between feeding circuits females usually perched near one of the larger clumps of *Besleria* from which conspecifics were driven off.

Periodically during a bout of aerial nectar extraction, both male and female Mountain Gems perch to feed at one particular flower, and re-perch at the same flower at each subsequent visit. This was noted when they were feeding at *Besleria*, *Quararibea*, and the epiphytic heath. Skutch (op. cit.) also noted this behavior of Mountain Gems feeding at epiphytic heaths. Observations on the insect searching strategy of Mountain Gems produced 2 records of males hawking for aerial insects from their territorial perches 6 to 12 m up, and 2 records of females searching amongst very dense vegetation, presumably for resting insects, once in the herbaceous layer at 60 to 120 cm and once in the foliage of a small tree at 3 to 6 m. On each occasion the female's wings were audibly hitting the leaves as she hovered amongst them.

While Skutch (op. cit.) has described the nesting of the Mountain Gem and once observed a young male, still being fed by his mother, who was persistently singing a very faint song, he has never heard song from adult males or observed any other courtship activity. During my observations both male and female Mountain Gems were usually silent except for occasional flight notes uttered during longer flights between nectar sources. But on 11 June I observed a male briefly uttering an insect-like song from a perch beside a *Palicourea* shrub at which it was periodically feeding. Another observation suggested that there may at times be a sharing of nectar resources between the sexes. Between 11:40 and 12:00 on 13 June I watched a male Mountain Gem which held a feeding territory over 3 flowering *Palicourea* shrubs. During this time he was observed both feeding at the shrubs and chasing off a female from them; then at 12:00 a female came to one of the *Palicourea* shrubs and began to feed, and between each probe she uttered a short call which I transcribed as *trrrt.* While she fed, the male was perched immediately below her on the same perch he had been using the previous 20 min. He remained perched there throughout the female's feed and once uttered an answering *trrt.* The only other occasion when this call was heard was earlier on the same day when a female, feeding at the same *Palicourea*, was noted as uttering the call between each feeding probe.

Interpretation of this behavior on a single observation would be premature, but it suggests that males may have a special relationship with particular females, and may allow them to share the nectar in their feeding territories. Wolf and Stiles (Evolution 24:759–773, 1970) found that male Fiery-throated Hummingbirds allowed females with whom they mated to feed within their defended territory.

I acknowledge with thanks financial assistance from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. I should also like to thank Dr. Luis Poveda and Dr. Richard Baker for botanical identifications.—BARBARA K. SNOW, *Old Forge, Wingrave, Aylesbury, Bucks, England.* *Accepted 12 Oct. 1976.*

Black-legged Kittiwakes nesting on snowbank.—On 4 July 1975 we found 20 nests of the Black-legged Kittiwake (*Rissa tridactyla*) being built on a snowbank at St. Paul Island, Pribilof Islands, Alaska (Fig. 1). The snowbank, approximately 10 m high, 100 m long and sloping at an angle of 75°, was blocking access to an area of south-facing cliff just east of Southwest Point. More Black-legged Kittiwakes and several other species of seabirds were nesting on the cliffs on either end of the snowbank.

The nests on the snowbank were not noted on 28 June, the date of the previous visit to the area. During the next 10 days after 4 July, the nests disintegrated and fell as the snow melted. No eggs were seen nor were the adults noted incubating. These nests were built relatively late in the breeding season, as the first eggs of this species on the island were seen on 27 June. On 7 July 85% of the Black-legged Kittiwake nests in a nearby study area were being incubated.

It is unclear whether this use of a snowbank as a nest substrate was the result of site tenacity on the part of the kittiwakes or of the lack of suitable alternative nest sites. Sealy (Auk 92:528–538, 1975) discusses a similar situation in which Least Auklets (*Aethia pusilla*) and Crested Auklets (*A. cristatella*) on St. Lawrence Island laid eggs on snow. Snow nesting of the auklets was restricted to those birds faithful to nesting habitat that remained snow covered until mid-July. Belopol'skii (Translated from Russian book *Akademiya Nauk SSSR, Karel'skii filial.* U.S. Dept. of Commerce 61-11487, p. 118, 1957) states that Herring and Great Black-backed gulls (*Larus argentatus* and *L. marinus*)

Fig. 1. Black-legged Kittiwakes building nests on a snowbank, St. Paul Island, Alaska, 4 July 1975.

nesting on Kharlov Island in the Barents Sea occasionally build nests on snow, although the majority of pairs wait until the snow has melted.

The support of contract number 03-5-022-72 from the National Oceanic and Atmospheric Administration to the senior author is gratefully acknowledged. We thank the National Marine Fisheries Service, St. Paul Island Project, for logistical support.—George L. Hunt, Jr., *Dept. of Ecology and Evolutionary Biology, Univ. of California, Irvine 92717 and* Max C. Thompson, *Dept. of Biology, Southwestern College, Winfield, KS 67156.* *Accepted 3 May 1976.*

Evidence of double brooding by American Kestrels in the Colorado high plains.—Double brooding, although considered uncommon in the Falconiformes, has been reported in the Harris Hawk (*Parabuteo unicinctus*) in southern Arizona (Mader, Living Bird 14: 59–85, 1975), Caracara (*Caracara cheriway*; Bent, U.S. Natl. Mus. Bull. 170, 1937), and the American Kestrel (*Falco sparverius*) in Florida (Howell, Florida Bird Life, Coward-McMann, New York, 1932). Captive American Kestrels have also produced second clutches after fledging the first brood (Porter and Wiemeyer, Condor 74:46–53, 1972). Observations at 2 nest boxes in southeastern Colorado during 1975 and 1976 breeding seasons suggest that double brooding also occurs in American Kestrels under natural conditions in a temperate climate.

The boxes, 2 of 25 attached to wooden H-frame towers of a 230 kV transmission line, were approximately 13 km SSE of Ellicott, El Paso County, Colorado. The terrain is rolling sandhills vegetated with yucca (*Yucca glauca*), sand sagebrush (*Artemesia filifolia*), and a variety of herbs and grasses. Insects (Orthoptera, Coleoptera), small lizards, and Horned Larks (*Eremophila alpestris*) were available and used as prey items.

An adult female American Kestrel was flushed from 5 eggs in Box A on 19 April 1975. She was brooding 3 recently hatched chicks on 14 May, and on 5 June, three 3½-week-old young were banded. Two infertile eggs were also removed. The empty box and its heavily muted top on 17 June suggested successful fledging; 1 kestrel was heard but not seen. On 8 August, 4 infertile eggs and a 2-week-old nestling were found in the box.

Four 2½-week-old young were banded on 25 May 1976 at Box B, 7 km northeast of Box A. On 24 June an ASY female, aged according to Parkes (Wilson Bull. 67:194–199, 1955), was captured on 5 warm eggs. A male escaped from the box while the female was being removed for banding. Another male and female were perched on the tower above Box B. The latter male aggressively defended the nest box suggesting that it was the mate of the incubating female. The other 2 kestrels were passive and less wary than the occupying adults, remaining perched throughout the nest visit. Young kestrels tend to remain in the breeding territory of their parents until fall migration (Balgooyen, Univ. Cal. Publ. Zool. 103, 1976). Since the nesting pair tolerated the extra kestrels in and near the nest, we believe that they were progeny of the first nesting attempt by the occupying pair. The 5 eggs were warm on 16 July but cool on 7 August and showed no development when opened. Handling the female during early incubation may have caused a temporary abandonment, killing the embryos, or all eggs may have been infertile.

We realize that our evidence is circumstantial. The 2 passive kestrels at Box B could have been members of an adjacent breeding pair. Nests of American Kestrels have been reported within 34 m of each other (Nagy, Wilson Bull. 75:93, 1963) and no territorial defense was observed between pairs nesting within 60 m (Smith et al., Southwestern Nat. 17:73–83, 1972). However, Balgooyen (op. cit.) found that Kestrels defended their territories from other Kestrels primarily by mutual avoidance rather than repeated defense of borders. It is also possible that the 2 extra birds at Box B were nest helpers (Wegner, Wilson Bull. 88:670, 1976). However, nest helpers at Red-tailed Hawk (*Buteo jamaicensis*; Wiley, Condor 77:480–482, 1972) and Harris Hawk (Mader op. cit.) nests were as aggressive as the nesting pair. The combined evidence from the 2 breeding seasons suggests that double brooding may occur in American Kestrels in southeastern Colorado.

Data for this note were collected as part of a study of impacts of transmission lines on wildlife and funded by Tri-State Generation and Transmission, Denver, Colorado, Colorado Division of Wildlife, and Colorado State University. We thank Clait E. Braun and Ronald A. Ryder for their critical review of this manuscript.—DALE W. STAHLECKER and HERMAN J. GRIESE, *Dept. of Fishery and Wildlife Biology, Colorado State Univ., Ft. Collins, 80523.* *Accepted 22 Feb. 1977.*

Further comments on sexual size dimorphism in birds.—Ralls (Wilson Bull. 88:149–150, 1976) published a note on extremes of sexual size dimorphism among birds. We corresponded on the subject and this was useful to me as I was then writing on the selective basis for the "reversed" dimorphism that exists in birds of prey (Amadon, Raptor Research 9:1–11, 1975). I did not, however, see her manuscript and here offer a few additional comments on the subject. Ms. Ralls observed that Lack (Ecological Adaptations for Breeding in Birds, Methuen, London, 1964:161) quoted me (Amadon, Proc. Am. Phil. Soc. 103:531–536, 1959) as source that the Australian Brown Songlark *Cinclorhamphus cruralis* is an extreme example of sexual size dimorphism in passerine birds, while the hawk *Accipiter fasciatus vigilax* shows the extreme of size divergence among those birds in which the female is the larger size. She adds for both examples: "the figures Lack gives are not in the paper by Amadon he cites." Of the *Accipiter* this is literally true; they are from an earlier paper (Amadon, Wilson Bull. 55:164–177, 1943) and are for *weight*, not *wing length* as Lack has it. The measurements of *Cinclorhamphus* are in the 1959 paper but again are for weight not wing length!

This confusion does raise the question: What is the best general measure of difference in body size? In my 1959 paper, cited above, which is a review of the subject, I noted that in most species of birds and mammals males compete for females and are the larger sex; while in the few groups in which females compete for males (phalaropes, for example) females are larger. Furthermore, dimorphism is usually greater in polygamous or polygynous species in which a few males do most of the mating and individuals of that sex are hence to a degree, expendable. Competition for mates often consists largely of display and threats but actual physical conflict is always latent, and overall body size and prowess, of which gross weight is the best available measure, provide the basis for the selection.

Considering now the extremes of sexual size dimorphism in the Class Aves, in a few polygynous or promiscuous species such as the Capercaillie (*Tetrao urogallus*) the weight of males averages a trifle more than twice that of females. *Cinclorhamphus cruralis*, mentioned above, is uniquely dimorphic for a passerine bird (and perhaps for all birds). Combining weights of several individuals from South Australia for which I am indebted to Dr. L. L. Short, with those I (1959:533) published earlier, we have the following: 6 ♂♂, 65–83 (69) g; 4 ♀♀, 28–32 (31) g; the males thus average 2.2 times heavier than the females. A few weights of the smaller and only other species of the genus, *C. mathewsi*, also supplied by Dr. Short, indicate that it is less strikingly dimorphic: 6 ♂♂ average 39 g and 3 ♀♀ 23.5 g; thus the males average 1.6 times heavier than the females. Dr. Short informs me that the flight displays of the large males of *Cinclorhamphus cruralis* cover a wide area and he thinks it highly likely that the species is polygynous.

In birds in which secondary sexual behavior is "reversed," such as phalaropes, females, as noted above, are larger, but not greatly so; perhaps they weigh 10 or 15% more than the males. In hawks and owls also females are larger than males, even though courtship and parental care roles are not reversed. The selective basis for this dimorphism is debated; I (Amadon 1975) think it is because in these aggressive, taloned, predatory species females would be in peril from males at pairing time, were they not larger and able to be the dominant partner. In various species of *Accipiter*, females average about 1.7 times as heavy as males, and if pairing is random some males will have mates of twice their own weight. For example Piechocki (*in* Glutz, Bezzel and Bauer, Handbuch Vogel Mitteleuropas, 4, Akademische Verlag, Frankfurt, 1971:420) gave the weights of a series of *Accipiter nisus* as 13 ♂♂ 134–162 (149) g; 58 ♀♀ 220–310 (258) g. Dimorphism in some of the other species of the genus *Accipiter*, for example the American *A. striatus*, is similar; I (1943 op. cit.) used *A. fasciatus vigilax* of New Caledonia merely because a series of weights was available. Judging from skins, I suspect there may be a few species of raptors in which females will be found to average twice as heavy as males: for example *Erythrotriorchis radiatus*, or *Hieraaetus kienerii*.

Some of the data presented by Ralls are in the form of cube root of weight. This statistic is useful when it is necessary to compare weights with linear measurements—it reduces the weight to a linear equivalent (Amadon 1943); but, as stated above, it would appear to be the weight, mass, or bulk of a bird *per se* that provides the selective material for sexual size dimorphism, and the raw weights themselves should be used.

Ralls used 2 other measurements in her comparisons: wing length and total length. The latter is rarely employed because differences in the make of museum specimens, and other factors, render it somewhat unreliable. Also, total length in birds as usually defined includes the tail (feathers), which are not really part of the body. This measurement does, however, suggest a different category of sexual dimorphism in birds; one that reaches its extreme in such species as the African Long-tailed Whydah, *Euplectes progne delamerei*. In breeding plumage males of this weaver-finch are 50 to 60 cm long, of which 75%, roughly, is represented by the very long tail feathers. Females are only about 15 cm long, so measured this way the males are about 4 times as long as the females. Such dimorphism is based largely upon insubstantial feathers and does not reflect true body size. But in another sense it is size dimorphism: the male whydah looks very much larger than his mates, and does fill more space. Some pheasants (*Rheinardia, Pavo*) and a few other birds equal or approach the dimorphism in display characters found in *Euplectes*.

This kind of dimorphism, unlike that in weight, is presumably based not upon physical competition for mates but rather upon sexual selection in a Darwinian sense. During the evolution of such species, females have tended to prefer males that were superior in display and the "ornaments" that go with it. Not unexpectedly this type of sexual dimorphism also has been able to proceed further in polygynous or promiscuous species such as those cited. Still, some monogamous species such as the Quetzal, *Pharomachrus mocinno*, are strikingly dimorphic.

As to comparative sexual size dimorphism in birds and mammals, no birds, as Ralls noted, approach the degree of disparity in weights found in a few mammals (elephant-seals, *Mirounga*, etc.) in which the male weighs several times as much as the female. Mammals are also far ahead in the development of bulky weapons (antlers), though a few birds are spurred. On the other hand, as befits their visual orientation and the structural plasticity yet light weight of feathers, some birds far exceed mammals and perhaps any other group of animals in the size of display ornaments.—D. AMADON, *American Museum of Natural History, New York, NY 10024.* *Accepted 7 Sept. 1976.*

Response of incubating Black-bellied Whistling-ducks to loss of mates.—Earlier work reported that Black-bellied Whistling-ducks (*Dendrocygna autumnalis*) mate for life and that both sexes in this species share incubation duties (Bolen, J. Wildl. Manage. 35:385–388, 1971). There is no verification from field studies of shared incubation among the other seven species of whistling-ducks except for the single observation of Flickinger (Wilson Bull. 87:106–107, 1975) for the Fulvous Whistling-duck (*D. bicolor*). This poses the question as to whether the loss of one member of a pair of Black-bellied Whistling-ducks might cause nest failure during incubation. Experimental evidence has thus far been lacking, although our field records include an instance when the death of a male led to nest abandonment by the female. We attempted to experimentally examine this question by removing 1 mate of 2 pairs of incubating whistling ducks and then observing the nest and the remaining mate to determine whether incubation would continue or whether the survivor would remate and renest during the current season.

On 28 June 1975 we removed 2 Black-bellied Whistling-ducks from separate nests in boxes designed for their use (Bolen, J. Wildl. Manage. 31:794–797, 1967); a male was taken from one nest and a female from the other. We held these birds in captivity for 4 days, then released them 60 km distant from the nesting site. The respective mates of each bird had been previously banded and marked prior to our experiment. In each case the nest was abandoned following the removal of the incubating bird. In one instance, we know that the surviving mate (female) was immediately available to assume incubation as she was repeatedly seen loafing on the pond near the nest box; she was seen in virtually the identical spot the day following the removal of her mate from the nest. Furthermore, a small string placed atop the eggs at the time the male was removed remained undisturbed for 24 h, indicating that the hen had not entered the nest box unseen. The male was not seen again following his release, and we likewise have no further history of the hen following 29 June.

In the second case, the nest also failed although the female returned to the nesting area on 2 July following her release; this hen's mate was noted in the company of a banded bird on 26 July (presumably the pair was then reunited), and on 16 August the male was captured incubating a clutch apparently begun about 24 July. On 27 August the female was captured on this nest and confirmed by her band number as the bird captured and released earlier. The nest successfully hatched by 4 September, and represented a successful renesting attempt on the part of this pair (cf. Delnicki and Bolen, Auk 93:535–542, 1976).

These observations support the earlier observations of Bolen (Ph.D. thesis, Utah State Univ., 1967) and Delnicki (M.S. thesis, Texas Tech Univ., 1973) that the exchange of incubation duties is initiated by the bird (of either sex) on the nest; this is accomplished simply by the incubating bird leaving the nest and flying to a loafing area where it joins the waiting mate. The loafing mate thereafter returns to the nest to continue incubation without further behavioral interaction or nest exchange ritual. Thus, the simulated or actual death of the bird on the nest interrupts the sequence and the nest is abandoned when the incubating bird fails to join its mate at a loafing site. This study was part of a M.S. thesis accepted by the faculty of Corpus Christi State University.—RICHARD E. MCCAMANT AND ERIC G. BOLEN, *Rob and Bessie Welder Wildlife Foundation, P.O. Drawer 1400, Sinton, TX 78387.* (Present address REM: *Buffalo National River, P.O. Box 1173, Harrison, AK 72601.*) *Accepted 5 May 1977.*

Late Pleistocene Williamson's Sapsucker from Wyoming.—Archaeological excavations at the Casper Site, a bison kill site in Casper, Natrona Co., Wyoming, yielded a single left humerus referable to *Sphyrapicus thyroideus*, Williamson's Sapsucker. The site, described by G. C. Frison (The Casper Site: a Hell Gap Bison Kill on the High Plains, Academic Press, N.Y., 1974), has been radiocarbon dated to 10,060 ± 170 years B.P. (8110 B.C.: RL-208) and 9830 ± 350 years B.P. (7880 B.C.: RL-125), and therefore lies on the Late Pleistocene-Holocene boundary. The extinct camelid *Camelops* is also present in the fauna, lending it a Late Pleistocene aspect. Dental eruption and attrition in the bison population, referred by M. Wilson (*in* G. C. Frison, op. cit., p. 132) to *Bison bison antiquus*, suggest a late autumn kill event. Shed coyote (*Canis latrans*) deciduous premolars also suggest a late summer to autumn occurrence. If a natural occurrence, the sapsucker could have been a migrating individual, as the sand-dune setting of the site is at variance with modern habitat preferences of this species. However, its emplacement in the bone bed may have come through the action of human or other predators.

TABLE 1

MAXIMUM MEASUREMENTS OF SAPSUCKER HUMERI

	UWA27269	*S. thryoideus*[1]	*S. varius*[2]
Mid-shaft diameter	2.85	2.85	2.70
Breadth distal end	6.70	6.55	6.45
Ectepicondylar prominence to external trochlear condyle	4.00	3.75	3.70

[1] N = 3. [2] N = 6.

Asyndesmus lewis and species of *Melanerpes* were eliminated on the basis of size as well as characters of the distal end (the proximal head of the fossil is missing). The similar humerus of *Picoides villosus* differs in having (1) a larger, more deeply excavated olecranal fossa, (2) a larger depression of brachialis anticus, and (3) a shorter ectepicondylar prominence. The external trochlear condyle of *Sphyrapicus thyroideus* appears more bulbous than that of *S. v. varius* and *S. v. nuchalis.* In addition, the larger size of the fossil indicates *S. thyroideus* rather than *S. varius* (Table 1). The specimen (NC2559, recatalogued UWA27269) is in the University of Wyoming Anthropology collections.

P. Brodkorb (Catalogue of Fossil Birds, Part 4, Bull. Florida State Mus. 15:162–266, 1971) lists 2 Pleistocene records for *S. varius* (1 of them uncertain), but none for *S. thyroideus.* The Casper Site specimen therefore appears to be the first Pleistocene record of the species.

We are grateful to Dr. George C. Frison for his loan of the specimen and for financial assistance to the senior author through the Wyoming Recreation Commission and the University of Wyoming, for the analysis of the Casper Local Fauna.—MICHAEL WILSON, *Dept. of Archaeology, Univ. of Calgary, Calgary, Alberta, Canada T2N 1N4; and* AMADEO M. REA, *Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson 85721.* *Accepted 14 April 1976.*

American Kestrel rejects captured spadefoot toad.—Although the diet of the American Kestrel (*Falco sparverius*) includes a wide range of prey items (Heintzelman, Wilson Bull. 76:323–330, 1964), I could find no records of American Kestrels preying on toads. Therefore, the following observation of a kestrel capturing but not eating a toad is of interest.

On 17 October 1975 at 09:40, about 5 km west of Elgin, Arizona, I observed a female American Kestrel fly about 50 m from a utility pole to the ground in an open short-grass field. Shortly she returned to the pole carrying a toad in one foot. The kestrel picked at the head of the toad sporadically and occasionally shook her head from side to side. After 2 min 55 sec, when she was frightened by a passing vehicle, she carried the toad about 150 m to another pole. She held the toad 3 min 45 sec on this perch before making an attempt to eat it, then began biting the head again but shook her head violently after each bite. After 5 min 55 sec of intermittent bites and head shakes she carried the toad about 200 m to a fence post. Soon she flew a short distance to the ground and returned to the post without the toad. She sat on the post with her feathers ruffled, constantly changed foot positions, and continued the head shaking. After 2 min she flew to the ground and captured a grasshopper which was carried to a utility pole farther out in the field. After eating the grasshopper she still occasionally shook her head.

I found the toad on the ground near a small bush. It was crawling feebly and the rostrum was covered with blood but it had no other injuries. The toad, a western spadefoot (*Scaphiopus hammondi*), measured 44 mm SVL and weighed 14 g. It exhibited normal locomotion and behavior within 24 h and lived for 22 days before being released.

Bent (U.S. Natl. Bull. 170, 1937) lists "toads" in the diets of 4 species of Accipitridae and Sexton and Marion (Wilson Bull. 86:167–168, 1974) report evidence of Swainson's Hawks (*Buteo swainsoni*) feeding on plains spadefoot toads (*Scaphiopus bombifrons*). Perhaps there are differences in the tolerances of different hawks to the distastefulness of toads and differences in the distastefulness of different species of toads.

That the toad was carried to the ground and released rather than dropped from a perch is probably explained by the food storing behavior of American Kestrels. Tordoff (Wilson Bull. 67:139–140, 1955) and Stendell and Waian (Condor 70:187, 1968) reported food storing by American Kestrels, and I have observed it in the Elgin area on 5 occasions; 3 times prey was stored in a small bush.—G. Scott Mills, *Dept. of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson 85721. Accepted 20 July 1976.*

Winter distribution of Red-tailed Hawks in central New York state.—The winter distribution of raptors in relation to their prey has seldom been investigated systematically. Several authors (e.g. Snyder and Hope, Wilson Bull. 50:110–112; Weller et al., Wilson Bull. 67:189–193) have noted concentrations of raptors where meadow voles (*Microtus* sp.) were abundant and Craighead and Craighead (Hawks, Owls, and Wildlife, Dover, N.Y. 1969:144) concluded that in a 90 km^2 study area in Michigan raptor density in winter was highest where vole density was highest.

While driving between Ithaca and Albany, New York I noticed on several occasions that Red-tailed Hawk (*Buteo jamaicensis*) density along the route varied greatly. This study was undertaken to determine whether the differences in hawk density were correlated with density of meadow voles (*Microtus pennsylvanicus*), one of their principal prey species (Craighead et al., USDA Circ. 370, 1935).

Methods.—Five surveys were made on clear days between 1 February and 1 March 1974 on the 241 km route which followed US Rt. 13, NY Rt. 26, and US Rt. 20.

TABLE 1

RELATIVE DENSITY OF RED-TAILED HAWKS, FREQUENCY OF VOLE HABITAT, AND VOLE RUNWAYS BETWEEN ITHACA AND ALBANY, NEW YORK IN WINTER, 1974

Hawk density Hawks/km	Frequency of good habitat	Runways in good habitat Mean* (SD)	Frequency of fair habitat	Runways in fair habitat Mean* (SD)
0.016 (low)	.006	54.8 (15.0)	.458	4.0 (4.9)
0.067 (medium)	.050	44.7 (7.4)	.372	1.0 (1.7)
2.190 (high)	.440	93.5 (10.7) **	.125	1.0 (1.5)

* N = 6 fields in each case (20 samples/field).

** Use of the Student-Newman-Keuls test (Sokal and Rohlf, Biometry, Freeman, San Francisco, 1969) showed that in good habitat there were more ($p \leqslant .01$) runways in high hawk density areas than in medium or low hawk density areas. No other differences in runway density were significant.

I measured *Microtus* habitat by driving the route slowly and visually classifying the habitat every .32 km on both sides of the road as "good," "poor," or "unsuitable." Good habitat consisted of recently abandoned fields with a matted, grassy cover. Grass shoots, on which voles feed, were common under this cover. Poor habitat included fields without the distinctive matted cover and had few grass shoots for voles to feed on. Unsuitable habitat included all areas such as plowed fields or woodlots where voles would not be found or where Red-tails would not hunt.

Hawk density was particularly high in a short 4.2 km section at the east end of the route. To measure *Microtus* habitat frequency more accurately in this section, I used aerial photographs and ground surveys to prepare a habitat map of the entire area within 400 m of the road (the average maximum distance at which I recorded hawks).

Using the results of the roadside survey (1480 samples) and the habitat map prepared for the short section at the east end of the route, I calculated habitat frequency for the entire route (Table 1).

Microtus population levels were then measured in good and poor habitats by counting the number of runways crossing the perimeter of a randomly placed .25 m^2 wire frame. Twenty samples were obtained in each of 18 good and 18 fair habitat fields regularly spaced along the route (Table 1).

Results.—Starting at the east end of the route, hawk density per kilometer varied from 2.19 in the first 4 km to .063 in the next 51 km to .016 in the final 186 km. Paralleling the change in hawk density, the frequency of good vole habitat dropped from .44 to .05 to .006 in the high, medium, and low hawk density sections respectively (Table 1). Good vole habitat thus varied about as much, and in the same direction, as hawk density.

There were few vole runways in any of the poor habitats sampled (0–4 runways per field). The number of runways in good habitat was about equal in low and medium hawk density areas but significantly higher ($p \leqslant .01$) in high hawk density areas (Table 1).

The number of Red-tailed Hawks observed was thus correlated with the frequency of good *Microtus* habitat and with high *Microtus* population indices within good habitat. These results support the hypothesis that, in the study area, *Microtus* distribution is a major factor determining the distribution of Red-tailed Hawks in winter.

The *Microtus* sampling method was suggested by M. Richmond who also greatly improved the manuscript. T. Cade and L. Oring offered additional helpful suggestions on the manuscript.—Jonathan Bart, *New York Cooperative Wildlife Research Unit, Dept. of Natural Resources, Cornell Univ., Ithaca, NY 14853. Accepted 14 Sept. 1976.*

Osprey catches vole.—On 3 October 1975 at Lighthouse Point Park, New Haven Co., Connecticut, I observed an Osprey (*Pandion haliaetus*) circle low over a salt marsh, rise slightly, hover in the same pattern it would in catching a fish and then plunge to the ground. It sat motionless for a moment in the short *Spartina patens* grass looking at its feet then took flight clutching a small rodent. It flew to the ridgepole of a nearby cottage and through a 20× spotting scope I watched it tear its prey apart. When it had finished and left, I retrieved all that remained: the skin from the sides, feet and some entrails of a meadow vole (*Microtus pennsylvanicus*).

Brown and Amadon (1968. Eagles, Hawks, and Falcons of the World. McGraw Hill, New York) list numerous vertebrates as acceptable Osprey prey including birds, frogs, and crustaceans in addition to its normal diet of fish. Wiley and Loher (Wilson Bull. 85:468–470, 1973) give detailed lists of Osprey prey including 12 species of birds, several reptiles and amphibians, and 8 species of mammals, but not *M. pennsylvannicus.* Spitzer (pers. comm.) found what he believed to be *M. pennsylvannicus* remains in at least 1 Osprey nest. The literature is lacking in actual sightings of how these mammals are taken.—Noble S. Proctor, *Biology Dept., Southern Connecticut State College, 501 Crescent St., New Haven 06515. Accepted 6 Aug. 1976.*

Patterns of feeding Field Sparrow young.—As part of a study of Field Sparrow (*Spizella pusilla*) breeding ecology (Best, Ph.D. thesis, Univ. of Illinois, Urbana, 1974), I recorded the activities of parents feeding nestlings on the 6th day after the first young hatched. Observations were made from a blind and covered the periods: dawn–08:00, 09:00–12:00, 13:00–16:00, and 17:00–dusk. A mirror positioned above the nest permitted observation of its contents. Airplane paint was applied to each nestling's bill for individual recognition (this had no noticeable effect on parental feeding behavior) and adults were marked with colored leg bands. Besides documenting the frequency and temporal distribution of feeding visits (Best, Auk, 94:308–319, 1977), the pattern of food delivery to individual nestlings was also recorded for 6 broods. The pattern of food delivery, which is rarely reported, is the subject of this note.

To determine if the sequence of feeding nestlings was random, an interval-distribution test (Ghent and Hanna, Am. Midl. Nat. 85:188–195, 1971) was employed. In only 2 of the 16 nestlings tested (representing 2 of 6 broods), were the intervals between feedings significantly different from a random sequence ($P < 0.05$). Although this implies no sequential pattern in feeding most nestlings, certain nonsignificant trends were evident. In all 16 nestlings the "observed" frequency of consecutive feedings (the same nestling being fed twice in immediate succession) was less than the "expected" frequency, while the observed frequency of alternate feedings (another nestling being fed between successive feedings of the nestling in question) was greater than the expected frequency in all but 3 nestlings (representing 2 broods). These trends indicate that on the basis of

Table 1

The Distribution of Feeding Trips (Male/Female/Both) Among Nestlings Within Each Brood

Brood[a]	Individual nestlings			
20 June	15/11/26 (7.8/1.8)[b]	6/13/19 (8.3/1.8)	9/17/26 (6.0/1.6)	10/14/24 (7.9/1.8)
24 June[c]	8/15/23 (8.0/1.8)	17/ 7/24 (8.7/1.9)	9/15/24 (9.1/1.8)	
5 August	20/28/48 (7.0/1.6)	25/21/46 (6.8/1.7)	30/26/56 (8.4/1.8)	
7 August[c]	44/22/66 (8.3/1.8)	32/26/58 (8.0/1.8)	33/12/45 (6.7/1.7)	3/10/13[d] (3.5/1.3)
28 August	15/28/43 (8.5/1.8)	12/27/39 (7.9/1.8)		
1 September	17/21/38 (7.4/1.8)	13/25/38 (6.8/1.8)		

[a] Date when brood was observed being fed.
[b] Nestling weight (g) and tarsal length (cm) measured the day before the feedings were recorded.
[c] Significant differences in the proportion of feedings by the male and female to each brood member.
[d] This nestling had a broken leg.

chance alone, nestlings are fed less often than expected on consecutive feedings but more often than expected on alternate feedings. There were no consistent departures from expected feeding frequencies for intervals greater than 1.

The distribution of the total feeding trips among nestlings of a given brood was not significantly different from uniformity in 5 of the 6 broods observed (Chi-square goodness of fit test) (Table 1). In the brood fed differentially, 1 nestling had a broken leg. This nestling was fed much less frequently than the others and could not reach as high when begging for food. When the analysis was restricted to the remaining nestlings, the difference was not significant. The above results suggest that size differences among nestlings did not significantly influence the number of feedings each received, although there was a tendency in most cases for the larger nestlings to be fed more frequently (Table 1). Brood reduction resulting from starvation was not observed during the entire study and the only nestling exhibiting abnormally slow growth was the one with a broken leg. Availability of nestling food did not appear to limit breeding success on the study area (Best, Auk, op. cit.).

The proportion of feeding trips by the male and female to each nestling of a brood generally differed (Table 1), although in only 2 of 6 instances (both broods of the same pair) was the difference statistically significant (Chi-square contingency analysis). In most cases differences were complementary, tending to balance the frequency of feeding each nestling.

The influence of spatial arrangement in the nest on how frequently each nestling received food was determined for 4 broods by comparing the positions of all nestlings during each visit with the position(s) of the nestling(s) receiving food (occasionally 2 nestlings were fed during a visit, but usually only 1). Twelve positions were selected reflecting the hours on a clock face (e.g. during a visit the 3 brood members were at 01:00, 05:00, and 10:00 with the nestling at 05:00 receiving food). The adult's position on the nest rim was also recorded during each visit. A Chi-square test for goodness of fit was used to determine if the frequency of feeding nestlings at various positions departed significantly from the frequency nestlings occupied those positions during feedings. Adult male and female feedings were considered separately as well as combined. In only one instance were the results statistically significant (Fig. 1) and then only for the spatial feeding pattern of the male ($P < 0.005$). Apparently the frequency of feeding nestlings in various regions of the nest is usually determined by how frequently those positions are occupied by young, and not by the adults' preference to feed in particular areas. All adults did, however, show strong preferences to feed from specific areas on the nest rim (see Fig. 1 for example). In some instances both members of the pair used the same feeding position while in other cases they did not.

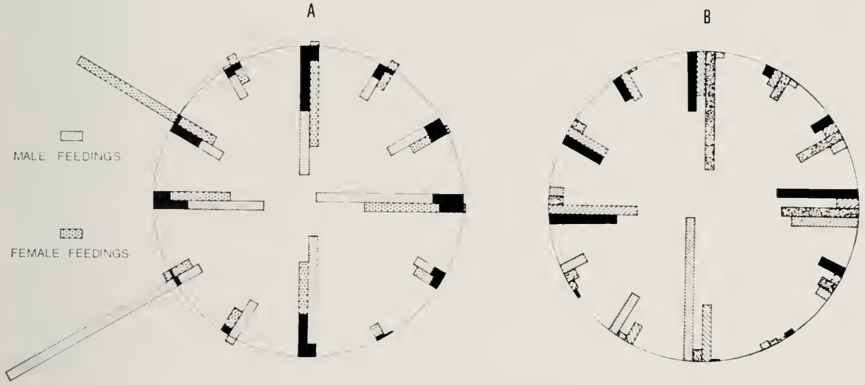

Fig. 1. The positions of adults and nestlings during feedings of the 7 August brood. Bar lengths indicate frequencies. Diagram A shows the feeding positions of the adults from the nest rim (bars outside circle), the positions of all nestlings during feeding visits (bars inside circle), and the positions of the nestlings actually receiving food (black portion of bars). Diagram B illustrates the positions of the 4 individual nestlings during feedings.

Although the young rearranged their positions in the nest frequently throughout the day, brood members showed a strong propensity to occupy different regions of the nest in all 4 broods considered ($P < 0.005$, Chi-square contingency analysis) (see Fig. 1 for example). When parents feed the young preferentially in different regions of the nest (which generally appeared not to be the case in this study), the nestlings' spatial arrangement in the nest could result in differential feeding.

The referees' suggestions for revising the manuscript were appreciated.—Louis B. Best, *Dept. of Animal Ecology, Iowa State Univ., Ames 50011.* *Accepted 3 Nov. 1976.*

Avian bone pathologies from Arikara sites in South Dakota.—Vertebrate remains recovered in aboriginal sites often provide the archaeologist with valuable data pertaining to the economic and social use of animals by various Indian groups. Certain groups of birds such as the Anatidae comprised a significant part of their diet (Howard, Univ. Calif. Publ. Zool. 32:301–387, 1929; Parmalee, Bull. Ill. Arch. Surv. 10:137–155, 1976) while others, for example representatives of the Accipitridae and Corvidae, played a major role in ceremonial and related customs (Ubelaker and Wedel, Am. Antiquity 40: 444–452, 1975). The identification of avian bones found during archaeological excavations may provide the zoologist with noteworthy prehistoric or early historic species' distribution and abundance records. Data pertaining to sex and age ratios of certain species, season of death (collection by the Indian), significant taxonomic characters, and osteological anomalies may also be obtained from archaeologically derived faunal samples.

The occurrence of mammalian bones which exhibit some form of anomaly or pathology are recovered occasionally in Indian refuse deposits, but similar elements of birds are extremely rare. This may be due to the fact that birds were seldom taken in numbers comparable to those of mammals and, consequently, fewer elements were preserved. However, the chances of a bird with a broken leg or especially a wing surviving during the period necessary for healing are probably small. Even if such a break would heal in a manner that would allow the individual to again function normally, the possibility that the Indian would later kill such a bird and its bone be preserved in the midden debris is even more remote. Therefore, the recovery of 3 extreme cases of bird bone pathology encountered during identification and analysis of an avifauna from 51 Arikara sites in South Dakota are worthy of description.

Archaeological salvage work was carried out along the Missouri River in North and South Dakota from about 1950 to 1965 prior to the construction of 5 major dams by the U.S. Army Corps of Engineers. During this period considerable quantities of animal refuse were salvaged from several Plains Indian village sites which were to be inundated. I have examined nearly 3100 bird bones from 51 of these South Dakota sites which were formerly occupied by groups of Arikara. This Plains tribe was originally a part of the Pawnee confederacy; these Indians migrated to the Middle Missouri River area from Nebraska and established numerous villages along the river. Approximately 68 species of birds, representing 22 families, were identified. Remains of waterfowl, hawks and eagles, grouse, and corvids comprised about 84% of the total.

A minimum of approximately 870 individuals were represented in these 51 sites and of this total, elements of only 3 birds, 2 hawks and 1 duck, exhibited a pathological condition. Four such elements, occurring in the same archaeological excavation unit and undoubtedly from the same individual, were recovered at the Crow Creek site (39BF11: occupied ca. AD 1400–1550). The bones consisted of a right tarsometatarsus and radius/ulna and a left humerus (Fig. 1) and were those of a hawk (*Buteo* sp.). Several of the broad-winged hawks are extremely difficult to separate osteologically even when the elements are normal, so these distorted bones make a specific determination more uncertain; however, these compare most closely with the Rough-legged Hawk (*B. lagopus*).

The most interesting of the 4 elements are the radius and ulna which had been broken about ¼ the distance from the distal end. During the healing process these bones became fused at or near the point of fracture by a bridge of callus bone. The distal ⅓ to ½ of these elements was greatly swollen with porous new bone which resembles a tumor. This swollen appearance is apparently due, in part, to the overlapping broken ends of the bone which double the normal diameter of each; healing in such a manner would tend to shorten the length of the wing. The distal articulating surfaces of the radius and ulna appeared only minimally affected and there was probably little or no disruption in free articular movement with the cuneiform, scapholunar, and proximal end of the carpometacarpus. Once complete healing had occurred, the bird was probably able to again fly.

Neither the humerus nor the tarsometatarsus recovered in the same unit with the pathological radius/ulna had been broken, but the deformities and surface irregularities apparent in both suggest they may well have been from the same hawk. It is possible that these 2 elements, as well as others, could have been affected as a result of the traumatic condition of the broken wing and/or possibly inadequate diet during the healing process. The proximal end of the humerus is bent upward (anconal view) and the area of attachment of the latissimus dorsi, pneumatic fossa, bicipital surface, and bicipital furrow appear granular or roughened. The proximal end of the tarsometatarsus is also bent upward (anterior view) and slightly twisted (Fig. 1). Although the break in the wing of this hawk healed completely, the total effect osteologically may have been detrimental to a normal existence.

The second incidence of pathology involved the left tarsometatarsus of a hawk, possibly Rough-legged Hawk or Red-tailed Hawk (*B. jamaicensis*) found at the Black Partizan site (39LM218: occupied ca. AD 1550–1675). The element had been broken near the distal end (Fig. 2, A) and, as evidenced by the deposition of porous new bone, a certain amount of healing had taken place. Whether or not the fracture had completely healed at the time of the bird's death is uncertain since the proximal section of the tarsometatarsus was not recovered. The callus bone was extremely irregular, however, and the use of the tarsometatarsus was probably considerably reduced as evidenced by the thin areas of ossification. In any event, this hawk had survived long enough before being killed to permit a considerable amount of healing at the fracture.

In his study of bone injuries in birds, Tiemeier (Auk 58:350–359, 1941) found that nearly 13% of 256 skeletons of the ducks he examined possessed one or more broken or otherwise damaged and repaired elements. Generally, for all groups of birds he examined, wing and leg elements were the ones most subject to injury, although damage to skulls, sterna, and furcula, especially in the passerines, was not uncommon. Of 6212 bird skeletons (59 families) examined by Tiemeier (op. cit.) from the collections of the Museum of Natural History, University of Kansas, Lawrence, no injury to the coracoid was mentioned. Therefore, the apparent rarity of injury to this element, coupled with the extreme pathological condition of a left coracoid from the Hosterman site (39P07: occupied ca. AD 1550–1675) is of particular interest.

This duck coracoid (Fig. 2, B–D) appears to have been broken or at least severely damaged in the area of the glenoid and/or scapular facets. Unlike the hawk elements described above, the callus was small and very compact, although the bone exhibited an extreme degree of deformity. The shaft was divided into 2 sections, producing 1 large and 1 small hole (viewed laterally) between them; the scapular facet appears as a deep U-shaped groove; the glenoid facet is reduced, or divided, and bent at about a 45° angle; and the surface of the ventral "half" of the shaft possesses an oblong depression in which the head of the humerus may have articulated. Because of its deformed condition, this element could not be specifically identified; the overall length and general configuration of the head and sternal facet compare with that of the Mallard (*Anas platyrhynchos*). There is little doubt that such an injury to the coracoid would have inhibited the wing from functioning normally and would have limited or entirely prohibited its use for flight until healed.

At least 1 tribe of Plains Indians, the Mandan of North Dakota, are known to have kept live owls as soothsayers (Thwaites, ed., Early Western Travels, Vol. 23, Arthur H. Clark

Fig. 1. Pathological conditions of hawk (*Buteo* sp.) elements from the Crow Creek site, South Dakota. A: left humerus, anconal view; B: fused right radius and ulna, palmar view; C: tarsometatarsus, anterior view.

Co., Cleveland, OH, 1906), but there is no evidence suggesting that hawks were kept alive for any reason. In discussing animal ceremonialism of the Miwok Indians of California, however, Heizer and Hewes (Am. Anthropologist 42:587–603, 1940) state that "Eagles, condors and falcons were kept captive, and might be traded from tribe to tribe," but apparently such birds were held only temporarily. Eagle trapping was a significant trait of all Plains tribes and a ritual which involved a considerable amount of preparation and

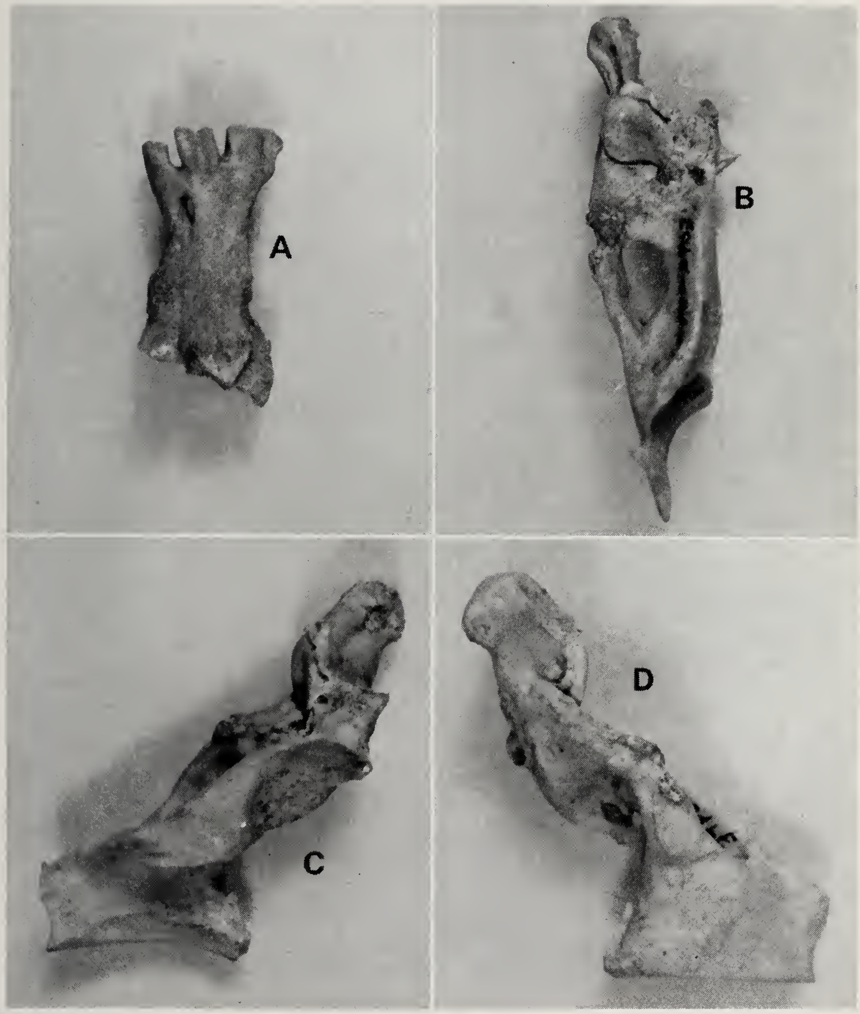

FIG. 2. A: anterior view of a fractured left tarsometatarsus of a hawk (*Buteo* sp.) from the Black Partizan site, South Dakota. Three views (B, lateral; C, dorsal; D, external) of a fractured left duck coracoid from the Hosterman site, South Dakota.

organization (Wilson, Am. Mus. Nat. Hist. Anthro. Papers 30:99–245, 1928). Large numbers of hawks and eagles were often taken during these hunts and, although the first few eagles caught were sometimes kept as decoys, most were killed at the end of the hunt. There is no mention of hawks being used in a like manner. Hargrave (Univ. Ariz. Anthro. Papers No. 20:1–67, 1970), in his osteological study of macaws (*Ara* spp.) from prehistoric Pueblo sites in Arizona and New Mexico, found that 47% of the 145 individuals examined displayed pathological bones; he concluded these conditions reflected normal accidents or dietary deficiencies.

The high percentage of bone pathologies evident in the macaws are indicative of a captive state with inadequate diet and generally poor treatment contributing to this condition. With no evidence of the Plains Indian keeping captive hawks, it may be reasonably assumed that the 2 birds exhibiting fractured bones were injured in "natural" accidents. Regardless of the cause, the fact remains that many wild birds which suffer severe fractures are able to survive adverse conditions during the healing period and eventually return to their natural mode of life. The broken and repaired humeri of ducks described and illustrated by Abbott (Auk 60:447, 1943) and Dillon (Auk 78:273–274, 1961) exemplify the fact that a healed break of a major wing element, even though distorted, may enable the bird to regain the power of flight. The extremely deformed coracoid from the Hosterman site is of special interest, however, both from the standpoint of how such an injury occurred and its possible effect on normal wing movement.—PAUL W. PARMALEE, *Dept. of Anthropology, Univ. of Tennessee, Knoxville 37916. Accepted 1 Nov. 1976.*

Nest reciprocity in Eastern Phoebes and Barn Swallows.—A few investigations of the Eastern Phoebe (*Sayornis phoebe*) and Barn Swallow (*Hirundo rustica*) have revealed use, with modification, of old nests of 1 species by the other (Stoner, New York State Mus. Circ. 22:1–42, 1939; Graber et al., Ill. Nat. Hist. Surv. Biol. Note No. 86, 1974; Jackson and Weeks, Alabama Birdlife 24:7–9, 1976).

In March 1970 on Crane Naval Ammunition Depot (NAD Crane), Indiana, I examined and marked all Eastern Phoebe and Barn Swallow nests that remained under bridges and culverts from previous nesting seasons. Of the 242 old nests examined, I found 7 instances of reciprocal use—3 former Barn Swallow nests modified by phoebes, 1 phoebe nest converted by a Barn Swallow, and 3 nests illustrating multiple reciprocity. In these and subsequent modifications, the pattern was similar, with Barn Swallows adding mud and dried grass, and phoebes adding moss to the nests' rims; each species also lined the nest with the appropriate material.

The multiple reciprocity nests were all found beneath bridges. The largest nest, 32 cm in height, was composed of 7 alternating Barn Swallow and phoebe nests beginning with a Barn Swallow base (Fig. 1). Another nest was of similar construction but composed of 4 tiers of alternating nests built on a phoebe base and 24 cm in height. A third nest appeared to be a single, excessively large (21 cm in height) Barn Swallow nest modified by phoebes, and only at removal at the end of the season did the nest separate to reveal a second, intermediate layer of phoebe nesting material.

Of the 235 normal nests marked prior to the 1970 nesting season, 8 were modified and used during the season by the other species. Six old Barn Swallow nests were adapted by phoebes, and 2 old phoebe nests converted by Barn Swallows. One of these latter nests and another phoebe nest, built early in the 1970 season, fledged broods of phoebes prior to their modification and successful late season use by Barn Swallows.

Since old nests were removed at the end of the 1970 season, no nests were available for reuse in spring 1971. However, 1 phoebe and 1 Barn Swallow nest built early in the 1971 season were subsequently converted and used by the alternate species. All nests

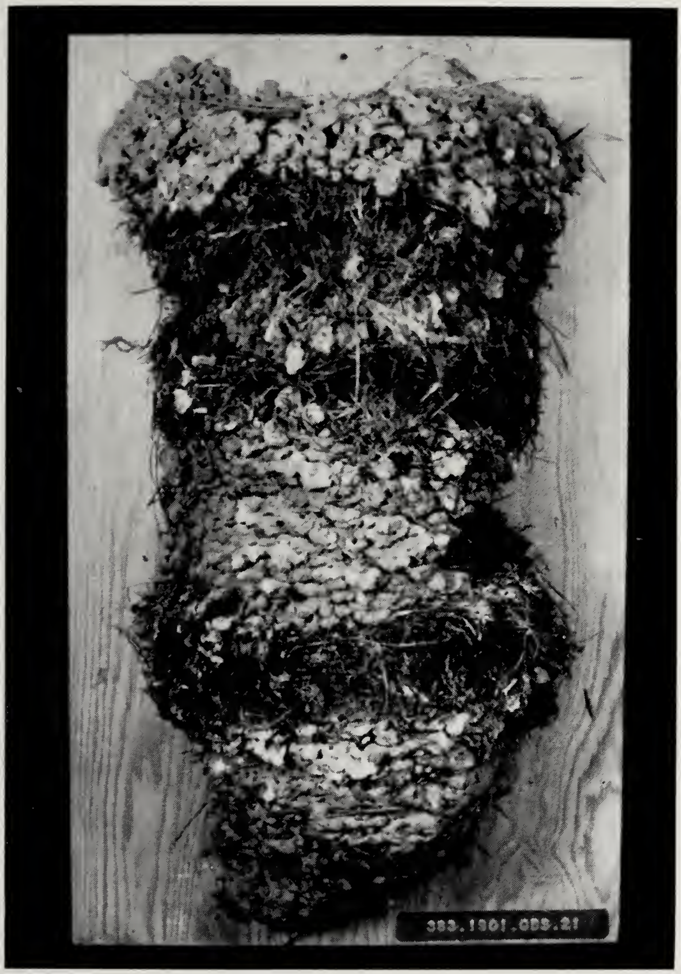

FIG. 1. An extreme example of successive nest use by Barn Swallows and Eastern Phoebes.

were removed at the end of the 1971 season with only sporadic examinations made from 1972 through 1975. At the close of the 1976 breeding season, I found 6 Barn Swallow nests altered by phoebes and 3 phoebe nests remodeled by Barn Swallows; all were under bridges.

Both species regularly nest under bridges and add material to and use old nests of conspecifics, so it is perhaps not surprising that these birds occasionally demonstrate reciprocal use. It seems that in most instances both species recognize and prefer old nests of their own species. The question then arises as to why a bird chooses an old nest of another species while one or more conspecific nests are available. And furthermore, why is a particular nest chosen from among all those available?

The possibility exists that certain sites are optimum, representing the ultimate combination of location parameters for both species. However, I compared empirically the site parameters for all modified nests and found no consistent relationship between nests in such features as height above ground or water, location over land or water, direction faced, distance from nearest side of bridge, and distance from nearest end of bridge or culvert. There was, however, a definite tendency for birds to choose nests that were adherent, as opposed to statant (Samuel, Wilson Bull. 83:284–301, 1971), and in which the distance to overhead cover was relatively great. This was especially evident in the selection of Barn Swallow nests by phoebes. In 5 instances phoebes chose (from among 5–30 available nests under a single bridge) the one with the greatest rim-to-overhead cover distance. Phoebes generally prefer a greater distance to overhead cover than do Barn Swallows; significantly ($P < 0.05$; χ^2) more phoebe than Barn Swallow nests had rim-to-overhead distances $\geqslant 6$ cm. Of adherent Barn Swallow nests, 35.6% had <5 cm rim-to-overhead distance. In addition to giving the incubating phoebe abnormally little head space, the typical Barn Swallow nest would prevent the addition of any substantial amount of moss to the nest rim. Barn Swallow nests that phoebes modified were usually built lower on the supporting beam to take advantage of some feature, e.g., mud dauber (*Trypoxylon politum* or *Sceliphron caementarium*) nests, wood splinters, or rough concrete, that facilitated initial attachment of nesting material. Although the top rim of the multiple nest in Fig. 1 was within 7 cm of overhead cover when discovered, the initial nest had 28 cm rim-to-overhead cover distance.

There seems to be no consistency with respect to distance to overhead cover or other location parameters in the few phoebe nests modified by Barn Swallows. Of the 6 nests for which complete data are available, the distance to overhead cover ranged from 6 to 25 cm and height from 1.1 to 3.4 m; nests faced 3 cardinal directions and both upstream and downstream. The fact that reciprocal nests are usually adherent is not surprising since both species prefer these types of locations. Over 92% of all Barn Swallow nests and 54% of all phoebe nests were adherent.

The size of the prospective nest may also play a role in its selection for modification. Once a nest is modified, it appears to be used year-after-year with greater regularity than nests without reciprocal alteration. Six of 7 nests (86%) built and modified prior to 1970 were used in 1970, while only 54% of all other nests present before 1970 were used during that year. Converted nests don't seem to accumulate, e.g., about as many nests were adapted in 1970 (8 nests) as had accumulated from all seasons prior to the 1970 (7 nests) season and in the years from 1972 to 1976 (9 nests). Modifications are likely more frequent than observed from periodic counts, with the intervening rim-tailorings being masked by material added in the successive species shift. The result of these annual additions, whether reciprocal or conspecific, is a larger nest. Birds frequently selected one of the largest available nests for repair or modification and use. The selective advantage to birds in choosing large nests may be that such nests are more durable. While nest turnover is not excessively high, 5 to 10% are lost each season. Those nests that survive many years undoubtedly have firm initial attachments, resulting in less likelihood of destruction during the nesting cycle. As did Jackson and Burchfield (Am. Midl. Nat. 94:503–509, 1975) in Mississippi, I found mud dauber nests of utmost importance in facilitating a firm initial attachment, with 38.0% of adherent Barn Swallow and 51.5% of adherent phoebe nests receiving some support from these insect nests.

I wish to thank C. M. Kirkpatrick and F. H. Montague for critical review of this manuscript. This is Journal Paper No. 6464 from Purdue Agricultural Experiment Station.

—HARMON P. WEEKS, JR., *Dept. of Forestry and Natural Resources, Purdue Univ., West Lafayette, IN 47907. Accepted 12 Jan. 1977.*

REQUESTS FOR ASSISTANCE

Colored-marked Sandhill Cranes.—During summers of 1975 through 1977, researchers at Clarence Rhode National Wildlife Range on the Yukon-Kuskokwim Delta, Alaska, banded and color-marked Lesser Sandhill Cranes. In July and August of each year, chicks were marked with black-numbered yellow collars and leg bands as well as standard Fish and Wildlife Service aluminum bands. To date, 10 resightings have been reported, yielding valuable information on migration routes and wintering areas. More information is needed on timing and pathways of migration, however. Observers are asked to report the date and location of sightings, size of the flocks with which marked birds were seen, whether color bands were on the birds' right or left legs and, if possible, the numbers on the collars and leg bands. Report sightings to Cheryl Boise, Wildlife Research Unit, Irving Building, Univ. of Alaska, Fairbanks, AK 99701.

Sightings of Sandhill Cranes in northwestern Ontario.—The Greater Sandhill Crane breeds throughout the Great Lakes states and parts of Saskatchewan and Manitoba. However, in northwestern Ontario (area south of 51° latitude and west of Sault Ste. Marie) they are considered rare transients. Over the past decade, cranes believed to be Greater Sandhills have been sighted with increasing frequency throughout this area. Occurrences of immatures in the last year suggest that there is a population of Greater Sandhills breeding in N.W. Ontario. Information from sightings will be used to estimate the population distribution and to determine an area for an intensive study of biology, migration, and taxonomic verification. Please include date, location, and number of birds. Dr. C. D. Ankney, Department of Zoology, University of Western Ontario, London, Ontario, Canada, N6A 5B7.

ORNITHOLOGICAL LITERATURE

The Birds of the Bahamas. By P. G. C. Brudenell-Bruce. Taplinger, New York, 1975: 142 pp., 4 color and 9 black-and-white plates, 2 maps. $10.95.—The first thing that confronts a reviewer of this book is the title. Apparently the American publisher decided that a field guide to "The Birds of New Providence and the Bahama Islands," the title of the British edition, would sell better under the broader designation. Accordingly, although this book is printed in England and to all intents *is* the British edition (complete with British spellings), the dust jacket cover, end flaps, and title page of the "American edition" have been changed. Taplinger did not go to the expense of altering the title on the book spine (*under* the dust jacket, from a purchaser's viewpoint) or on the half title page; these still declare it to be "The Birds of New Providence and the Bahama Islands." And so it is.

A field guide to Bahamian birds has long been needed. The only other recent book on the subject is so poor as to be useless. Therefore, until the present guide appeared, one had to carry both North American and Bond's West Indies guides to identify birds seen in the Bahamas. Now one still has to carry a North American guide, but Brudenell-Bruce's book weighs less than Bond's and is limited to the Bahamian fauna. It includes all the species recorded in the Bahamas (206, plus 69 accidentals), but illustrates only 31 native land birds in color and another 61 species in black-and-white. The remaining 111 species are referenced by plate number to Peterson's eastern guide. Apparently by error, illustration references to 3 species are omitted; all 3 are available in Peterson.

The book focuses on the birds of New Providence both because that island is by far the best known ornithologically, and because the author could draw on his own experiences during the 4½ years he lived there. New Providence is a small island, with only 1.3% of the land area of the country. Nevertheless, it has over 60% of the human population, the capital city of Nassau, and a busy tourist trade. From the Bahamian point of view, Nassau/New Providence are of paramount importance—hence the custom of collectively calling all the other islands the "Out Islands" (or, more recently, the "Family Islands") even though they make up 98.7% of the total land area. The Bahamas contains approximately 17 major islands and some 700 smaller ones. Ornithologically, New Providence is both typical and atypical of the country. It is one of the 4 northern islands to contain pine forest. It also receives more rainfall than do the southern islands, and is not subject to the extreme drying effects of the southern trade winds. New Providence is by far the most disturbed island in the Bahamas, but it may also be the most diverse in terms of numbers of habitat types. It has more cleared land, flowering gardens, and large trees (other than pines) than do the others. Approximately 222 species of birds have been recorded there—with only an additional 53 known from all the rest of the country. Of the New Providence species, 40 are year-round residents, 9 are summer breeders, 70 are winter visitors, 71 are passage migrants only, and 32 have been listed as vagrants.

The text arrangement and nomenclature follow the AOU Check-list and Bond. Each species account begins with the English language name (occasionally supplemented with older, British, or local synonyms) and the scientific name. The body of most accounts is divided into: status (first on New Providence, then in the Out Islands); description and habits; voice; and nest. The thoroughness of each account is heavily influenced by Brudenell-Bruce's experience with the species. The treatment of birds he knows well is generally excellent, filled with useful, often new, information. If a species does not occur on New Providence, however, it is too often given short shrift. For example, the interesting and rare endemics that are found only on other islands: the Cuban Parrot, *Amazona leucocephala bahamensis*, rates only 4 lines (and those partly inaccurate); the Black-cowled Oriole, *Icterus dominicensis northropi*, another 4 lines (vs. the New Providence passage migrant *Icterus galbula* with 14 lines); and the West Indian Red-bellied Woodpecker, *Melanerpes superciliaris* (3 endemic subspecies), only 6 lines. Even the national bird, the American Flamingo (*Phoenicopterus ruber*), is granted only 9 lines, heavily devoted to explaining that it can be seen on New Providence only in captivity. Thus the author not only skimps on Bahamian specialties, but also generally ignores the fact that many are conservation/protection problems. Of the endemics listed above, only the oriole is not a "Red Data Book" bird.

As Brudenell-Bruce has visited only 4 other islands for brief periods, most of the information on Out Islands species is drawn from the experience of others, notably from James Bond's writings and records obtained from C. Russell Mason. Granted that many of these islands are poorly known ornithologically, more information is available than the author found. Even in the references he used, he sometimes missed pertinent information. For instance, he states that the Bobwhite is not found in the Out Islands, yet Bond (at least as early as 1961) gives it as also introduced on Andros and Eleuthera. From personal experience I know it is doing well on Andros. The author curiously ignores Rock Doves (which I have seen at least on New Providence, Eleuthera, and Great Exuma), but he includes Starlings and House Sparrows as well as more exotic introductions such as White-bellied Doves (*Leptotila jamaicensis*) and 2 species of grassquit (*Tiaris*).

In a field guide it is never possible to cite references for all records, but I wonder on what authority the author suggests that the Northern Mockingbird (*Mimus polyglottos*) might not occur on Crooked Island (I saw it there in March 1976). The author's lack of experience outside New Providence also shows in some of his species descriptions. No one familiar with the *Melanerpes* in the field would italicize *red belly* as an important field mark. The upper border of the face mask on Bahama Yellowthroats (*Geothlypis rostrata*) is only lightly washed with yellow in some individuals, and is a poor field character. The wintering North American race of Yellow-throated Warbler (*Dendroica dominica*) is described (as having white underparts), but not the distinctive endemic race (with yellow underparts) on Grand Bahama and Abaco; nor is the reader aided by the black-and-white illustration.

The plates by Hermann Heinzel range from good to excellent. Some of the species that apparently were unfamiliar to the artist look a bit wooden, but most are good field guide renditions. I noticed, however, a few errors: for example, the *Melanerpes* woodpecker is far too white on the head and underparts; and the Bananaquit (*Coereba flaveola*) lacks its distinctive red mouth corners. Interestingly, the Bahama Yellowthroat male was painted with a gray-blue-white mask border, while the plate caption states it is "Distinguished from Common Yellowthroat by . . . yellowish upper border to mask . . . ," and the Greater Antillean Bullfinch (*Loxigilla violacea*) plumages are marked ♂ and ♀ on the plate, but adult and immature (correct) in the caption.

This book clearly has drawbacks, especially as a guide to the Bahamas as a whole. Many of the descriptions are too brief, especially of birds that are not illustrated, absolutely requiring the supplementation of a North American guide. My main objection, however, lies with the too-brief accounts of many of the native species—the sort of material not easily found elsewhere and surely to be expected in a guide to a limited avifauna. Certainly the resulting book is slim enough that much more text could have been included.

On the positive side, the author has done a generally competent job on New Providence birds, and has included several useful features such as local common names, appendices with details of accidental records and song periods of 9 breeding species, and a good index. The book is well bound—my copy has had hard use in the field and is still in fine condition—especially for an English binding. But mostly this guide is, at last, a field book limited to Bahama birds—a relief after years of picking through Bond's guide which, excellent as it is, covers a much larger fauna.—MARY H. CLENCH.

ORNITHOLOGICAL GAZETTEER OF ECUADOR. By Raymond A. Paynter, Jr., and Melvin A. Traylor, Jr. Museum of Comparative Zoology, Cambridge, Mass. and Field Museum of Natural History, Chicago, Ill., 1977: viii + 151 pp., 2 maps, paperbound. $5.00. Order from Bird Dept., Mus. Comp. Zool., Harvard Univ., Cambridge, Mass. 02138 *or* Bird Division, Field Mus. Nat. Hist., Chicago, Ill. 60605.—This is the second in a series of gazetteers of Neotropical localities where birds have been collected or observed. With a few exceptions, the format of the first (Bolivia) gazetteer has been maintained (for review, see Wilson Bulletin 88:679–680, 1976). The bibliography of the Bolivian volume listed only publications cited in the text, but nevertheless amounted to what the authors had described as "virtually a complete bibliography of Bolivian ornithology." Paynter and Traylor, in their new volume, have tried to assemble "a complete list of all publications concerned primarily with Ecuadorian birds (exclusive of the Galápagos), not merely those that have been cited in the gazetteer." I need hardly say that this bibliography of 198 titles will be invaluable to workers on South American birds, and the authors are to be congratulated for their decision to augment the list of references cited.

Paynter and Traylor explain that preparation of a gazetteer for Ecuador was vastly more difficult than was true for Bolivia. The literature pertaining specifically to Bolivia is relatively small, and only a few museums have significant collections from that country. Ecuador, on the other hand, has a long and complicated history of ornithological exploration, much of it by professional collectors who sent birds by the tens of thousands to museums and private collections around the world. Label data from many of these specimens are inadequate or misleading. The authors' introduction goes into some detail as to specific problems encountered in trying to verify itineraries and localities.

An innovation is a second map (in addition to that showing major political subdivisions and rivers) of Ecuador on which all collecting sites (and a few observation sites) have been dotted—the only other information on the map is the 1000 meter contour. "This should help the zoogeographer to decide whether a gap in a distribution may be of biological significance or whether it may merely reflect the absence of collectors." The map certainly calls attention to those portions of Ecuador that have been relatively neglected, notably the Amazonian east and the northwest, in contrast to the heavily collected high Andes in the vicinity of Quito.

The authors have done such an important service to Neotropical ornithology that a reviewer must seem to be a cranky ingrate for wanting even more. Yet the gazetteer could have been substantially more complete and its accuracy improved had the authors followed the suggestion made in my earlier review, and circulated a preliminary copy among museums with major holdings in Ecuadorian birds. The amount of additional work that would have fallen on the shoulders of the authors themselves would have been minimal. For example, there are nine localities listed as "not located" that are cited only from publications of J. T. Zimmer of the American Museum of Natural History. During a visit to that museum, I was able to solve six of these problems in less than an hour. As Paynter and Traylor suspected, some of these were typographical errors or were mistranscribed from labels by Zimmer: "Guapiles" and "Guapilo" for Guápulo, and "Lonambo" for Conambo, for example. "Río Yamisa," which they could not locate, is "Rio Yamasa" on the specimen label. This spelling is not in the gazetteer, but the label data also include the altitude, date, and collector's name, which might have helped to identify this locality. The authors were unable to find "Chitoque," a locality listed by Zimmer for *Tangara nigroviridis consobrina.* By looking up the cited specimen, I was able to determine from the label that Chitoque is or was on the Alamor-Guachanama trail, Prov. de Loja, at an altitude of 57 feet, and that the specimen had been taken by Cherrie and Gill on 13 September 1921. I have been assured by ornithologists at the American Museum that they would have been delighted to provide this kind of information had the authors so requested.

Carnegie Museum of Natural History has relatively few birds from Ecuador. Most of these were obtained by exchange from the Moore Laboratory of Zoology, Occidental College. In checking the collecting localities represented in our Moore material, I found ten that are not listed at all by Paynter and Traylor, and supplementary information (such as alternative spellings and extensions of collectors' itineraries) for 19 more. Although I have not discussed this with staff members of the Moore Laboratory, I have no doubt that they would have been happy to cooperate in this important project by consulting the itineraries and maps of Robert T. Moore that are housed at Occidental, thus filling in some significant gaps in the gazetteer.

The Bolivian and Ecuadorian gazetteers will be extremely valuable assets to the working libraries of students of Neotropical birds, as will, I am sure, additional volumes in this series. Again I urge the authors to take the time (I see no reason why there should be critical publication deadlines for works like these) to circulate copies of future manuscripts among those of us who might be in a position to help make the gazetteers even more nearly complete. Few ornithologists of my acquaintance would begrudge the time needed to assist such a worthwhile project in view of the tremendous effort already made by the authors.—KENNETH C. PARKES.

MAINTENANCE BEHAVIOR AND COMMUNICATION IN THE BROWN PELICAN. By Ralph W. Schreiber. Ornithological Monographs No. 22, 1977: 78 pp., 38 figures. $6.00 ($5.00 to A.O.U. members).—This highly detailed description of Brown Pelican colony behavior is the first full ethogram for any pelican, and will doubtlessly become the basis for comparison with other species in the family. Schreiber's presentation is well organized, thorough, and usually very clear. The rather scanty extant literature on other pelicans is integrated throughout.

A major drawback for anyone other than a pelican worker is that the monograph is boring to read. Few readers will care to plod through 34 pages of raw descriptions of comfort activities, and the "communication" half is not much more exciting. Schreiber's carefully worded descriptions of motor patterns are frequently interspersed with lengthy quotations from his own field notes, as if they were a special source that must be quoted verbatim. Only rarely is the reader's perserverance rewarded with an eyebrow-raising anecdote (for example, if a male pelican drops a stick while flying back to the nest he usually completes the elaborate Nest Material Presentation anyway). The monograph contains little quantification, mostly just the statement of how many times Schreiber observed a particular behavior in the field.

Considering that Schreiber has spent several years doing the field work (his diligence and care are apparent on every page), I was disappointed in the monograph on two counts. First I felt that Ornithological Monographs got stuck with the driest material from a very holistic field study. (Schreiber notes on page 1 that his data on nesting cycles, population fluctuations, age-class composition, reproductive success, and plumage characteristics will be published elsewhere. His data on chick growth patterns, feeding behavior, pesticides, and population history have already been published.) I wonder if the monograph series might not have rated something beyond raw ethological description. Secondly I felt that Schreiber could have posed some more fundamental (and interesting) evolutionary questions about the behavior he described. For example, he explains that Brown Pelicans have remarkably sluggish social lives. They use only 5 displays and generally keep things very simple. By contrast, many other colonial birds, some of which nested in the study colonies near the pelicans, have highly complex social interactions. *Why* are the pelicans so simple? How can they accomplish the many tasks of pair-formation and successful reproduction with only 5 signals? Schreiber is probably the only person in the world sufficiently knowledgeable about pelicans to intelligently ponder such matters and his speculations could have been provocative.

The paper begins with maintenance behavior (shaking, stretching, scratching, preening, bathing, locomotion, and thermoregulation) because some of these motor patterns have been modified by evolution as social signals. Then comes a brief transitional section on "Attack and Escape" before the concluding "Social Behavior." The generally lucid descriptions are profusely illustrated with 270 mediocre line drawings, including 30 of preening and 10 more of a comfort activity called "glottis exposure." Do we *need* 10 illustrations of "glottis exposure?" There are no photographs, though many of the drawings were derived from original photos and a few are even called "photos" in the text (p. 61).

The volume is reasonably free of editing errors though "flys" and "uropygeal" were found. Display names are capitalized in accordance with Moynihan's established convention and then the word *display* is redundantly tacked on (e.g., Bowing display). The caption for figure 25 is nonsensical. On page 36 an apparent error in paragraph organization implies that courting male pelicans may go as long as 3 weeks without food! (If this is not an error then it deserves considerably more explanation!) Elsewhere the description slips occasionally into vagueness (e.g., we are informed that the Upright is often maintained ". . . for some time"). One popular but unfortunate descriptive trick that Schreiber uses repeatedly is the concept of behavioral "intensity." This is a nonterm referring to variability in the broadest sense. We read about high- and low-intensity display performances, high- and low-intensity courtship activity, etc. In "high-intensity Bowing," for example, the pelican's head is held below foot level while in "low-intensity Bowing" the head is above foot level. There is also some suggestion that the bird is somehow more excited when it is involved in "high-intensity" behavior. Schreiber also uses the word in its general sense ("intense eye contact") which makes things even more confusing. It seems paradoxical that the concept of "intensity" should have such sustained popularity among ethologists who generally credit themselves with using only descriptive terminology. Schreiber could as easily have subdivided the variability observed in Bowing into "high-neck" and "low-neck" descriptive categories.

Perhaps a more crucial problem is that Schreiber frequently overstates his evidence. At times this could have been avoided by the editorial insertion of a qualifying adverb (e.g., "probably" or "apparently") that would have softened the sentence's tone. Elsewhere he seems to have overstepped the limits of scientific prudence, as in the following generalization: ". . . the subtle and highly variable differences in context in which the displays are performed and received modifies these messages, and thus each encodes different precise probabilities of further action" (p. 72). This is an attractive working hypothesis—being the basic premise of W. John Smith's message-meaning approach—but it is not *fact.* Schreiber gives no evidence to support even the broadest outlines of the claim, much less to demonstrate "precise probabilities."

My last complaint concerns the widespread opinion that pair-formation in many monogamous species can be justly characterized as a "female-choice" system. Schreiber shares this view as shown by his statement that ". . . mate selection is accomplished by the female, who selects the male" (p. 37). It is true that in many colonial birds, including pelicans and herons, the males take fixed positions and display while females move about as if "shopping" among them. Outwardly it *looks* as if females do the choosing and the males are merely passive merchandise. The theoretical implication is that natural selection acts only on the females despite the fact that these males make enormous parental investments. Actually, of course, males are very choosy about their mates; a preference they show by driving away (or ignoring) any females they wish to reject. Schreiber's own observations confirm this view just 3 sentences after the female-choice statement: ". . . some females are not allowed on the perch, and frequently a female will be allowed onto the perch but then is kept off the nest site. In these cases pair bonding does not occur." As evolutionary theory would predict, both sexes choose carefully. The lengthy courtship is clearly a period of *mutual* assessment.

In conclusion I should like to stress the strengths of this paper because it does provide remarkably detailed information on Brown Pelican behavior. I expect Schreiber's collective works to become the starting place for an exciting comparative literature on the ecology and behavior of pelicans. His work may become to the Pelecanidae what Bryan Nelson's Gannet study was to the Sulidae. Its tedium does not detract from its value as a reference work, though it will probably not attract a wide readership.—Douglas W. Mock.

Alberta Birds, 1961–1970, with Particular Reference to Migration. By Thomas S. Sadler and M. Timothy Myres. Occasional Paper No. 1, Provincial Museum of Alberta, Natural History Section, Edmonton, Alberta, Canada, 1976: 314 pp., 1 map. $3.25.—This work summarizes many bird observations by 225 observers in various parts of Alberta and taken from the published literature. Major justification for the book is to "provide basic data for subsequent analysis by . . . students of the migratory behaviour of particular groups of Alberta birds." The main part of the work is 233 pages of "species records and summaries, 1961–1970." Each entry begins with a brief summary of the decade's records on migration, distribution, breeding records and population status and trends. Records are then listed by year in a telegraphic style, with each entry prefaced by an alphabetical code identifying the kind of observation it is, i.e. spring arrival, peak numbers recorded in migration, and so on. The observations usually include the number of birds seen, date, locality, and the observer or source of the data.

Occasional comments show, for example, that the spring of 1967 was particularly harsh for migrants as indicated by the following observations: a Pygmy Owl was found "frozen to death in a blizzard" in April, the Tree Sparrow migration was "interrupted by a mid-April snow-storm" and in late April about 1000 Lapland Longspurs were seen "in the shelter of a barn during a snow-storm." Some observations are also of ecological interest as, for example, the observation of very high nesting densities of Short-eared Owl in the Calgary area in 1969 because of a high spring vole population.

Several short sections precede the species list. There is an Introduction, a tabulation of the bird highlights of the decade, and a brief section on birds and main weather events of the decade. The latter section and the Introduction are attributed to the junior author. There is also a section listing the place names mentioned in the text with references to a map of Alberta by which they can be located. Another section lists the dates of the Sundays in the decade, and finally a section explains the symbols used in the species accounts.

The contributors to the volume are listed immediately after the species accounts. Then follows a bibliography of 259 publications concerned with Alberta birds in the decade covered by the book. Separate indexes to scientific names and English common names conclude the work.

The book discusses 341 species. These include confirmation of the historic presence of the Passenger Pigeon in Alberta, the recent so-far-successful establishment of Wild Turkey, and a recent unsuccessful release of Chukar. Other first occurrences in the decade were Cattle Egret, Ruff, Black-necked Stilt, Band-tailed Pigeon, Yellow-billed Cuckoo, and Scarlet Tanager. Of more significance are changes in the status of some species, such as the continued decline of the White Pelican and the Peregrine, and the apparent decline of the Burrowing Owl. The Black-crowned Night Heron, Cinnamon Teal, White-breasted Nuthatch, and Yellow-headed Blackbird are regarded as increasing, while such species as the Cooper Hawk, Blue Jay, and Herring Gull are reported to be more widespread than previously.

Considering the authors' stated objectives this work is fairly successful. It does provide many records of arrivals, departures, flock sizes, breeding records, and distribution data. Students of Alberta bird populations will find this a very useful source of such information. However, I would have liked to see more analysis of the data, more effective presentation of climate data, and more discussion of the interactions of birds and climate. Had this been done the work would be a more important contribution than it is.

The book seems free of minor typographical errors, but there is a major problem with the indexes. The page references in the scientific and vernacular indexes are all incorrect although they agree with each other. The publishers should correct this error as soon as possible. The last four items in the Table of Contents are also incorrect.

I recommend this book to anyone interested in the birds of Western Canada. It may be purchased from: The Bookshop, Provincial Museum of Alberta, Edmonton, Alberta, Canada, T5N 0M6.—WILLIAM J. MAHER.

BIRD POPULATIONS OF ASPEN FORESTS IN WESTERN NORTH AMERICA. By J. A. Douglas Flack. Ornithological Monographs No. 19, 1976: viii + 97 pp. $7.50 ($6.00 to A.O.U. members). (Obtainable from Glen E. Woolfenden, Department of Biology, University of South Florida, Tampa, Florida 33620.)—Aspen forests in western North America constitute a physiognomically distinctive community, somewhat isolated from other broad-leaved vegetation types. In this important study the avifauna of this community is examined through the strip censusing of 41 plots, each in a homogeneous aspen forest. Two visits were made to each plot, the area censused in most cases being 12.5 acres. The stands censused fall into 2 regional groupings, western montane (27 plots) and prairie parkland at lower elevations in Canada. Aspen forests of the 2 regions, which are disjunct in Montana, differ in that summer nights in the parkland are warmer, and summer moisture greater, contributing to faster growth, greater incidence of diseases and shorter life spans of the trees there. Undergrowth usually is more dense in the parkland forests which have experienced more disturbance in pre-settlement time. In contrast, the montane stands tend to be mixed in their age composition.

The population data are minimal but the relative values are used to probe significant ecological and evolutionary questions. Species composition and total numbers are considered in relation to many vegetational parameters that relate to the birds' habitat requirements. Such responses are analyzed further by the grouping of species into 5 nesting guilds to which species are assigned by the positions of their nests. This categorization points to regional differences in the representation of certain groupings, such as a paucity of cavity-dependent nesters in the parkland. Although there are fewer species and individuals in the montane stands, bird species diversity (Shannon-Wiener function) in both regions appears greater than expected on the basis of foliage profile features. Size, spacing and health of the trees emerge as other factors contributing to bird species diversity.

Species compositional differences between the two regions receive considerable attention. Twenty aspen-dwelling species are considered restrictedly montane, 24 occur only in the parkland and 24 are shared. The greater number of species in the parklands is attributed to the proximity of a larger pool of prospective colonizers of aspen stands in the eastern deciduous forests. Representation of species derived from that source decreases progressively southward in montane aspens. In the absence of 10 species found in such timber farther north, species diversity in aspen forests in Arizona is maintained by such characteristic conifer forest species as the Evening Grosbeak and Western Bluebird.

The last example points to a considerable contrast in the avifaunas of the 2 regions that is only partially borne out in a schematic summarization of "Geographic Replacement of Morphologically Similar Species" (Table 5). Here, species of minor occurrence (= frequency), such as the Western Tanager, are not distinguished from those that are widespread and/or numerous. In a succeeding table the species are ranked according to their importance regionally. Table 5 would have been more meaningful had the relative importance of the species included been denoted by size or boldness of type. The contrast between the avifaunas of the 2 regions is diminished further by the omission of other species (such as the Broad-winged Hawk, which lacks a counterpart in montane aspen).

With reference to ecological equivalence, I question the author's view (p. 64) that the more rigorous montane climate does not limit species composition. Several western forms equivalent to or conspecific with parkland inhabitants appear confined to levels below the aspen belt in the central Rocky Mountains (Bullock's Oriole, Gray Catbird) or they reach greatest abundance at lower elevations (Brown-headed Cowbird). The role of the elevational difference is conceded indirectly by Flack in his discussion of foothill aspen stands in Alberta as being faunistically and climatically intermediate (p. 77).

The topics discussed above demonstrate the emphasis placed upon historical factors, many of which (e.g., routes of colonization) are elusive. Ecological questions, however, receive at least equal attention. Attempts are made to explain abundance or absences on the basis of vegetational features, and the question of saturation in this community is weighed carefully.

The success of Flack's study derives from the application of relative abundance values based upon standard censuses by one investigator to comparisons of broad geographic scope, and from a thorough integration of his findings with a diverse literature. Many of the questions raised, such as fluctuations in populations of widely distributed species, can be answered only by long-term studies that should be undertaken by resident naturalists.

The reader's task would have been aided by the provision of a map showing the extent of the parkland in relation to other vegetation types. Membership in the seven somewhat subsidiary foraging guilds might have been coded in the nesting guild lists. The few proofreading lapses (even "Red-bellied Sapsucker") do not hinder the reader's understanding. However, these criticisms detract but little from an informative and thought-provoking monograph.—KEITH L. DIXON.

WATCHING BIRDS. By Roger F. Pasquier. Houghton-Mifflin Co., Boston, 1977: 301 pp., 100+ black and white drawings by Margaret La Farge. $10.00.—"*Watching Birds* is . . . intended to unite the bird watcher's perception of specific details with the environmentalist's awareness of general truths" (p. viii). This handsome elementary ornithology book is dedicated to the amateur birdwatcher who wishes to advance beyond the mere "life list" stage of his hobby and expand his understanding of most aspects of bird biology, including the relationships of birds to each other and to their environment. Any non-professional ornithologist could profit from reading this book, which is mercifully free of jargon and which sticks to basic facts about birds. This volume would serve as a high school ornithology text, or for a reference to supplement the library of a bird aficionado. Chapters cover such aspects of avian biology as Origin, Evolution and Speciation (Chap. 3), various aspects of anatomy and locomotion (Chaps. 4 and 6), Behavior (Chaps. 5, 7, 8, 10, 11), and Zoogeography (Chaps. 10 and 12). Also included are discussions on conservation, general birdwatching, and an overview of current progress in ornithology (Chaps. 1, 13, 14, 15).

By and large the text is quite enjoyable and complete. Occasionally, some statements smack of dogma (e.g. "In every case the individuals that are going to survive and reproduce will be those best adapted to their niche . . ." p. 27), and the discussion of speciation (p. 28) is superficial. But there is little sense in cluttering up a very basic and readable text with current and sometimes confusing problem areas of biology.

Mr. Pasquier has a feel for birds, and his text imparts this delight of the subject matter to the reader. Reading it could mark a turning point in the life of those birders whose major thrill is hunting down and checking off a new trophy on their lists. New observations of behavior of familiar species can be as exciting as, and certainly more enlightening than, the hunt involving pad and pencil.

The illustrations by Margaret La Farge are superb, both scientifically and aesthetically. They are well chosen and delightful. Both the author and artist would likely agree with Thoreau who said. "The wood thrush is a more modern philosopher than Plato and Aristotle. They are now dogma, but he preaches the doctrine of this hour." Their book reflects such thinking and I recommend it to anyone who loves birdwatching, and, more importantly, birds.—MICHAEL A. MARES.

A GUIDE TO BIRD FINDING EAST OF THE MISSISSIPPI, Second Edition. By Olin Sewall Pettingill, Jr., illus. by George Miksch Sutton. Oxford University Press, New York, 1977: xxvii + 689 pp. $15.95.—The standard guide to finding birds in the eastern United States has been revised to take into account changes in distribution, changes in habitat, and to provide new travel directions resulting from an expanded road network, especially the interstate highway system. For each of the 26 eastern states the major birding localities are listed, and for each there are instructions for reaching it, a brief description of the habitats, and comments on the kinds of birds to be found there at various times of the year.—R.J.R.

SUMMER BIRDS OF THE SAN JUAN VALLEY, NEW MEXICO. By Carl Gregory Schmitt. New Mexico Ornithological Society Publication No. 4, 1976: 22 pp., no price given.—An annotated list of about 147 species observed during the summers of 1971 and 1972, with comments on numbers, breeding status, and habitats.—R.J.R.

PLUVIANELLUS SOCIALIS: BIOLOGY, ECOLOGY AND RELATIONSHIPS OF AN ENIGMATIC PATAGONIAN SHOREBIRD. By Joseph R. Jehl, Jr. Trans. San Diego Soc. Nat. Hist., 18 (3): 25–74, 1975. 28 figs., 3 tables.—In recent years there have been a number of studies on the ecology and behavior of shorebirds, many dealing with social organization. However, a clear picture of the evolution of social systems within a group is only possible once the behavior, ecology, and taxonomy of many species is described. Although not complete, such baseline information exists for shorebirds and the task at hand is to add basic information on key species. *Pluvianellus socialis* is such a species and Jehl has provided an excellent description of its behavior and ecology. This paper concerns such topics as habitat and distribution, vocalizations, pre-nesting and nesting behavior, growth and care of the young, foraging and feeding behavior, molts and plumages, and systematic relationships.

Jehl studied *Pluvianellus* on its wintering grounds in 1971 and 1972 and on its breeding grounds in 1973. The total population, which may not exceed 1000 individuals, breeds along lakes from the Rio Grande (Tierra del Fuego) north along the southeastern coast of Patagonia to Puerto Deseado. It winters along the coast from the Strait of Magellan to the Valdes Peninsula. *Pluvianellus* has been considered a plover, but Jehl, whose knowledge of shorebird taxonomy is considerable, suggests from his observations that "its relationships are far less obvious."

Pluvianellus returns to the breeding grounds in early September and begins breeding up to several weeks before other Fuegian shorebirds. The chicks hatch before most North American migrants arrive. The birds nest on the shores of shallow ponds, lagoons, and lakes in the steppe region of northern Tierra del Fuego and southern Patagonia. They nest along brackish and fresh water lakes, but not along streams, rivers, or the ocean. Obvious requisites are beaches of intermixed small stones and mud with adjacent stretches of open shoreline. The number of pairs at a lake was limited by the amount of suitable habitat and the presence of other shorebirds, but not by the size of the lake.

Due to the arrival time of the investigator, information on pair formation and territory acquisition are omitted. However, renesting by one pair allowed Jehl to describe this phase qualitatively. *Pluvianellus* defends linear territories of 300 to 500 m along the shoreline. The complicated territorial defense displays, described with diagrams and photographs, involve the members of a pair acting as a unit as is typical of oystercatchers and plovers. Territorial clashes increase in frequency and intensity as the chicks become more mobile. Although Jehl's descriptions of these clashes provide an excellent qualitative picture of the behaviors involved, quantitative data are necessarily lacking on daily and seasonal variations since the rarity of the species in general, and the small number of pairs on any one lake make it difficult to quantify the behavior described.

Nests, located 0.7 to 25 m from water in fully exposed situations, were excavated by digging and lined with small bits of gravel. *Pluvianellus* lays 2 eggs, but only one chick is actually raised. Egg laying occurred from 4 September to 17 November. Both sexes incubate. Jehl observed no exchange displays and no distraction displays by adults incubating or caring for chicks.

Jehl notes that the young chicks are less agile than plover or sandpiper chicks of the same age. The 2 eggs hatch 8–14 h apart, and the chicks leave the nest the day after hatching. The slight age difference results in the success of only the older chick; the 5 families over 3 days of age observed by Jehl included only 1 chick. Both sexes feed the young by regurgitation as well as with food carried in the bill. Parental feeding is "extremely unusual in the Charadrii, and the use of the crop to regurgitate differentiates it from all other shorebirds." Chicks obtain all their food from their parents for the first 2 weeks, then begin to forage for themselves. During this dependency period chicks remain concealed and depend on their coloration for protection. Jehl concludes from the growth pattern that *Pluvianellus* chicks fledge at a much higher weight than that of similarly sized shorebirds that forage for their own food.

Pluvianellus' foraging and feeding behavior parallels that of turnstones. It is apparently the only Charadriiform bird that digs for food.

Wintering behavior is also described. The species' winter requirements are intertidal rocky areas and debris covered sandy beaches on which to feed. The species is uncommon and irregularly distributed along the Patagonian coast. In contrast to its breeding season behavior, the species avoided the water's edge in winter and fed in flocks with other shorebirds.

The concluding section on systematic relationships lists the aspects of *Pluvianellus*' morphology and behavior that differ from the usual plover condition: turnstone-like body, short stout legs and blunt claws, foraging pattern which includes digging, territorial defense behavior involving the pair acting as a unit, complex pre-copulatory and scrape displays, courtship feeding, small eggs, clutch size of 2, rearing of only 1 chick, absence of distraction displays, semi-precocial chicks, slow chick growth, prolonged dependence of chicks, unique natal down color, parental feeding of chick, and apparent dove-like drinking behavior. After an excellent discussion of the problem, Jehl concludes that the species should be in a new monotypic family Pluvianellidae.

In general, the problem is clearly defined, the paper is succinctly written, and the diagrams and photographs are clear and contribute to the descriptions. This first detailed study on *Pluvianellus* provides excellent descriptive data on breeding and nonbreeding behavior so necessary for the comparative approach to shorebird behavior.—JOANNA BURGER.

BIRDS OF THE ANTARCTIC AND SUB-ANTARCTIC. By George E. Watson, in collaboration with J. Phillip Angle and Peter C. Harper, illus. by Bob Hines. American Geophysical Union, Washington, D.C., 1975: 350 pp., 11 color plates, 55 black-and-white illustrations, 51 range maps, 11 numbered text figures, 7 tables, hardbound. $15.00.—This is the most unusual book review that I have written, because long before the book's release, I was asked by George A. Llano of the National Science Foundation to field test the original manuscript in the Weddell Sea off Antarctica. In late December of 1972 I boarded the Coast Guard Icebreaker *USCGC Glacier* at the American base McMurdo by the Ross Sea. The voyage that followed took a course nearly 180 degrees around the Antarctic continent, including a northward thrust to southern South America and a southward one that penetrated pack ice deep within the Weddell Sea. My travelling companion was S. D. MacDonald of the National Museum of Canada. He was especially valuable to the project because of his keen eyes and exceptional ability at identifying objects far off.

MacDonald and I are experienced birders, and have often worked as a team in the High Arctic, but we were totally inexperienced at identifying southern sea birds. Up to the time the *Glacier* broke free of the pack ice in the Ross Sea and entered the open ocean, neither of us had seen an albatross or the many petrels and storm-petrels that cover these southern waters. We were truly in a good position to test Watson's descriptions and Bob Hines' illustrations.

Many people have had important input in the production of the handbook. Foremost among these was George Llano, who thought not only in terms of a handbook of birds to serve the growing number of people visiting far southern places, but of a series of handbooks covering various biological disciplines for these areas. With the financial backing of the National Science Foundation and continued assistance by Llano, the handbook on birds became a reality. The selection of George Watson as author was a very good choice. He, J. Phillip Angle and others had earlier finished an important scientific work entitled "Birds of the Antarctic and Subantarctic," edited by Vivian Bushnell and published in 1971 by the American Geographical Society as Antarctic Map Folio Series 14. No doubt this work formed the skeletal structure of the present handbook.

At the beginning of our voyage, MacDonald and I experienced difficulty in identifying southern sea birds, especially prions and immature albatrosses, but by and large things went well. The manuscript and illustrations were indispensable, really a tremendous aid, and there is no question in our minds that we would have been severely handicapped without them. We caught some inconsistencies, a few errors or oversights, and pointed out a number of troublesome areas dealing mostly with at-sea identifications. Hopefully, our efforts produced a better handbook.

As good as the text and illustrations are, there still remain shortcomings that only too soon became apparent to the user. There is to my knowledge no easy method for separating at a distance Antarctic Terns in first-year plumage from either young or old Arctic Terns in winter plumage, especially in areas where both species occur. This point really struck home as I recently observed a number of experienced birders aboard the *Lindblad Explorer* chalk up Arctic Terns when in fact they were seeing immature Antarctic Terns. I knew this to be the case for I had learned by experience that immature Antarctic Terns often associate with adults at or near the breeding colonies, as were the birds observed by the *Lindblad* birders.

The void between research and publication is always a hopeless matter. Months before publication of the handbook we had new information on terns and skuas that should have been included, but there is no stopping the publication machinery once set in motion. How I wanted to tell artist Bob Hines not to use large pupils in the eyes of his penguins, for even in fairly poor light the pupils of most penguins seen by us appeared as pinpoints, giving the penguin its colorful but blank, pupilless appearing eye.

Be as it may, the handbook contains a wealth of useful information. Included in this durable pocket-size book, in addition to species descriptions and much life history information, are accounts of the geography and environments of the southern lands and seas, including climate, vegetation, record taking, preserving and shipping specimens, conservation, and specially protected areas. The distribution maps and tables are very useful. The references are extensive and the index complete. All these many facets, really an amazing assemblage of material for a small size book, are logically arranged and written in a clear, succinct manner.

The black-and-white illustrations play their role well, but it is the color plates that one will return to time and again throughout one's voyage. Composites showing many birds in flight are a difficult, dreary proposition for any artist. Bob Hines is to be congratulated for pulling it off as well as he has, for his was an especially tough assignment with so many birds with similar shapes and colors.

Perhaps the most pertinent question that can be asked of a work of this kind is, "who will be able to use it effectively?" On this point there is little doubt that almost any experienced birder, professional or non-professional, will be able to do so. For the inexperienced person it may be a different matter. From the start it was hoped that the handbook could be used effectively by non-birders, even highly trained scientists, in making records during voyages when an ornithologist or bird watcher was not present. But a good friend, an expert on invertebrates, confided that it took more than the handbook to enable her to identify sea birds accurately. She discussed the need for large, highly demonstrative illustrations (preferably color *plus* black/white prints *plus* line drawings and written descriptions) of each species in different conformations, which could be mounted (for instant comparison) on the bridge and the pilot house. If such identification sheets were available to relevent ships' personnel, perhaps more realistic bird censuses could be taken. This is a big order to be sure. Maybe for these special cases the only solution is a short course in bird watching along with the handbook. But whether best for the experienced or inexperienced, the handbook nevertheless is indispensable for anyone contemplating observations of far southern birds at land or at sea.—DAVID F. PARMELEE.

PENGUINS, PAST AND PRESENT, HERE AND THERE. By George Gaylord Simpson. Yale Univ. Press, New Haven and London, 1976: xii + 150 pp., 10 color and 24 black-and-white photographs, 9 maps. $10.00.—In 1933, George Simpson and his party made a collection of fossil mammals in Patagonia and incidentally accumulated the best collection of fossil penguin bones of its time. Unable to find an ornithologist willing to study the collection, Simpson took up the cudgel himself and published his well-known monograph on fossil penguins in 1946. Since then he has continued his studies of fossils and has seen most of the living species in the wild as well. His infatuation with penguins inspired him to write this book "for adults who do not necessarily know much about penguins but for whom there is nothing that they do not really want to know." With such readership an author is presumed relieved of the necessity of commanding attention by irresistible prose.

The first chapter on the earliest accounts of penguins is nevertheless sprightly and almost irresistible. The next chapter on naming penguins begins in the same vein but it becomes more pedantic and ends with a discussion of each species' scientific name. Subsequent chapters continue as competent accounts of general features of penguin biology, fossil penguins, distribution and speciation of extant penguins, breeding behavior and ecology, and exploitation of penguins by man. Except for occasional light touches, however, this major portion of the book is likely to lose readers who want more than just facts. Unfortunately, neither the black-and-white, nor the color photographs are exceptional, and the distribution maps are sometimes difficult to interpret.

Dr. Simpson's book provides broad coverage of penguins for the layman. It falls short of Pettingill's "Another Penguin Summer," however, in presenting "the singular charm of penguins."—RICHARD L. ZUSI.

PARENT BIRDS AND THEIR YOUNG. By Alexander F. Skutch. Univ. of Texas Press, Austin, 1976: xviii + 503 pp., 116 plates, 18 tables, 19 figs. $27.50.—In this large volume, Skutch presents his synthesis of the reproductive activities of birds and the characteristics of young birds, bringing together a wealth of useful facts and his evolutionary interpretations of the major patterns. The facts are drawn from over 40 years of painstaking observations in the New World Tropics and from an extensive literature survey.

The text is divided into 34 chapters, each covering one topic. These are arranged as follows: pair formation and mating systems (3 chapters), territoriality (1), timing of nesting (2), nest form, materials, construction, and maintenance (4), egg size and color (1), incubation patterns (5), hatching process (1), developmental state at hatching (1), parental care of nestlings (4), nestling interactions (1), fledging, care and education of fledglings (4), inter- and intraspecific helpers (2), nests as dormitories (1), concealment and direct defense of the nest (2), reproductive rate and its regulation (2).

Skutch set himself the formidable task of preparing a comprehensive, yet detailed, treatment of reproduction to satisfy the amateur naturalist as well as the professional investigator. He has succeeded rather well, largely because his mastery of the written language makes for an eminently lucid style, readable by most laymen, and because the examples discussed are interesting. Some of my favorite sections are the accounts of manakin behavior on the lek, megapode habits, procedures whereby non-incubating males learn that their offspring have hatched and require feeding, and birds feeding nestlings of other species. For the investigator, the book will be valuable chiefly for the sheer mass of facts arranged for easy comparison among birds, and for the 18 tables. These include data on age at first breeding, nesting periodicity of seabirds, incubation patterns and duration, feeding rates, nesting success, and clutch size. The figures are well chosen to illustrate points in the text (except that I could find no text reference to fig. 19). The 116 black-and-white photographs are of generally good quality and appropriate to the discussion at hand, but many could have been omitted. In the text, species are identified by common name and alternate common names and scientific names are given in the index at the end of the book. Common names do not always follow American use, e.g. Common Bluebird for *Sialia sialis*.

The text is nearly error-free; I found only 2 typographical errors and 1 factual mistake (using a linear instead of a logarithmic model to calculate daily rates of nest loss from overall nest mortality). Nevertheless, the objective scientist may find fault with some of the concepts expressed, as that "birds often sing from pure ebullience or joyousness . . . and females sitting in the nest sometimes hum little ditties expressive of contentment" (p. 336), and that "those (birds) that maintain their population with the smallest reproductive effort, are the truly efficient species. They enjoy the longest, and doubtless most satisfying, lives" (p. 376). It must be pointed out that many of Skutch's evolutionary interpretations do not jibe with currently accepted views on the nature of natural selection. In particular, Skutch fails to provide a plausible selective mechanism when he argues that because species in stable environments produce only enough young to replace annual losses, despite being able to feed additional offspring, they are limiting their reproductive rate to avoid depleting their resources.

In summary, in spite of some questionable interpretations, *Parent Birds and Their Young* is easy to read, well-organized and factual, and, especially for the amateur, may serve to alert observers to phenomena worth recording.—SUSAN C. WHITE-SCHULER.

Bird Sounds. By Gerhard A. Thielcke. University of Michigan Press, Ann Arbor, 1976: 190 pp. (First Published as *Vogelstimmen*, Springer-Verlag, 1970.) $2.95 (paper), $6.95 (cloth).—This book, written in semi-popular style, begins with a chapter on methods of analysis of avian acoustic signals, comparing the oscilloscope and the sound spectrograph as research tools. Thereafter are chapters on vocal versus mechanical sounds, neuro-anatomical studies, functions of calls vs. songs, ontogeny of vocalizations, vocalizations and speciation, evolution of sounds, annual and diurnal cycles, and finally bird sounds and music.

The translator has retained the German word "strophe" throughout the text, but the term appears to have two different meanings. On page 3 it is stated that: "Several strophes are called a song." Presumably then, "strophe" is equivalent to the term "phrase" of other investigators. Thereafter, however, strophe appears to signify "song types" or "themes," e.g. when discussing songs of Marsh Tits and treecreepers (pp. 35 and 36). Breeding season (Brutperiode) is referred to as "brooding period" throughout. "Clutch" (Gelege) was translated as "egg-lay" (p. 69), and "altricial" appears as "insessorial" (p. 65). "Sibling species" appears as "twin species" (p. 137) and "domestic cockerels" (pp. 164 and 165) has become "turkey cockerels." But these are not serious; all-in-all the translator has done an excellent job.

The author states (p. 96) that: "The ability to learn song begins around the thirtieth day of life in song birds." This is contradicted on p. 115 in which he informs us that White-crowned Sparrows, captured at 30 days of age and then isolated, sang their home dialect the following spring. Marler has refined these data further (J. Comp. Physiol. Psychol., Mongr. 71(2), 1970).

In the chapter on sound-production (p. 26) the author informs us that the interplay of sound-production and breathing is an unsolved problem, and that surely birds must inhale and exhale as they sing. Recent attempts to tackle this question have been summarized by Gaunt et al. (Condor 78:208–223, 1976). In the section on antiphonal singing, the author asks (p. 45) whether or not duetting is correlated with pair-contact in dense vegetation or with nocturnality when pairs are visually separated. Recent surveys by Payne (Ostrich Suppl. 9:125–146, 1971) and Kunkel (Z. Tierpsychol. 34:265–307, 1974) indicate that duetting is most often found in birds with long-term pair bonds, and not necessarily in areas of poor visibility. Indeed, Kunkel points out that duetting is often associated with elaborate visual displays during which singing pairs are very close to each other.

The author also asks (p. 117) how a new dialect can come to exist. Several authors have tried to provide answers to this. Field studies (Payne, Ornithol. Monogr. 11, 1973; Lemon, Condor 77:385–406, 1975; Baptista, Univ. Calif. Publ. Zool. 105:1–52, 1975) on song variation in natural populations indicate that song learning is an imperfect process. Due either to copy errors, or in Lemon's view, and improvisational process that he calls "drift," new themes or variants of existing themes continue to emerge. Given geographical isolation, oral tradition, the accumulation of copy errors (or Lemon's "drift"), new dialects may eventually devolop.

The chapter on "sound parasitism" (pp. 155–159) summarizes Nicolai's studies on viduine brood parasitism on estrildid finches, in which he suggested that each viduine parasitizes and mimics songs of only one host. Payne (Auk 93:25–38, 1976) has cautioned that the one-host-one-parasite theory is good in only some parts of Africa. In other areas (e.g. in West Africa) one viduine form may mimic as many as four different fire-finch hosts.

My comments are not meant as criticisms of the author's work, but merely indicate the popularity of the field and the speed at which new data are being accumulated. The author has brought together a fine review of the field up to 1970. Especially notable are his chapters on functions of calls, functions of songs, evolution of species, and evolution of sounds, in which he summarizes many important studies from the German literature. The latter include his own extensive work on geographical variation and ontogeny of vocalizations, and playback experiments with treecreepers (*Certhia* spp.), tits (*Parus* spp.) and other species that will, I am sure, stimulate others to exciting research. "Bird Sounds" is definitely a *must* for students of ethology, systematics, and avian bioacoustics. The price is right to boot!—LUIS F. BAPTISTA.

SONG DIALECTS AND DEMES IN SEDENTARY POPULATIONS OF THE WHITE-CROWNED SPARROW (*Zonotrichia leucophrys nuttalli*). By Luis F. Baptista. University of California Publications in Zoology, Vol. 105. University of California Press, Berkeley, Los Angeles and London, 1975: 52 pp., 25 plates. $4.00—In his introduction Baptista speaks of the White-crowned Sparrow as the white rat of the ornithological world. Certainly insofar as vocalizations are concerned it is among the most thoroughly studied of all birds, providing some of the most complete documentation now available on song variation within and among wild populations. The work described here extends and amplifies previous studies by Marler and Tamura (Condor 64:368–377, 1962; Science 146:1483–1486, 1964) as well as previously reported studies by Baptista himself (Z. Tierpsychol. 34:147–171, 1974).

As a basic framework for his investigation, Baptista asks the following questions: (1) does gene flow occur between demes, as indicated by song characteristics?; (2) what occurs in contact zones between neighboring demes?; (3) what barriers exist between populations?; (4) how large is a dialect group?; and (5) what are the effects of visiting migrants on the songs of local populations? The study included various localities in the San Francisco Bay area and extended from April 1968 through July 1971. Based on an analysis of over 2400 song spectrograms of over 400 birds it was found that there is not one single song theme in each area, but rather a dominant motif or "dialect" with a number of minor variations in song.

Song variants were not found randomly dispersed throughout the populations, but were clumped, forming a number of subdialect areas within each dialect region. Although most individuals sang only one theme each, a few sang from two to four. Some birds were apparently "misimprinted" with songs sung by wintering migrants belonging to the subspecies *pugetensis*.

Dialect or "theme" areas varied in size from the rather small Brooks Island and adjacent mainland to the much larger Berkeley area. Some populations were separated by ecological barriers, and their song themes thus developed in isolation. Others seem to be separated only by distance. The mosaic distribution of subdialect groups and dialects in a continuum points to a population structure of genetically semi-isolated neighborhoods. Between contiguous dialect areas Baptista found a narrow mixed zone of song themes. Many individuals within this zone maintain their separate and distinct dialect forms, while some sing a mixture of the 2 in a repertoire of more than one song pattern, or a single song containing elements of the two separate dialects.

Most of the publication is taken up by the description of song characteristics of the various San Francisco Bay area populations sampled, and therein lies its main strength. The remarkably thorough documentation of song characteristics of the birds throughout this topographically and ecologically complex area provides the basic data upon which to begin to understand the distribution and dynamics of song dialects. The amount of work involved in the analysis of the recording is enormous, although Baptista does not mention it.

Perhaps the greatest weakness in the paper is the author's failure to nail down solidly the answers to the questions he asked at the beginning. Most of them are answered, more or less, but some, such as question number 4, are left pretty much up to the reader to figure out for himself. There are some grammatical and spelling lapses that indicate a lack of thorough editing. On the whole, however, this publication provides a remarkable record of song variation within and between adjacent populations of the White-crowned Sparrow (*Zonotricha leucophrys nuttalli*), and is a very important contribution to the literature on song dialects.—WILLIAM L. THOMPSON.

SOCIAL ORGANIZATION AND BEHAVIOR OF THE ACORN WOODPECKER IN CENTRAL COASTAL CALIFORNIA. By Michael H. MacRoberts and Barbara R. MacRoberts. Ornithological Monographs No. 21, American Ornithologists Union, 1976: viii + 115 pp., 39 figs., 13 tables. $7.50.—The Acorn Woodpecker (*Melanerpes formicivorus*) is a fascinating species because of its unusual social system. At least in California, the birds live in permanent groups of up to 12 or more individuals of both sexes and all ages. In the fall the groups communally harvest, store and defend caches of acorns, which are their major food. In spring the colonies breed as units, with most or all members helping to incubate and feed 1 or (rarely) 2 broods of young. These facts about Acorn Woodpecker natural history were discovered long ago, but no comprehensive studies were undertaken using marked birds to determine such important aspects as the genealogical relationships among group members, the amount of movement between groups, or even who lays eggs fertilized by whom. With the current flurry of interest in group and kin selection, and "sociobiology" in general, it is not surprising that several such studies are now in various stages of completion. This is the first to reach publication.

The study was conducted at The Hastings Natural History Reservation above the Carmel Valley in California. This is prime Acorn Woodpecker habitat because of the abundance and diversity of oaks present (6 species and 5 hybrids grow on the reservation). Most of the fieldwork was carried out between October, 1971, and August, 1974; 149 birds were individually color-banded and 60 groups were studied, 32 intensively enough to appear in an appendix describing their individual histories. Extensive observations were made from blinds. The authors did not include a methods section and we do not know exactly how many hours of observation were involved. Also, no mention is made of techniques for capturing birds. This is unfortunate, since Acorn Woodpeckers are notoriously elusive and anyone who captures 149 of them has learned something useful.

The monograph is well-written and a pleasure to read. Following introductory remarks and a description of habitats occupied, the MacRoberts' discuss the all-important topic of group composition. They found that group size varied from 2 to 15, with a mean between 5 and 6; all groups had both male and female members, and sex ratios were about equal. Most recruitment to groups was by reproduction, although 9 individuals, mostly adults, were observed to move from one known group to another; some 87 birds disappeared during the course of the study, unknown proportions dying or moving off the reservation. The MacRoberts' write in their summary (p. 82) that "the Acorn Woodpecker is a sedentary species," and that "each group maintains a year-round, all-purpose territory." This picture of extreme stability appears true only to a degree. For example, of the 32 groups discussed in detail in an appendix, 19 either appeared on the reservation from unknown areas, left the reservation for unknown areas, or made documented moves on the reservation during the study. In some cases these moves were attributable to acorn crop failures.

Acorn Woodpeckers, acting as groups, vigorously defend their territories against intra- and interspecific intruders. In a species that caches immense quantities of food, the defense of that food supply becomes a major operation. The MacRoberts' were fortunate to be able to document several inter-group conflicts that resulted in complete or partial displacement of one colony by another. In no cases did smaller groups displace larger ones. There also is a highly significant figure showing a strong positive correlation between group size and territory size. These observations suggest that one reason for the evolution of group living in this species may be the advantages gained in defense of food resources.

The reproductive effort of Acorn Woodpeckers at the Hastings Reservation was very low—between 0.2 and 0.3 young per adult per year. Many groups failed to breed at all in any given year. The MacRoberts' were unable to explain this phenomenon, although it seems perhaps consistent with a strongly K-selected life history strategy. Indeed, the authors note that Acorn Woodpeckers on their study area live at high, relatively stable population densities. In most years food supplies are good and populations remain at or near carrying capacity. Young stay with their groups, presumably because there is no place for them to go and because there is little or no chance for them to breed on their own. Even though groups may move, they appear to do so as intact units.

In this environment, and if the colonies are made up of related individuals, K and kin selection will be powerful forces shaping the social system of the species. It may not be that simple. One would predict that small groups might breed more than large ones, since recruitment would be both possible (more "room" for additional birds) and advantageous (more efficient defense of territories). However, the MacRoberts' data show, if anything, that it was the small groups that more often failed to breed. As the authors observe (p. 71), "the exact genetic relationship among group members was not known in most cases." Their data suggest that most recruitment to groups occurs via reproduction, but in order to say anything conclusive about kin selection or group selection it would be necessary to learn what happened to those 87 individuals that disappeared during the course of the study.

The social behavior of Acorn Woodpeckers appears very complex, and is not fully described in this study. There is a long appendix on visual and vocal displays, with high-quality audiospectrograms. The vocal repertoire is large and the function of many calls remains unclear because of the variety of situations in which they occur. The Acorn Woodpecker almost certainly evolved from a non-social melanerpine relative, but the MacRoberts' make no attempt to compare the displays and vocalizations of their species with those of close relatives. This should be done, because it could provide an excellent example of the ways in which display behaviors evolve to fit a new social system. The authors found that dominance hierarchies exist within groups, males and older birds being dominant; but there is no discussion of the role of calls or displays in the maintenance of these hierarchies. In several instances, adults excluded young of the year from acorn stores, but did not expel them from the territory. The young either fed on secondary stores, or were rationed acorns by the adults. The significance of this behavior remains obscure.

Much remains to be learned about the Acorn Woodpecker. We still do not know which group members are parents and which are helpers during nesting. Long-term studies will be necessary to determine genealogical relationships among group members. The question of population regulation remains unanswered, and we still have no clear idea why certain groups breed while others do not. These comments are intended not as criticisms but as encouragement for further work. The MacRoberts' have written an excellent account based on an intensive and highly successful three-year field effort. In so doing they have made by far the most significant contribution to date toward an understanding of this remarkable species.—CARL E. BOCK.

THE HABITAT GUIDE TO BIRDING. By Thomas P. McElroy, Jr., Albert A. Knopf, New York, 1974: xvi + 257 pp. $8.95.—This book is far more than its title implies. It is really a text which, in addition to habitats, touches on such wide-ranging subjects as moonwatching (bird migration at night), choice of binoculars and spotting scopes, their use and care, precautions and clothing for different habitats, and tips on leading bird trips. It briefly discusses feeding stations and choice of bird food. It takes up the subject of bird communities and the niches filled by various species in the same habitat.

There are numerous drawings by Matthew Kalmenoff, almost all of which I found very pleasing. Some readers will not like the physical make-up of the book. The text covers a little over half of each 8 inch × 9 inch page, leaving a 3½ inch margin for the artist's illustrations. However, on some pages this margin is blank, and it seems a waste of space, although the author suggests using this space for notes or sketches, thus personalizing the reader's copy. There are no labels under the species drawings, and one must turn to a "Guide to the Illustrations" in the front if one cannot identify the bird or scene depicted. Therefore a beginner might well be confused when reading about the meadowlark and Killdeer, with an unlabelled drawing of a Horned Lark beside the text. In one place there are drawings of foot adaptations, but with no accompanying discussion. However, in most cases, text and illustrations are adjacent.

In a book which deals with a great variety of topics, the author has done a very good job of leading from one subject into the next. His bird categories are interesting and often unique. For example, in his chapter on common birds of country roadsides, he divides them into wire-sitters, fence-post-sitters, road-kill scavengers and "others." His descriptions and explanations of the stages of development of marshes and swamps, the eventual domination of old fields by forests, and the effect of such plant successions on bird life, I found excellent.

As the author himself points out, this book will be a source of help to the amateur and the experienced birder alike. I strongly recommend that the reader note carefully his early chapter called "Some suggestions for using this book." It should be read more than once. There is a species index and a good bibliography. The book is limited to the eastern half of the continent, and I hope that someday there will be a similar one for the west.—SALLY HOYT SPOFFORD.

ORNITHOLOGICAL NEWS

LOUIS AGASSIZ FUERTES AND MARGARET MORSE NICE AWARDS

Fuertes Awards are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists and students. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic institutions. Each proposal is considered primarily on the basis of possible contribution to ornithological knowledge. Although grantees are not required to publish their studies in The Wilson Bulletin, it is hoped that they will submit their manuscripts to the editor of The Wilson Bulletin for consideration.

Most of the statements applicable to the Fuertes Awards are also applicable to the Nice Award. However, the Nice Award is limited to applicants not associated with a college or university. It is intended to encourage the independent researcher without access to funds and facilities generally available at the college. High school students are eligible.

In some years two Fuertes Awards have been made, in some years, one. Amounts have been between $200 and $100. One Nice Award is made annually, in the amount of $100.

Interested persons may write to Eugene S. Morton, National Zoological Park, Office of Zoological Research, Washington, D.C. 20008. Completed applications must be received by 15 March 1978. Final decisions will be made by the Council at the annual meeting of the Society, 4–7 May 1978.

FRANK M. CHAPMAN FUND

The Frank M. Chapman Memorial Fund gives grants in aid of ornithological research and also post-doctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. 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, NY 10024.

1978 ANNUAL MEETING

The 59th annual meeting of The Wilson Ornithological Society will be held at Jackson's Mill, West Virginia, on 4–7 May 1978. The meeting will be hosted by the Brooks Bird Club, the Department of Wildlife Biology of West Virginia University, and West Virginia University. Information concerning lodging and field trips and abstract forms for submitted papers will be mailed to the membership early in 1978. The deadline for submission of abstracts will be 1 March 1978.

A special feature of the meeting will be a symposium titled, "Resource Use Strategies in Birds," to be held on the afternoon of Friday, 5 May. The symposium is organized by Dr. Elliot J. Tramer. The chairman of the local Committee is Dr. Robert Whitmore, Division of Forestry, West Virginia University, Morgantown, WV 26506.

INTERNATIONAL BIRDS IN CAPTIVITY SYMPOSIUM

The 1st International Birds in Captivity Symposium will be held in Seattle, Washington from 8–12 March 1978. Sessions will deal with husbandry, nutrition, medicine, sexing techniques, behavior, reproduction, and ornithological studies done in the wild. A panel discussion will be held after each topic session and there will be a special panel on conservation. All presented papers will be published after completion of the Symposium. For more information please write: Jan R. van Oosten. Chairman, IECF, 1008 James St., Seattle, WA 98104.

A SYMPOSIUM: ROLE OF INSECTIVOROUS BIRDS IN FOREST ECOSYSTEMS

The role of insectivorous birds in forest ecosystems will be the theme of a symposium co-sponsored by Stephen F. Austin State University (SFASU) School of Forestry and USDA Forest Service (USFS), Southern Forest Experiment Station, Nacogdoches, Texas. Conference chairmen are Dr. James C. Kroll (SFASU) and Dr. James G. Dickson (USFS). The symposium should provide a forum for exchange of current ideas between researchers and land managers. Tentative subject areas are: sampling bird populations, sampling prey populations, population dynamics of insectivorous birds, birds as biological control agents, and methods to increase bird populations.

Technical papers will be presented 13 and 14 July. and a field trip will be scheduled for the morning of 15 July.

Invited and volunteer papers selected for presentation by the editorial review board will be presented orally in abbreviated form and published in the symposium proceedings. Persons wishing to present a paper should submit manuscripts by 1 March 1978 to: Dr. James C. Kroll. P.O. Box 6109, Stephen F. Austin State University, Nacogdoches, Texas 75962.

OPINIONS OF THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following Opinions have been published recently by the International Commission on Zoological Nomenclature, c/o British Museum (Natural History), Cromwell Road, London SW7 5BD, United Kingdom (see Bulletin Zoological Nomenclature Volume 34, part 1).

1078 (p. 14) *Anas punctata* Burchell, 1822 (Aves suppressed under the plenary powers.

1081 (p. 25) Addition of Family-Group Names based on *Alca* (Aves) and *Alces* (Mammalia) to the Official List of Family-Group Names in Zoology.

The Commission cannot supply separates of Opinions.

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BY BONNIE J. TURNER AND WENDY J. WEBER

This issue of *The Wilson Bulletin* was published on 27 December 1977.

THE WILSON BULLETIN

SUGGESTIONS TO AUTHORS

See Wilson Bulletin, 87:144, 1975 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in duplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on 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. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Ernest E. Hoover, 1044 Webster St., N.W., Grand Rapids, Michigan 49504. 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.

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