THE
WILSON BULLETIN

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WHITE-RUMPED SANDPIPER *(Calidris fuscicollis)* chick, newly hatched. Painted direct from life July 13, 1962, by George Miksch Sutton. The egg, taken from a nest on Jenny Lind Island, was hatched on Victoria Island by a Semipalmated Sandpiper.

SUMMER SCHEDULE AND BREEDING BIOLOGY OF THE WHITE-RUMPED SANDPIPER IN THE CENTRAL CANADIAN ARCTIC

David F. Parmelee, Dale W. Greiner, and Walter D. Graul

During the summer of 1962, the senior author, George Miksch Sutton, H. A. Stephens, and Richard H. Schmidt visited Jenny Lind Island in the Arctic Archipelago and found an unusual breeding shorebird population. Among the many shorebirds, which included both high-arctic and low-arctic forms, the White-rumped Sandpiper (*Calidris fuscicollis*) was one of the commonest. Our stay on the island that year, from 19 June to 5 July, was much too brief to permit an extensive study of this highly provocative and puzzling species—the taxonomic position of which has been repeatedly disputed. Although the senior author wished to return soon to Jenny Lind Island for the purpose of studying White-rumps and other shorebirds, the opportunity did not occur until 1966 when he, accompanied by George Miksch Sutton, Dale W. Greiner, and Walter D. Graul, arrived there on 31 May and remained until 12 August.[1] The account that follows is an attempt to describe certain aspects of the White-rumped Sandpiper's complex breeding behavior, and thereby to clarify its relations to certain other scolopacids, particularly the Pectoral Sandpiper (*Calidris melanotos*). We concentrated on the incubation and fledging periods, and especially on the pair-bond relationships and role of the sexes in care of eggs and young.

STUDY AREA AND METHODS

Jenny Lind Island lies isolated in Queen Maud Gulf at the southern edge of Victoria Strait. The Royal Geographical and King William islands are to the east, the very much larger Victoria Island is north and west, and the sprawling mainland (Perry River area) is south. Less than 20 miles across, the total area of the island is only 167 square miles. The highest land hardly exceeds 200 feet elevation anywhere, and there are no precipitous cliffs either inland or at the coast. Innumerable lakes and ponds dot the landscape, although none is deep. The few streams that flow swiftly following the thaw are reduced to a series of stagnant pools by mid-July, when coastal shore leads are wide open and the last spots of snow disappear inland. Despite the unpretentious terrain, extensive wet tundras with networks of

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[1] The expedition to Jenny Lind Island in 1966 was financed largely by the National Science Foundation (GB 4904) and partly by Kansas State Teachers College at Emporia. George Miksch Sutton, Research Professor of Zoology of the University of Oklahoma, joined our group as an independent investigator and bird artist. He kindly gave us his notes on the White-rumped Sandpiper for inclusion in this report.

marshy ponds, sandy flats, raised beaches, stony ridges and prominences, and both sandy and rocky marine beaches provide a variety of habitats favorable to the many birds that inhabit the island.[2]

Though south of the 69th parallel, Jenny Lind Island is cooled by chilling winds that sweep down from the ice pack of Victoria Strait. The mean daily temperature for July is only 42 F and approaches a high-arctic condition, which in part accounts for a retarded vegetative cover most evident in the willows. No doubt the cool conditions contribute to the remarkable high-arctic avifauna that breeds on the island with distinctly low-arctic species.

Detailed studies on the White-rumped Sandpiper were carried out in a circumscribed area covering 2.5 square miles of variable terrain near the east coast. The southeastern end of the study area was a barren rocky ridge (50 to 100 feet elevation) that, except for a few isolated marshy ponds, was unsuitable for nesting White-rumps. Within and beyond the limits of the study area, the ridge gave way to a gentle, well vegetated slope that ended northwestwardly in a great marsh with myriads of lakes and ponds. A few White-rumps bred near the isolated ponds and vegetated traps at the higher elevations, but the majority were in the perpetually wet habitat of the low interior.

Many parts of the study area were visited at various times round the clock daily from 1 June through 12 August—a span that covered nearly all phases of the species' summer schedule. A light-weight tundra vehicle (Jiger) was used occasionally as a means of transportation, but most visits to the study area were made afoot. Nests were found by watching or flushing females. Choice areas containing fair numbers of birds were systematically covered by rope dragging, a technique successful enough for White-rumps but not for all scolopacids. Nest markers consisting of a wire rod with a small label attached were placed at least 15 yards from each nest in an attempt to avoid predator detection of nests. Certain eggs were marked with dots of red fingernail polish for identification purposes.

Incubating White-rumped Sandpipers were live-trapped at nests by means of a Myer's (1966) trap, an ingenious device designed for catching doves, but equally suitable for shorebirds. Eleven adult females were trapped at nests within the study area and released upon banding, color banding, and feather coloring with crimson, yellow, or green water-soluble dyes for convenient field identification. Two of the 11 abandoned their nests immediately upon being handled and were not seen again. The other nine soon

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[2] Notes on all bird species and subspecies recorded on Jenny Lind Island in 1962 and 1966 are included in a separate publication by the senior author, H. A. Stephens, and Richard H. Schmidt, entitled "The Birds of Southeastern Victoria Island and Adjacent Small Islands" and published by the National Museum of Canada (Bulletin 222, 1967).

returned to their respective nests, and we were thus able to follow the individual movements of these birds very accurately, in some cases up to the time the parent-offspring bond dissolved. We failed to trap a single male White-rump at a nest, since the male does not sit on eggs (see page 16, below). Incubating males of some other shorebird species were quickly caught, however.

Adults were sexed mainly on the basis of calls and behavioral characteristics, since it was not practical to kill the very birds we studied. We did, however, collect one of the marked females about the time its young fledged. Male White-rumps behaved so differently from females on the breeding ground that sex identification was no problem afield. Moreover, breeding males showed an enlarged throat, which readily identified them when seen at reasonable distances. In failing to color mark male White-rumps, we were unable to follow their individual movements. This proved a distinct disadvantage.

Most of the 55 young White-rumps handled by us in 1966 were banded on the left leg when newly hatched at the nest. Those young of uncertain age outside the nest were banded on the right leg as a rule. Only young with bands on left legs were later collected, thus giving us a useful series of sexed juveniles of various known ages. This method worked well with White-rumped Sandpipers, for even strong flying young were easily approached and the bands readily detected.

We considered the banding and color marking techniques essential. Without them we could not have pinned down many facts on breeding behavior. So many surprising phenomena concerning shorebird behavior came to light during the course of study, that we strongly feel that any comparable study should be based on marked individuals.

DISTRIBUTION AND BREEDING DENSITY

The White-rumped Sandpiper is a monotypic, Nearctic species that breeds commonly but discontinuously across Arctic Canada, and sparingly on the north coast of Alaska. On the mainland of Arctic Canada it probably breeds from near its southern limits at Chesterfield Inlet on Hudson Bay westward across northern Keewatin, Melville and Boothia peninsulas, and northern Mackenzie. On the Arctic Islands it breeds from the southern edge of the archipelago northward nearly to the 75th parallel on Melville Island, but apparently not at higher latitudes. Although a number of observers at various localities have reported on the breeding of this relatively unknown species, there are only a few detailed studies to date.

Population densities of White-rumped Sandpipers have been estimated for several localities by various means. Soper (1946) described the invasion of Bowman Bay, Baffin Island, by "almost incredible numbers" of these birds but gave no numerical estimates. Sutton (1932) stated that the birds were abundant and widely distributed over most of Southampton Island but were less common in the eastern, more rocky part; about 60 pairs of White-rumps occurred within a radius of about four miles of his base, an area equivalent to about 50 square miles. By use of the multiplier technique, Manning et al. (1956) converted the number of White-rumps recorded per hour in a given area to an estimated standard number per square mile and concluded that a total adult population of 25,000 birds summered on Banks Island (24,600 square miles) in 1953. However, the birds were not evenly distributed over the island and appeared to be common only in the southeastern part. By employing the same method, Manning and Macpherson (1961) arrived at a 1958 estimate of 15,000 adults for Prince of Wales Island and small adjacent islands, a total area of about 12,500 square miles. The number of White-rumps varied from one locality to another. Where found, the birds ranged in density from 0.5 to 10.2 birds per square mile. Drury (1961) concentrated his studies in a circumscribed area on Bylot Island and found six pairs (12 birds) in one square mile—apparently the densest population of White-rumps seen on the island by him in 1954.

The eastern half of Jenny Lind Island was surveyed for birds in general, but detailed studies on White-rumped Sandpipers were made in the 2.5-square-mile area already mentioned. At least 22 pairs occupied this area in 1966. This figure was based on 17 nests and five broods of young not more than three days of age. Older young from additional broods were not included, since they easily could have come from outside the study area. Ten of the 17 nests and four of the five broods were within a half-square-mile area: five nests and two broods were within one-eighth-square-mile area. The densest population was, therefore, seven pairs (14 birds) per 80 acres. Although these figures are minimal, they probably are fairly accurate considering the many hours spent traversing the area and observing both females and displaying males.

On the basis of 22 pairs per 2.5 square miles, one might assume a total population of 1,470 pairs for Jenny Lind Island in 1966. This figure is far too high, for much of the island is unsuitable for nesting White-rumps. Probably no more than 60 square miles would qualify as nesting habitat, and much of this ground would be marginal rather than choice. Our 2.5-square-mile area with its variable terrain, though hardly a random sample, is probably representative of the 60 square miles of seemingly suitable habitat. A generous estimate of the total breeding population based on the 60 square miles would be in the neighborhood of 528 pairs. Even this figure, though more realistic, seems a bit high on the basis of casual observation in most areas visited.

There can be no doubt that the number of breeding pairs fluctuates considerably from time to time. The 1962 season may well have been a peak year when the density conceivably attained 20 or more pairs per 80 acres. Sixteen nests were found without much searching in a square mile of choice ground, which we later used as part of our 1966 study area. There probably were two or three times that many nests judging from the number of birds seen.

ARRIVAL AT BREEDING GROUND

Arrival and early courtship dates for the White-rumped Sandpiper in Arctic Canada are poorly documented. The few records indicate that the dates vary considerably from one locality to another, and may vary yearly at a given locality. At Cambridge Bay on Victoria Island where the species is uncommon, the senior author first noted a displaying male in 1960 on 7 June. In the same area in 1962, he and Sutton first noted three males (no displaying) on 7 June, and a female on 8 June. But in 1966 the species was already at Cambridge Bay the day of our arrival on 28 May (one bird, sex not known to us). Flight displaying was not observed before 31 May, however.

In 1966 we especially looked for, but failed to find, the species before 2 June on Jenny Lind Island only 95 miles from Cambridge Bay. The first White-rumps seen—two birds seemingly not paired and a solitary individual—stood near partly open ponds several miles inland, where the species later bred. A single White-rump stood with a Pectoral Sandpiper in the same marsh on 3 June, and a solitary individual was seen several miles from there the following day. On 5 June scattered males performed aerial displays—the first observed on the island that year. Many males displayed and chased females on 6 June, and commonly thereafter.

Courting White-rumps appear to be highly sensitive to changes in temperature and wind velocity. Although an exceptionally early May thaw occurred on Jenny Lind Island in 1966, the first days of June were windy and raw (mean daily temperatures only 27 F on the 1st and 26 F on the 3rd). Temperatures rose during 5 June and were mild by the 6th, when there was much thaw accompanied by increased White-rump activity. Displaying decreased appreciably during the inclement weather of 8 June, but soared during a calm on the 9th; then it fell off during the next couple of days and picked up again on the 12th.

Delayed courtship has been noted elsewhere in Canada. The snow cover was deep and winds fierce on 3 June when Sutton (1932) first noted

White-rumped Sandpipers on Southampton Island. A few bare patches of ground were evident when he saw them next on 6 June. The birds were definitely on wet breeding grounds on 8 June, but the first pronounced courting activities apparently did not take place before 11 June.

Some ornithologists report a different arrival and early courtship. Soper (1928) did not see the species at Nettilling Lake, Baffin Island, before 10 June: by 14 June the species had become quite common. At Bowman Bay, according to Soper (1946), an intensive wave of migrating White-rumps persisted during 8–14 June, after which the numbers gradually diminished, though a large population remained to nest on the surrounding tundra. On Bylot Island, the northeasternmost breeding ground known for the species, the general arrival of White-rumps took place on the afternoon of 19 June, according to Drury (1961), who inferred that ground display followed by aerial display commenced soon after the birds had arrived. Both Soper and Drury believed that the arrival was precisely timed for breeding. According to Soper (1928), both sexes arrived together, with the females almost, if not quite, ready for immediate reproduction. Drury thought that egg laying started within two days after the species arrived on Bylot Island.

Records for other areas are less instructive. Sutton and Parmelee (1956) noticed a few migrating White-rumps near the head of Frobisher Bay, Baffin Island, during 15–21 June. Macpherson and Manning (1959) noted small groups and pairs on Adelaide Peninsula during 16–20 June. Manning and Macpherson (1961) first saw the species on Prince of Wales Island on 15 June, and fairly commonly thereafter. On Banks Island, Manning et al. (1956), collected a male at Egg River as early as 1 June, and noted an individual at Cape Kellett on 2 June.

Considering all these records, it is clear that the spring arrival on the breeding ground in the Canadian Arctic may cover a span of considerable magnitude, from at least 28 May to 19 June: and that the first displays may start as early as 30 May, or as late as 20 June. It can be said with some confidence that early arrivals may be few in number and do not necessarily display or breed immediately, especially when the weather is inclement and the snow cover extensive. But courtship and breeding may start almost immediately when the majority of both sexes arrives in force, especially when the arrival takes place after the first week or ten days of June when conditions are apt to be optimal.

TERRITORY—DISPLAY—PAIR BOND

Territories were established on Jenny Lind Island in 1966 as early as 5 June, when aerial displays were first noted. Some males that we watched closely on 6 June amorously pursued females that ran swiftly before them over exposed turf and banks of snow. Characteristically, the males walked and ran with tails elevated high and somewhat forward, and wings straight out with tips arched down, not fluttering. In attitudes precisely similar to those illustrated and described as the "Sharp-tailed Grouse dance" by Drury (1961), they displayed their white rumps, and fully their white under-tail feathers while uttering low buzzing notes or little growls. Paying no attention to us, one male followed a female attentively around a rather small area presumably within his territory for 20 consecutive minutes, attempting copulation not only on the run but on the wing as well. In fits of excitement it several times landed squarely on the back of the flying female, but the acts were hardly consummated. Other females seen that day were equally unreceptive. Eventually we discovered that a few had laid fertile eggs early, indicating that at least some females not seen by us had been receptive.

Sutton (1932) beautifully described the aerial hovering and calling of the male White-rumped Sandpiper on territory, and Drury (1961) elaborated further on the display with action illustrations. We, also, have noted these aerial displays many times. The hoverings and glides back to earth are used by other seemingly related sandpipers, notably the Knot (*Calidris canutus*), Baird's Sandpiper (*Calidris bairdii*), Stilt Sandpiper (*Micropalama himantopus*), and Semipalmated Sandpiper (*Calidris pusilla*). A less spectacular aerial display of the White-rumped Sandpiper, on the other hand, resembles rather closely one of the Pectoral Sandpiper, which normally does not hover or tred while calling in mid-air.

For example, the male White-rump has a horizontal flight that moves it fast and low across the tundra. The flight may terminate in a sudden rise followed by an abrupt descent. While flying horizontally, the displaying bird gives the familiar "*quo-ick*" calls, and some times the "typewriter carriage" series of rapid notes described earlier by Sutton. The male may drive an intruder far beyond the territory he is defending seemingly hundreds of yards at times, but then quickly flies back. Upon re-entering his favored ground, he may suddenly rise to heights of 20 or more feet and immediately glide swiftly down, calling as he goes. No hovering accompanies such displays, so far as we know. This flight, interestingly enough, appears to be remarkably like one described by Holmes and Pitelka (1961) for the Curlew Sandpiper (*Calidris ferruginea*).

Like the Pectoral Sandpiper, also, the male White-rump stands guard on some prominence in the wet tundra. From his perch he reacts quickly to strange males by driving them off, and seemingly to all females, even those of other species, which he attempts to court. Invariably when we flushed a female from its eggs in the presence of a male, there was an immediate response. With bill thrust forward, wings stiff, and tail tilted high, he growled and buzzed incessantly while moving in close to the displaced and unreceptive bird. The action eventually terminated in a swift flight chase or simple parting. This display, essentially the one used by males in early phases of courtship, was remarkably similar to one of the male Pectoral Sandpiper, which reacts in almost the same way to displaced females.

Detailed observations on an isolated nesting in 1966 revealed noteworthy features of the territory. The nesting area was unique in being near the summit of a stony ridge within a narrow but rather long depression containing several ponds fringed with wet, grassy hummocks. The rocky ground all around was a barrier to other White-rumps on territory, the closest of which was about a half mile away. One male, first noted while performing aerial displays on 11 June, occupied the entire pond area without interference or territorial pressure from adjacent areas. On occasion the male, presumably the same individual each time, flew from the area but returned to display. The one female (color banded and dyed) that nested in the area—in a spot not often visited by the male—completed her clutch on 19 June. This was the day the male was last seen. Here is one case where the pair bond terminated with the completion of the clutch, or soon thereafter. The female alone incubated the eggs and attended the young—invariably the case with all White-rump nestings studied by us. The territory of the male, therefore, has a sexual function of short duration. The pair bond, if it can rightly be called such, is of short duration also, suggesting an incipient kind of lek behavior.

Aerial displaying in 1966 appeared to have reached a peak of activity from 6 June to about 12 June, and then declined. It was decidedly sporadic by 20 June when most females were incubating steadily. A few males defended areas vigorously as late as 27 June, but they were truly exceptional. The last flight display seen by us occurred 4 July. In the same area in 1962, we last recorded aerial displaying on 30 June, though we continued to see a few males chasing about in the breeding areas as late as 5 July.

In visiting the Jenny Lind Island nesting ground late in 1962, when most clutches were completed, we found a preponderance of females, i.e., we saw many more females than males. No doubt, this was due largely to the fact that many males had already abandoned their territories. On the breeding ground the sex ratio appeared to be equal early in the 1966 nesting season.

NESTING HABITAT—EGG LAYING—INCUBATION

Female White-rumped Sandpipers appear to nest without regard to the male's territory, though they often do nest within a territory. This behavior may partly explain why nests may occur close together. Two nests on Jenny Lind Island in 1962 were only 13 yards apart (Parmelee et al., 1967). Indif-

Fig. 1. Female White-rumped Sandpiper at nest on Jenny Lind Island. From a Kodachrome transparency taken 18 June 1966.

ference to the male's territory is characteristic of female Pectoral Sandpipers as well.

The territory and nesting site both occur in essentially the same type of habitat—reason enough that the two often coincide. Choice habitat on Jenny Lind Island, and apparently all across Arctic Canada, is hummocky, well vegetated tundra that remains persistently wet and often occurs near marshy ponds and lake shores. Well vegetated hummocky ground on the higher slopes is used less often. These better drained areas, though wet and muddy when the eggs are laid, often are very dry by the time incubation draws to a close and the young hatch. Nevertheless, the vegetation is dense and concealing (Fig. 1). This is not true of the strictly dry tundra where the ground cover is thin and scattered. The dense vegetation often consists of sedges and numerous other plants.

All 47 White-rumped Sandpiper nests seen by us on Jenny Lind Island were well concealed, rather deep depressions in hummocks. All were lined copiously with dry willow leaves and bits of mosses and lichens. We do not know whether the female actively lines the depression, but it seems unlikely since plant materials readily fall into depressions situated in well vegetated hummocks. We suspect that many of the unused depressions seen in the breeding areas may be used from time to time by the same species. Presumably some individuals use the same ground, conceivably the same nest cup, in consecutive years. A male Stilt Sandpiper banded at the nest by the senior author one summer at Churchill on Hudson Bay was found nesting in the old depression the following year by Joseph R. Jehl, Jr.

Several species of sandpipers nested in wet tundra in proximity of the White-rumps on Jenny Lind Island: the Pectoral and Semipalmated sandpipers typically; the Stilt Sandpiper, and probably the Knot, occasionally. The latter two species, also, occupied dry tundra with scattered plants. Dry tundra was the preferred nesting habitat of Baird's Sandpiper, Buff-breasted Sandpiper (*Tryngites subruficollis*), and Sanderling (*Crocethia alba*).

In the case of the White-rumped Sandpiper, we failed to find incomplete clutches of one or two eggs and thus did not determine precisely the time interval between layings. Drury (1961) inferred that eggs were laid every other day. From our own experience we know that as many as two days sometimes elapse between layings in certain large shorebirds, e.g., the Black-bellied Plover (*Squatarola squatarola*). Our guess, based on our observations with Baird's and Pectoral sandpipers, is that the interval falls somewhere between 24 and 30 hours for the White-rumped Sandpiper.

For example, the second egg at one Baird's Sandpiper nest was laid about 0330 on 12 June, the third egg about 0900 on 13 June, and the fourth egg about 1515 on 14 June. The eggs, therefore, were laid 29 to 31 hours apart. At another Baird's Sandpiper's nest the third egg was laid the very moment we discovered the site. The female while standing in the nest laid her egg *pointed end first.* She laid her fourth egg 29 hours later on 13 June. The interval between laying of the third and fourth eggs at a Pectoral Sandpiper's nest observed earlier at Cambridge Bay was at least 24 hours, at most 28 hours and 40 minutes, the fourth egg appearing later in the day than the third. That eggs are laid about 30 hours apart explains why laying occurs at a later hour each day until completion of the clutch.

One of our White-rumped Sandpiper nests had three eggs when found 14 June. The fourth egg was laid 29 hours later at about 1600 on 15 June. The fourth egg (marked) was the first of the clutch to hatch; all four eggs hatched between 1605 and 1710 on 7 July. The period of incubation from laying to hatching of the last (fourth) egg was 22 days (error not greater than 1.5 hours). The period or duration, heretofore not reported for the species, is close to the 21-day-period first reported for Baird's Sandpiper by Drury (1961) and later confirmed by us. The Semipalmated Sandpiper

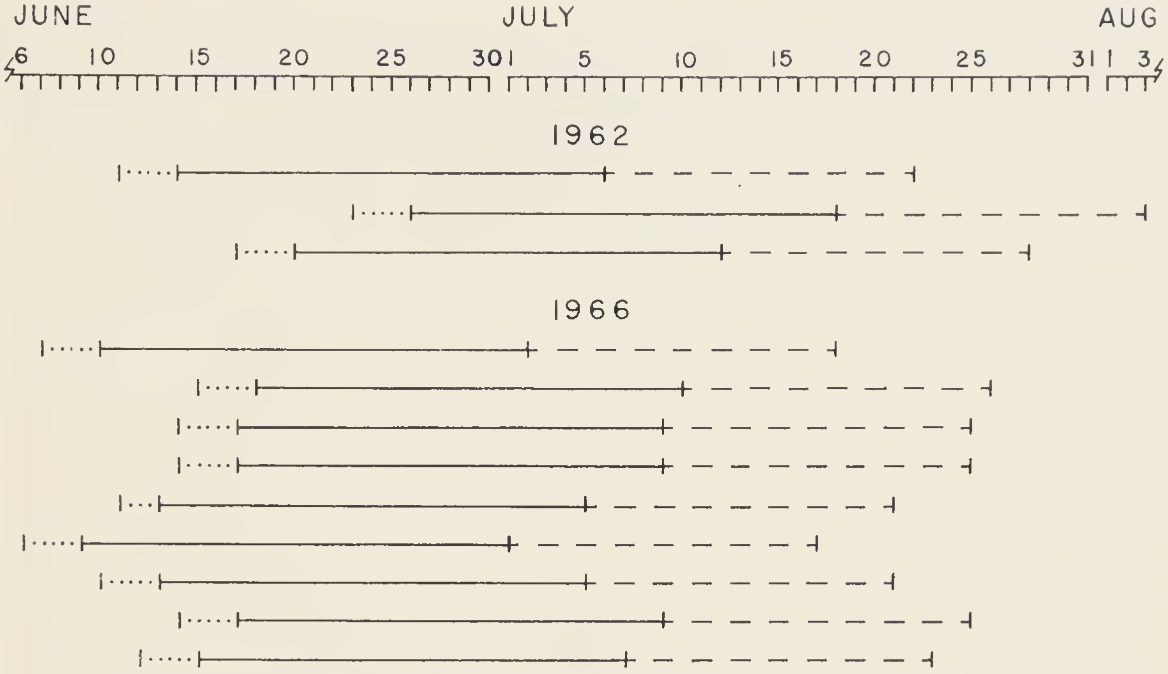

FIG. 2. Chart showing the spread of the egg laying period (dotted line), incubation period (solid line), and fledging period (dash line) for three White-rumped Sandpiper nests found on Jenny Lind Island in 1962, and for nine nests found there in 1966. Eggs presumably are laid daily at about 30-hour intervals. The period of incubation is 22 days, the period of fledging, 16 to 17 days. The period from first egg to fledging time is approximately 41 days. Egg laying may start as early as 6 June and young may fledge as late as 3 August—a span of 58 days.

appears to have a considerably shorter incubation period. Four of our records indicate that the period is only 19 days.

Assuming that White-rumped Sandpiper eggs are laid daily, and by using the 22-day incubation period as a fairly reliable standard, we have attempted to date the egg-laying and incubation periods for nine nests whose young hatched at known times in 1966 (Fig. 2). It appears that some birds had commenced laying as early as 6 June and others as late as 15 June, indicating a variation of nine days in the start of laying. Egg laying per se covered a span of 12 days (6–18 June). Seventeen or nearly 50 per cent of the 35 eggs in the nine nests were probably laid during 11–15 June, attaining a peak during 14–15 June.

Nesting data gathered on Jenny Lind Island in 1962 is of little value, since we left the breeding ground before hatching had commenced. Of 56 eggs (14 nests) examined during 20–26 June that year, all contained small embryos of various ages but indicated that egg laying had taken place chiefly in mid-June. Eggs with advanced embryos were collected early in July, and these later hatched artificially at Cambridge Bay, some as early as 6 July, and one as late as 12 July. The chick that hatched 12 July was painted directly from life by Sutton on 13 July (see frontispiece).

One clutch in 1962 was completed on 26 June—our latest date of laying for the species. Whether this late nesting was a first attempt or a repeat was not known. In any event. the egg-laying period for Jenny Lind Island was considerable. perhaps as much as 20 days. But despite the fact that some White-rumps nest very early and others very late. it is evident that most eggs are laid during mid-June. A late spring thaw probably would have little effect on the breeding schedule of the majority of White-rumps unless the season was much retarded.

The clutch size of 46 of 47 Jenny Lind Island nests was four. It may have been three at one nest. but we were not certain of this. Conceivably, an egg could have been lost to some predator before we discovered the nest.

Years ago Sutton (1932) reported that White-rumped Sandpiper males do not incubate. This observation. which is correct, had not been confirmed. Drury (1961) believed that only one sex seems to incubate, though he was vague as to which sex actually attended the eggs. In 1962 we flushed only females (three collected) from nests. But in marking nine females at nests in 1966. we were certain that the female alone incubated the eggs. Not once did we flush an unmarked bird from any of these nests. several of which were checked regularly at various hours around the clock. Observations at one nest in particular were convincing. The nest, alluded to earlier, was situated in an isolated marshy pond area between rocky ridges. The male had abandoned the territory following completion of the clutch on about 19 June. From that date the female was the only White-rumped Sandpiper on the eggs, indeed within the pond area. throughout the period of incubation. During 50 nest checks from 27 June to 10 July. this bird came off the eggs during 35 checks, or 70 per cent of the time. Seven times she appeared from over the grassy hummocks and scuttled along ahead of us, eventually returning to the eggs. Twice we watched her from afar feeding at the edge of the pond not far from the nest. Six times we failed to find her: evidently she had flown from the area before we had arrived. Our data substantiate Drury's (1961) belief that the incubating White-rump is off the nest 20 to 30 per cent of the time.

The time spent away from the nest varied. Incubating birds often left their eggs for considerable periods, at odd hours, and even during inclement spells. Some of the eggs we checked were so cold at times that we believed them to be deserted; but all these chilled eggs hatched. In this behavior the species closely resembles the Pectoral Sandpiper and Sanderling. For example. the female of a Sanderling nest we watched without letup for 21 consecutive hours frequently left her eggs unattended for short periods in late afternoon to feed close by or at a favorite lake shore fully a quarter mile away. Although she incubated her eggs constantly during the cool hours that followed when the sun was low, she suddenly left them at 0730 and did not return during the next six hours. Once back on the eggs in the afternoon, she could hardly be driven off, though she left to feed for short periods, evidently of her own volition. Most significantly, no male was seen at or anywhere near the nest throughout the 21-hour period. This female was later collected for positive sex identification.

Other scolopacids breeding on Jenny Lind Island behaved very differently. While checking the above-mentioned White-rumped Sandpiper's nest 50 times, we also checked Baird's, Stilt, and Semipalmated sandpiper nests that were near by. In these three species both sexes shared equally the duties of incubation. So regular was the twice daily turnover at the nest of the Stilt Sandpiper, that we recorded the marked male at the nest 25 times during the bright hours from 0730 to 1920: the marked female 25 times at various times during the remaining hours. The pattern was not so clearly defined in Baird's Sandpiper, and even less so in the Semipalmated Sandpiper. Nevertheless, the role of the sexes in all three was vastly different from that of the White-rumped Sandpiper.

HATCHING—CARE OF YOUNG—FLEDGING

Hatching was observed at nine nests from 1 July to 10 July in 1966 (Fig. 2). Young from six of these nests hatched during 5–10 July. Six additional broods from unmarked nests were noted during 7–11 July, indicating that many young hatched during this period. Hatching at one Jenny Lind Island nest in 1962 probably was as late as 17 July, since egg-laying was late (26 June).

Hatching dates for the species elsewhere have not been reported often. Soper (1928) first noted small young on Baffin Island on 11 July. Sutton (1932) first noted them on Southampton Island on 12 July. On Bylot Island, where arrival and egg laying may be late, hatching at four nests occurred during 15–22 July (Drury, 1961). Small downies (specimens in the National Museum of Canada) collected in southeastern Victoria Island by Captain Joseph Bernard during 7–11 August (year uncertain) were from exceptionally late nestings and probably represent an extreme case.

The period of hatching from the first to the last egg of a clutch may be rapid—as little as one hour and five minutes at one of our marked nests. At another it probably was close to 17 hours. At six nests it fell between six and 13.5 hours. These figures suggest that steady incubation usually starts about, or at most a few hours before, the time the clutch is completed.

When the large end or cap broke loose from the rest of the shell, the young chick emerged quickly. As soon as the female discovered the empty half shells, she grasped and flew off with them one at a time. One female flew about 80 yards, alighted, dropped the shell, and then promptly flew back to the nests. Another picked up a half shell which we placed two feet from the nest and carried it 150 yards before dropping it. So strong was the instinct to rid the nest of empty shells, that the attending bird quite forgot our presence, despite the fact that we held its young in plain view.

We witnessed a striking example of this type of behavior at a Stilt Sandpiper nest when we failed to entice one of the marked adults into our trap a second time in order to measure its bill. The bird repeatedly ran up to, but not into, the trap that we baited with its newly hatched young. We caught it immediately, however, when we baited the trap with an empty shell! Actually, many shorebirds show this behavior, which must have a high selective value in protecting young from the many predators that would surely detect conspicuous shells.

White-rumped Sandpiper downies remained in the nest for an indefinite period. One of our banded chicks had moved eight inches from the nest by the time it was 2.5 hours old. Another banded chick (about 7.5 hours old) having once left its nest, returned to the nest that held two siblings and an addled egg. Some chicks remained in the nest for upwards of 17 hours. Older chicks were not seen in nests. Drury (1961) stated that downy White-rumps spent the first night in the nest if they hatched in the afternoon, but did not return once they left.

The female alone attended the brood. Following the hatch we carefully checked the movements of the marked birds that we had observed earlier at nests. Females with broods generally remained within the vicinity of their respective nests for the first six or seven days, after which time some moved out into new areas. This was especially true of those White-rumps that had nested on the drier slopes. They and other shorebirds tended to move down slope toward marshy lake areas, not necessarily in the direction of the coast as might be imagined. One marked female and brood last seen in the vicinity of the nest when the chicks were six days old had moved a mile and a half down slope by the time the young were 12 days old.

Those families moving down slope within our study area tended to pile up at the lake shores or at the maze of ponds and swales between the lakes. Many of them progressed no farther until fledging time. Those young that

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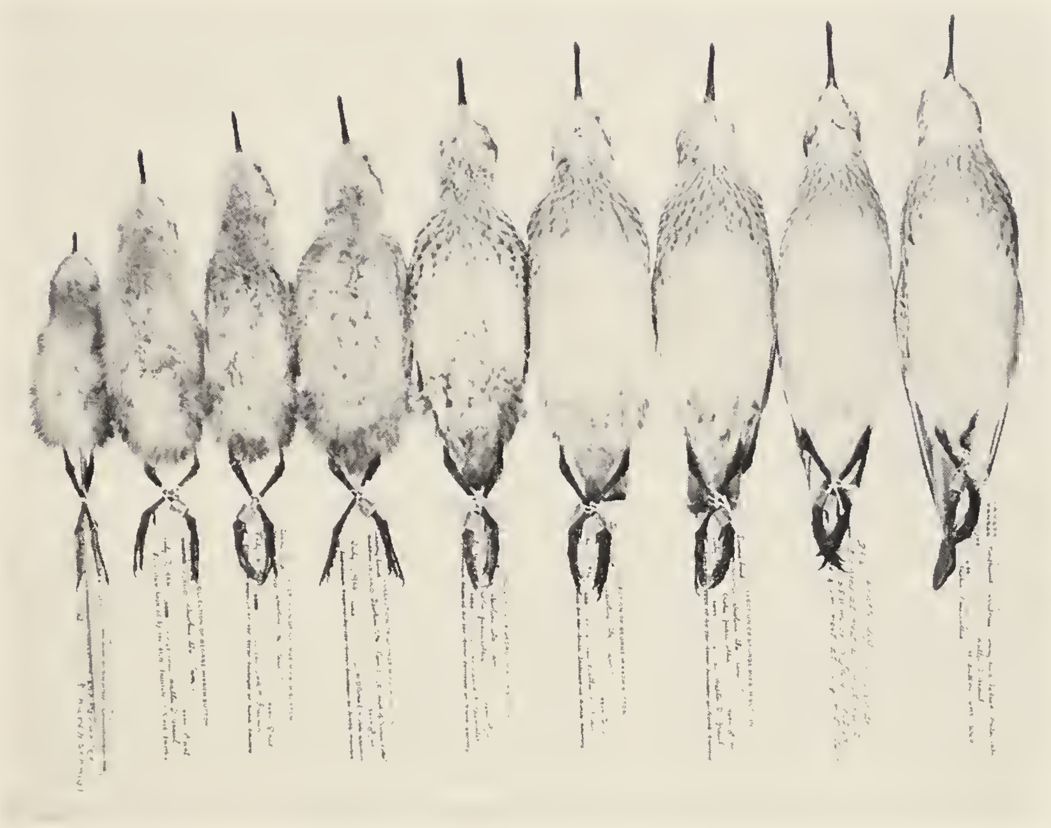
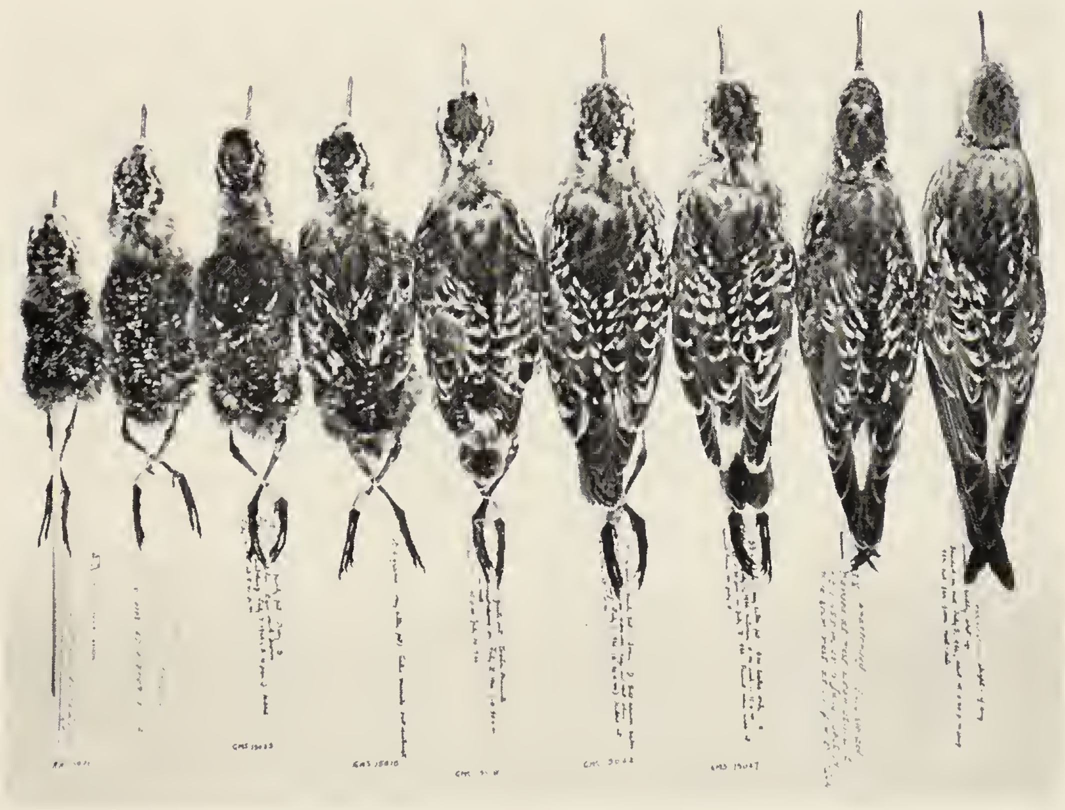
Fig. 3. Ventral and dorsal views of nine White-rumped Sandpiper young. The newly hatched downy on extreme left is six hours old. The eight banded juveniles from left to right are approximately six, nine, 11, 13, 15.5, 17, 22, and 27 days old (six, 11, 15.5, 17 day-old birds are siblings). All eight were collected on Jenny Lind Island by the authors in 1966 during 6 July 1 August and preserved by George Miksch Sutton.





had hatched near or within this labyrinth did not move very far. Broods continued to pile up until by late July the area swarmed with young of various species.

Some of the White-rumped Sandpiper females with broods we saw daily. From one such family which could be found almost any time, we collected all four siblings (Fig. 3) when six. 11, 15.5. and 17 days old respectively. The female remained with the brood to the last young. which was a strong flying juvenile when shot. At no time did we see males attending marked or unmarked broods.

Inasmuch as the female has sole charge of the brood, it was at first difficult for us to explain the occasional occurrence of two equally solicitous adults with young White-rumps. such as witnessed by Drury (1961) and others. We. also, have seen this phenomenon not only in White-rumps but in other species as well. An odd White-rump in our study area exhibited so much interest in one of our marked females. that we first thought it to be a male, possibly the mate. For at least two days the bird followed the female both in flight and on the ground. and on occasion to the nest: but it did not settle on the eggs to our knowledge. nor did it call or display. All doubts were dispelled upon collecting the bird. It proved to be a female. perhaps one that had recently lost her eggs or young.

Male White-rumped Sandpipers that are still on the breeding grounds by the time the first young hatch exhibit interest in females, but we do not know if they evince interest in chicks. At Cambridge Bay. the senior author actually witnessed a male Pectoral Sandpiper defending small downies of his kind. But the interest was short lived. for he soon abandoned the young to chase females. Both Pectoral and White-rumped sandpiper males have no real role in care of young. They differ greatly in this respect from male Knots. Baird's. Semipalmated. and Stilt sandpipers. all of which are even more solicitous and persistent than females in rearing young.

On Southampton Island, Sutton (1932) noted well developed but flightless White-rumped Sandpiper young which he felt were entirely on their own. We several times found unattended White-rump chicks. some only a few days old. One such individual, banded 621–08*174* when about three days old on 13 July. we found running alone a good half mile from the point of banding on 17 July. The female and two siblings (621–08*172.–73*) were later found near the original banding site on 18 July, the birds evidently having remained close by since the 13th. Chick number *74* was not with them and was presumably lost to the brood. Unless adopted by another adult. a small chick would have little chance of survival. It seems likely that unemployed females would quickly adopt unattended chicks. but we do not know that this is actually the case with White-rumps. Adults of other shorebird species, notably males of Baird's and Stilt sandpipers, may at times attended young other than their own—highly interesting behavior brought out in our banding studies.

Lost members of a brood cannot be ascribed to accident alone. Female White-rumps will fly off and temporarily abandon even small young. The best example of this behavior seen by us occurred on 11 July. A female left three newly hatched chicks and flew directly to and joined a circling flock of five White-rumps, at least one of which was a male. The latter occasionally set his wings and called "*quo-ick*" while flying with the group. When the flock ranged too far, the female quickly flew back and gathered up her brood, which in the meantime had scattered. But when the flock wheeled in close again, up she went for another spin.

The fledging period, heretofore not reported for the species, is 16 to 17 days. A marked 13-day-old juvenile captured by hand was fleet afoot but not capable of even short flights. Two siblings that were captured by hand when 15.5 days old were not quite fledged, though capable of flying weakly for short distances. One of them was flying strongly and could not be caught by hand 36 hours later when it was 17 days old. It flew well over a hundred yards per flight and was, in our opinion, fledged.

Allowing 16 days for fledging, young from nine nests in 1966 fledged during 17–26 July, the majority of them during 21–25 July (Fig. 2). Strong flying young were first seen that year on 18 July. Young from a late nesting in 1962 may have fledged as late as 3 August. Conceivably there could have been some overlapping between late hatchings and early fledgings that year.

The adult female-offspring bond dissolved soon after the young fledged. By the time unattended juveniles became conspicuous on the breeding ground, adult females became scarce. Lone females seen 31 July and 2 August were the last seen inland by us in 1966.

One of the marked females was collected 22 July when its young were 17 days old and fledged. The loss of the parent did not preclude further development of the young, for one was collected in good condition five days later on 27 July.

DEPARTURE FROM BREEDING GROUND

The small flocks of White-rumped Sandpipers that we saw circling low over the breeding grounds and nearby coastal areas throughout most of July were puzzling. Presumably they were composed mostly of adult males that had entered their post-breeding period. Collecting of specimens from such flocks would have been desirable, but we failed to take even a small sample.

Sutton (1932) observed that migratory tendencies were in evidence during

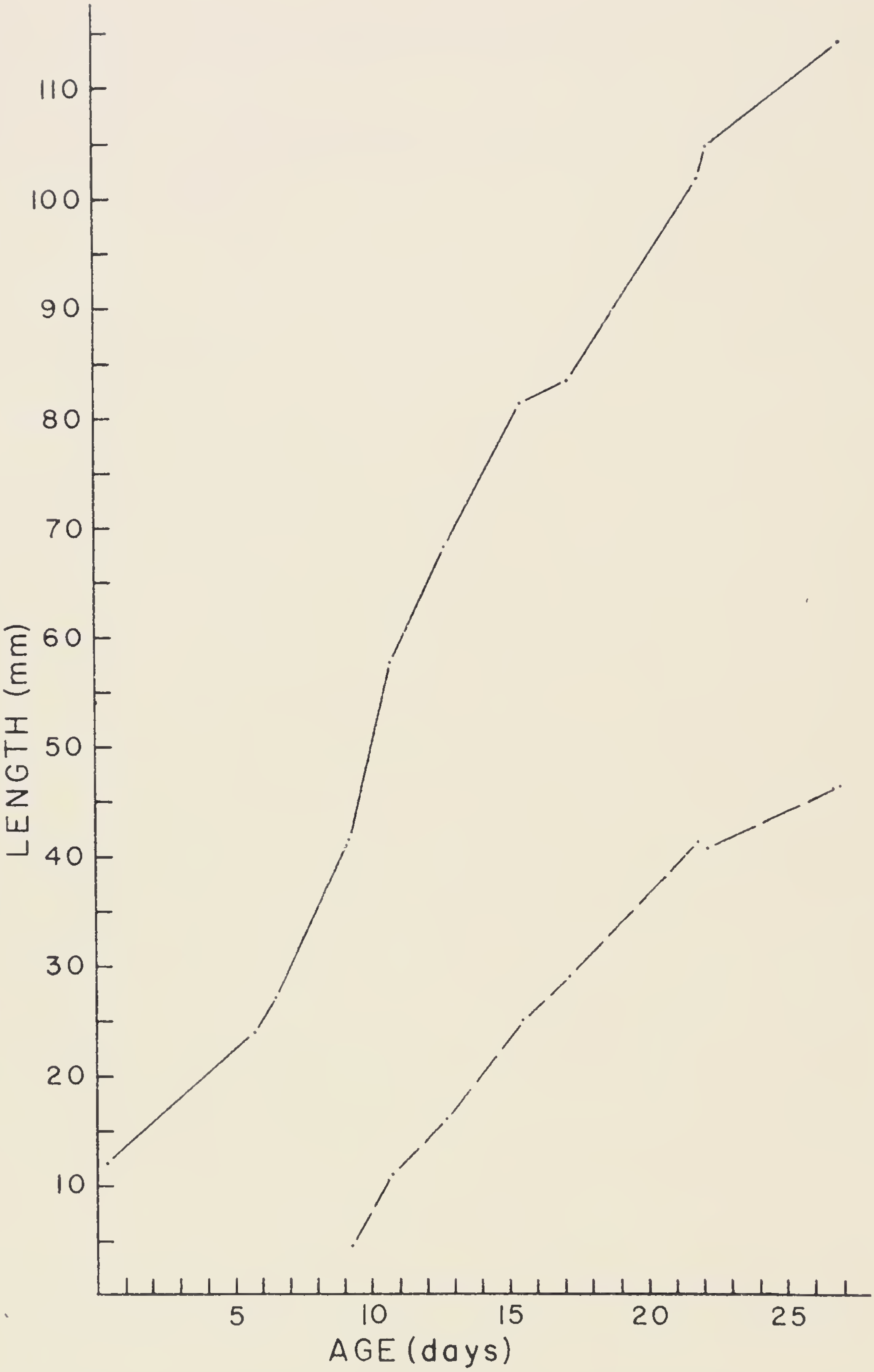


Fig. 4. Wing (solid line) and tail (dash line) growth in White-rumped Sandpiper juveniles. Curves based on measurements of wing chords and rectrices of birds of known age. Juveniles begin to fly when chord measurements exceed 80 mm.

early July before the young hatched on Southampton Island. From 9 July he observed small loose flocks of adults which he believed to be composed chiefly, if not altogether, of male birds. By mid-July males appeared to be by themselves in flocks near the coast, though not necessarily on the beaches. He witnessed a build-up or increase in the size of one flock from day to day. From these and other observations he concluded that by the time the eggs are all laid the males leave the females, go to the outer beaches, and finally flock together in small bands.

Following departure from the Jenny Lind Island breeding areas, most adult females vanished from the scene. Presumably they left the island. A few in worn and molting feather were seen occasionally among the many unattended juveniles at the marine beaches: one female each date on 3, 4, and 5 August; three on 6 August. We saw no migratory flocking of females anywhere, including the beaches of nearby Victoria Island where a single female was collected with several unattended juveniles on 13 August 1960.

Although juveniles were at the lakes and inland marshy ponds up to the time of our departure on 12 August, their numbers had fallen off appreciably inland from about the 5th. A banded juvenile 27 days old was collected within a short distance of its hatching place on 1 August. Two banded young (age uncertain) were seen on the breeding ground on 2 August, but none thereafter.

No juveniles were seen at the marine beaches during July, but when first seen there on 2 August, they had arrived in force and were second in abundance only to Semipalmated Sandpipers. Both species remained common at the beaches until 6 August, after which time their numbers fell off sharply. Macpherson and Manning (1959) reported that White-rumped Sandpipers commonly associated with the migrating flocks of Semipalmated Sandpipers that passed through Adelaide Peninsula southeast of Jenny Lind Island.

As many as 50 juveniles were seen by us at the marine beaches on 12 August, but some of these birds may have been from afar. Juvenile White-rumps are known to remain at northern beaches for a long time. It seems likely that a few remain at the Jenny Lind Island beaches after August.

SPECIMENS

Ten banded White-rumped Sandpiper juveniles from approximately six to 27 days of age were collected on the Jenny Lind Island breeding grounds in 1966 during 6 July–1 August. Data concerning their weights (gm) and measurements (mm) are given in Table 1 with those of a recently hatched chick taken from an egg collected on Jenny Lind Island in 1962.

From this table it is evident that wing chord and tail measurements increase steadily in length with age (see Fig. 4). Measurements of two juveniles (Nos. 621-08046 and -43) of approximately equal age are very similar, suggesting that during the period of

TABLE 1

Band Number	Sex	Age	Weight	Wing (chord)	Tail	Culmen	Tarsus
	F	6 hours	5.0	12.0		9.8	20.2
621-08010	M	5 days 20 hours**	?	24.0		14.2	21.9
621-08042	F	6 days 11 hours*	18.0	27.0		15.2	22.7
621-08085	F	9 days 4 hours	19.8	41.5	4.5	15.3	23.1
621-08009	M	10 days 20 hours**	25.2	57.5	11.0	17.3	24.5
621-08015	M	12 days 19 hours**	29.2	68.0	16.0	19.0	24.0
621-08011	F	15 days 13 hours	29.7	81.0	25.0	20.9	26.3
621-08012	M	17 days 5 hours	33.4	83.0	29.0	19.4	23.7
621-08046	F	21 days 23 hours	33.8	101.0	41.0	21.7	25.5
621-08043	M	22 days 6 hours*	36.3	104.0	40.5	21.4	24.0
621-08047	?	27 days 2 hours	32.5	113.0	46.0	22.6	24.0

** ± 8 hours
* ± 3.5 hours
The error for the five unstarred birds is less than one hour.

rapid growth there may be relatively slight differences in feather length of individuals of the same age. Wing chord and tail measurements probably can be used to some advantage in determining approximate ages of unbanded juveniles in the breeding areas. Verification by additional specimens of known age is needed, however.

Wing chords 80 mm long approach a critical length with respect to fledging in White-rumped Sandpipers. Chords of a 15.5-day-old juvenile that was capable of weak flight are 81 mm, whereas those of a 17-day-old sibling that was capable of strong flight are only 83 mm. Remiges continue to lengthen appreciably following fledging, chord measurements attaining a length of 113 mm by the 27th day. According to Godfrey (1966), wings of adult males average 120.4 mm, those of adult females 120.6 mm.

An abbreviated description of the body plumage development is given below for the 10 banded juveniles:

No. 621-08010 Age 5 days 20 hours (± 8 hours)
Juvenal Plumage: inconspicuous; sheaths noticeable above on cervical, interscapular, and humeral regions; below on cervical, sternal, and axillar regions.
Down: everywhere conspicuous.
No. 621-08042 Age 6 days 11 hours (± 3.5 hours)
Juvenal Plumage: same as 621-08010 but sheaths in axillar region bursting at tips.
Down: same as 621-08010.
No. 621-08085 Age 9 days 4 hours
Juvenal Plumage: feathers fluffed and conspicuous above on auricular, interscapular, humeral, and dorsal regions; sheaths conspicuous on femoral and crural regions.
Down: more conspicuous than juvenal plumage.
No. 621-08009 Age 10 days 20 hours (± 8 hours)
Juvenal Plumage: sheaths conspicuous on coronal and pelvic regions; interscapular, humeral, sternal, and dorsal regions well

feathered; wing coverts fluffed out; sheaths bursting on abdominal, femoral, and cural regions.
Down: about as conspicuous as juvenal feather.

No. 621–08015 Age 12 days 19 hours (± 8 hours)
Juvenal Plumage: feathers conspicuous on coronal and pelvic regions; white feathers of rump clearly visible; abdominal, femoral, and cural regions feathered but quite downy.
Down: less conspicuous than juvenal feather except on head, mid-pectoral, abdominal, pelvic, femoral, and cural regions.

No. 621–08011 Age 15 days 13 hours
Juvenal Plumage: buffy pectoral region distinct from whitish or pale buffy underparts.
Down: conspicuous only at base of bill, throat, neck, pelvic, abdominal, femoral, and cural regions.

No. 621–08012 Age 17 days 5 hours
Juvenal Plumage: similar to 621–08011.
Down: similar to 621–08011 but less conspicuous, especially at lower extremities.

No. 621–08046 Age 21 days 23 hours
Juvenal Plumage: typical juvenal plumage.
Down: dense and conspicuous only on dorsal cervical region; traces at base of bill, throat, and rump.

No. 621–08043 Age 22 days 6 hours (± 3.5 hours)
Juvenal Plumage: similar to 621–08046.
Down: similar to 621–08046.

No. 621–08047 Age 27 days 2 hours
Juvenal Plumage: similar to 621–08046 and 621–08043.
Down: not conspicuous anywhere; trace on dorsal cervical region.

TAXONOMIC CONCLUSIONS

Drury (1961) studied the relationships of the *Calidris* species and concluded that if any were to be taken out of the genus, *melanotos* and *fuscicollis* should be the first.[3] He went so far as to revive the genus *Heteropygia* for the two species and included *acuminata,* but not *bairdii.* Holmes and Pitelka (1962) retorted by stating that Drury's conclusions did not reflect correctly the biological characteristics and phylogenetic relationships of the White-rumped Sandpiper. Evidence gathered by them on the Alaskan breeding ground indicated that *melanotos* differed from *fuscicollis* in displays. patterns of vocalizations, and lack of an expandable throat region. They believed that *fuscicollis* was similar to the majority of "eroliine" sandpipers while *melanotos* was unique in its characters.

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[3] The authors follow the British Ornithologists' Union (1952. "Check-list of the birds of Great Britain and Ireland," London.) usage of the genus *Calidris*, which includes those species placed in the genus *Erolia* by other sources.

Our numerous observations on certain *Calidris* species in the Canadian Arctic lead us to believe that there are many overlapping characters among these birds. This is especially true of flight and ground displays and vocalizations, many observations of which have received cursory treatment only. For example, it has been our experience that several call notes of *Calidris bairdii* and the monotypic *Micropalama himantopus* are so similar that they can hardly be distinguished by the unaided ear alone. Such observations suggest that the two species may be more closely related than heretofore suspected. But to our knowledge no real analysis has been made of their calls to date.

Holmes and Pitelka (1962) and Drury (1961) stress the importance of the pair-bond relationship and the role of the sexes in care of eggs and young. However, they present few data of this sort for *fuscicollis*, although Pitelka's (1959) study sheds light on the breeding behavior of *melanotos*. Many of his observations on that species are substantiated by our own studies. In carefully marking incubating birds of several species, we are certain that the pair-bond relationship, and the care of eggs and young, are indeed similar in *melanotos* and *fuscicollis*. And that in these characters *canutus, bairdii,* and *pusilla* differ greatly—as do most *Calidris* species judged by the literature.

The taxonomic position of *ferruginea* (Curlew Sandpiper), a species we have yet to see, takes on special interest in view of the findings of Holmes and Pitelka (1964). Classified as a *Calidris* species, it apparently shows affinities to both *melanotos* and *fuscicollis*, and to others as well, including *Micropalama himantopus*. Although there are conflicting views on the breeding biology of *ferruginea*, e.g., Birula (in Pleske, 1928) and Portenko (1959), it would seem that the pair-bond dissolves following completion of the clutch, at which time the territory is apparently abandoned; and that the female alone incubates the eggs and cares for the young. We do not suggest that this behavior in itself is sufficient to bind *ferruginea* with *melanotos* and *fuscicollis;* but the behavior points to a similarity in the breeding of the birds that demands an explanation.

With respect to the pair-bond relationship and care of eggs and young, it is clear to us that *Micropalama himantopus* is very similar in its breeding behavior (as well as vocalization) to *bairdii*, but not to *melanotos* and *fuscicollis*. What little we know about *Crocethia alba* suggests to us that its breeding behavior is somewhat similar to *melanotos* and *fuscicollis*, but much more investigation is needed here. The same can be said of *Tryngites subruficollis* (Buff-breasted Sandpiper), although its many strange behaviors indicate that it is rightly called monotypic.

Our data force us to agree with Drury (1961) that *melanotos* and *fusci-*

collis are closely related, contrary to the views expressed by Holmes and Pitelka (1962, 1964). However we agree with Holmes and Pitelka that taxonomic revisions of the kind attempted by Drury are not in order until more information is available on the many *Calidris* species and several moot monotypic genera. The genus may well include nearly all species mentioned in this paper. If this is true, we believe that *melanotos* and *fuscicollis* must not be separated from each other in the expanded genus, which in time probably will include *Micropalama* and perhaps *Crocethia*. This is our view as of now. The service of the category subgenus probably could be used to some advantage in separating these seemingly related species.

Additional research is needed for a better understanding of *fuscicollis*. Most pressing is a real assessment of its displays and vocalizations, including an anatomical examination of the male's throat. A better understanding of the male's territorial behavior and of its behavior in the post-breeding phase is highly desirable.

SUMMARY

1. The summer schedule and breeding biology of the White-rumped Sandpiper were studied on Jenny Lind Island in the central Canadian Arctic from 31 May to 12 August in 1966. Emphasis was placed on the pair-bond relationship and role of the sexes during the incubation and fledging periods.
2. Detailed studies were conducted in a 2.5-square-mile area of variable terrain. Of 11 nesting females that were live-trapped, banded, color-banded and dyed for positive field identification, the movements and behavior of nine were carefully observed.
3. Twenty-two pairs bred in the study area in 1966. The highest density within this area was seven pairs (14 birds) per 80 acres. Probably two to three times as many birds occupied the same area in 1962, when a preliminary investigation was carried out from 19 June to 5 July.
4. The total breeding population for Jenny Lind Island in 1966 was estimated at 528 pairs or less. Density in peak years probably attains a level as high as any reported for Canada.
5. Early arrivals on the Jenny Lind breeding ground were few in number and not all performed aerial or ground displays immediately, as may be the case at certain localities where arrival is late. Aerial displays were noted commonly from 6 June.
6. The territory of the male has a sexual function of short duration. Ground displays, at least one type of aerial display, and general behavior of the male on territory are similar to those of the Pectoral Sandpiper.
7. Female White-rumped Sandpipers nested without regard to the male's territory. Males generally abandoned their territories when the females settled down to steady incubation, at which time the weak pair-bond relationship of short duration dissolved.
8. The choice nesting ground was persistently wet, well vegetated hummocks. Well vegetated hummocks on better drained slopes were marginal sites that frequently became very dry by the time the eggs hatched.
9. The precise time interval between laying of successive eggs of a clutch was not

determined, but it was thought to be close to 30 hours. The period of incubation from laying to hatching of the last egg of the clutch was ascertained to be 22 days.

10. Some females started to lay eggs for the first time in 1966 as early as 6 June and others probably as late as 15 June. The period of egg-laying probably covered a span of 12 days (6–18 June). It may have been even longer in 1962 when egg-laying continued until 26 June. Most eggs were probably laid during mid-June of both years, however.
11. The clutch size almost invariably was four.
12. The female alone incubated. Adults occasionally seen with incubating females were stray females.
13. The spread of hatching was at least 9 days (1–10 July) in 1966. Most young probably hatched during 7–12 July. Hatching probably occurred as late as 18 July in 1962.
14. The period of hatching from first to last egg of a clutch was as much as 17 hours, indicating that steady incubation may have started some time between laying of the third and fourth eggs at certain nests. But in most cases it probably started about the time the clutch was completed.
15. As in many scolopacids, the instinct to rid the nest of empty shells was strong. Females immediately flew off with the half shells and dropped them some distance from the nest.
16. Some downy young left the nest when only 2.5 hours old. Others remained in the nest for at least 17 hours. One young returned to the nest having once left it.
17. The female alone took full charge of the brood. Some females with broods remained near the original nesting site until the young fledged. Others moved into new areas when the young were about a week old.
18. Flightless young became separated at times from the female and were seen occasionally wandering alone. Whether such young survived was not known.
19. The fledging period was ascertained to be 16 to 17 days, after which time the female-offspring bond quickly dissolved.
20. Young from early nestings in 1966 fledged by 17 July, those from late nestings by 26 July. Some young may have fledged as late as 3 August in 1962 when there may have been some overlapping between late hatchings and early fledgings.
21. Most males abandoned the breeding ground by the time the eggs were all laid. Their numbers declined noticeably from mid-June. The few that were still about in late June and early July presumably were accommodating late females, but this point needs further investigation, as does the post-breeding flocking behavior of males.
22. Females vanished from the breeding spots following fledging of young. Most left the island immediately, though a few in worn and molting feather were among the many juveniles at the marine beaches in August.
23. Juveniles remained inland for an indefinite period following fledging. Most flocked with Semipalmated Sandpipers at the marine beaches in August when peak numbers were recorded during the first week. A few occurred inland and at the marine beaches as late as 12 August, and probably much later.
24. Fifty-five downy White-rumped Sandpipers were banded in or near the nest on Jenny Lind Island in 1966. Ten of known age, ranging from six to 27 days, were collected for scientific specimens. Data on weights, measurements, and juvenal plumage were included in this report.

25. The breeding behavior of the White-rumped Sandpiper is remarkably similar to that of the Pectoral Sandpiper, but very different from certain other calidridine sandpipers.

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KANSAS STATE TEACHERS COLLEGE, EMPORIA, KANSAS, 12 JUNE 1967.

GEORGE MIKSCH SUTTON

Andrew J. Berger

Photo by Grace R. Ray

Had I been writing a hundred years ago, there could be no doubt but that a subtitle most certainly would have been mandatory. To wit:

Gentleman, Scholar, Author, Artist, Explorer, Raconteur, Philanthropist, and Connoisseur of Whale Blubber and Sundry Other Rare Culinary Delicacies.

Even this subtitle, however, would not encompass all of the talents and personality traits of the man whom it has been my good fortune to have known for over 20 years.

If one could ever epitomize with a single word any complex human being, that one word for George Sutton would be *enthusiastic.* This boundless and infectious enthusiasm he manifests both in the confines of his office, with only one or two other persons present, and in large gatherings. Moreover, the enthusiasm is in no way limited to his interest in birds alone, but in any aspect of biology, as well as in history, music, literature, and the fine arts, which is to say, in all of the good and desirable things in life itself.

George Sutton is a teacher *par excellence.* He did not teach a single formal course during his all too short tenure at the University of Michigan, and, yet, I and many other graduate students certainly learned more through our association with him than we did in much of our class work. George Sutton has an intuitive way of teaching by the example he sets.

George Sutton introduced me to proof-reading shortly after I entered the Graduate School of the University of Michigan in 1946 after nearly five years of military service. Meeting in the hall of the University Museums one day, he said something like this: "Andy, if you have the time, I'd appreciate it if you would give me your suggestions on a paper on the Green Jay that I have in galley proof." At that time, I probably had never even heard of the Green Jay, and George Sutton knew it, but this was his way of exposing a new student to taxonomic problems and to proofreading.

I have never ceased to be amazed at George Sutton's wealth of knowledge. During the period that I was reading intensively for the comprehensive examination, I frequently came across "new and startling" facts. I felt certain that sometime I would be able to add to George Sutton's store of facts about birds, and would innocently inquire if he had heard of such and such. He invariably had heard, and I gave up trying to educate him on the day I asked if he knew the color of the yolk of the oystercatcher's egg. He not only told me at once but proceeded to give a detailed lecture on variation in color of both the yolk and the albumen among birds' eggs, virtually all of which was new to me.

Insofar as it is possible in our time, George Sutton believes in the complete education of the man. This philosophy often expresses itself during Ph.D. oral examinations, much to the consternation of the nervous candidates. Knowing that H. B. Tordoff had a very good knowledge of world birds, for example, Sutton quizzed him on birds in literature. He grilled me thoroughly on the order Pelecaniformes, knowing full well that I had never seen more than one or two of the mainland species of this order in the field. This surely was the Master's way of pointing out to the student that there is never an end to learning, and, I presume, that the new Ph.D. should keep his ego in perspective.

His selection of me as his Assistant Editor for *The Wilson Bulletin* when he assumed the Editorship in 1950, was, I feel certain, purely and simply a matter of his seeing to my continuing education. My first assignments concerned general notes and book reviews, but we also made dummy layouts for each issue, and we proofread to each other *every* single word, comma, and period of both galley and page proofs; we routinely checked quotations against the original sources. There were days when it seemed to me that we spent most of the time thumbing through dictionaries and atlases, searching out the precise meaning and nuance of words or of the preferred spelling for some remote place name. I was being tutored by a true scholar in the finest tradition of the past.

Over the years The Wilson Ornithological Society and *The Wilson Bulletin* have invariably received George Sutton's first allegiance and support. His support has been demonstrated in innumerable ways. In addition to his term as Editor of *The Wilson Bulletin,* he served as President of the Society during 1942–43 and 1946–47. His paintings often have appeared in *The Wilson Bulletin.* He has sometimes financed the printing of his own art work as well as that of others. The fact is that, in true philanthropic manner, his numerous gifts for many purposes (beyond art work) have rarely been publicized, or even known to anyone except the recipient.

George Sutton has been a contributor to *The Wilson Bulletin* for 45 years. "Notes on the Road-Runner at Fort Worth, Texas" (accompanied by his black-and-white frontispiece of an adult Roadrunner on its nest) was published in Volume 34 in 1922. Many papers on a wide variety of subjects have been published since that time.

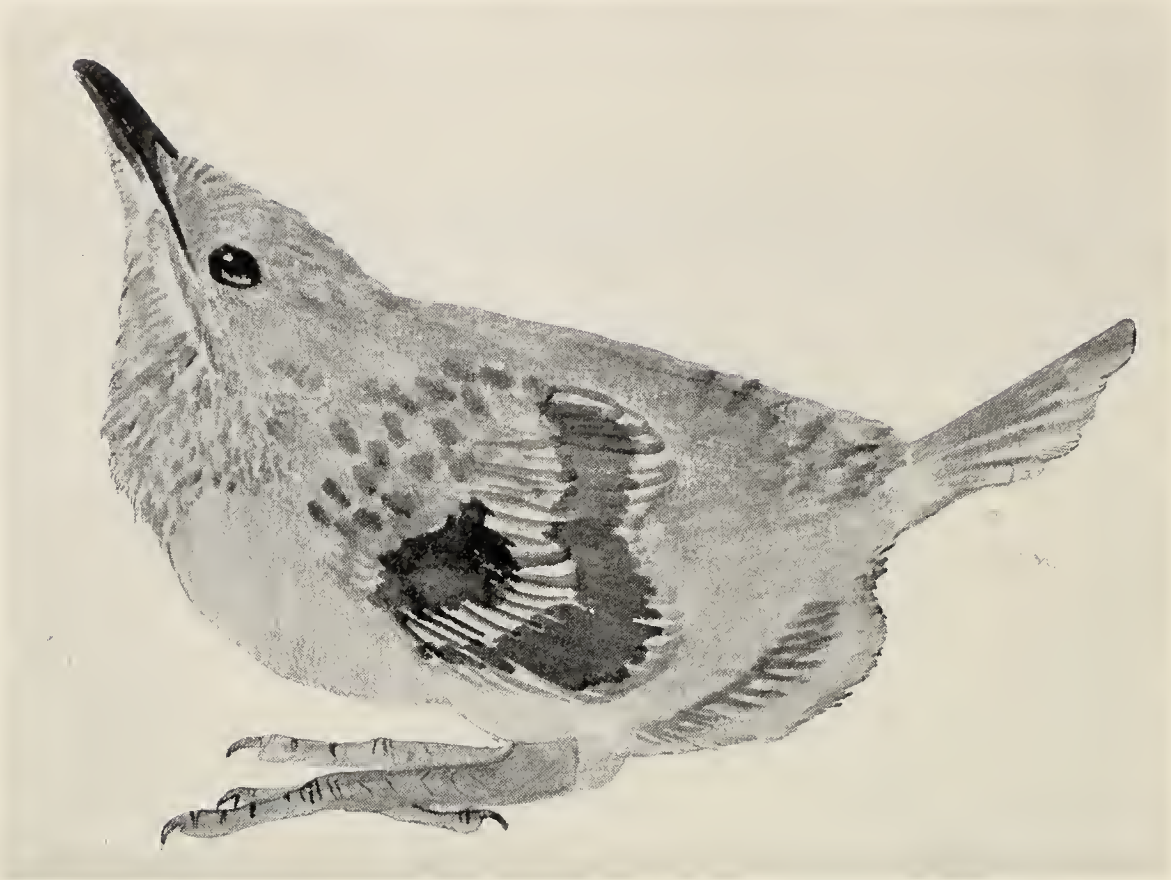

FIG. 1. A young Roadrunner still in the nestling stage. Dr. Sutton believes this to be his first direct-from-life bird drawing. It was made on 22 April 1913, a short time before the artist's fifteenth birthday. Reproduced here for the first time by courtesy of George Miksch Sutton.

George Sutton has contributed substantially to the Society by his attendance at annual meetings: by participating in the business sessions of the Council, by giving papers, or by delivering the main banquet address. He has, at the same time, over the years contributed both to the Society and to ornithology in general by his sincere interested and animated discussions with amateurs and graduate students, many of whom were attending their first scientific meeting. As every teacher knows, it is impossible to appreciate fully (or, sometimes, even to be aware of) the extent of the influence that such a dynamic man has upon the future of others, even as the result of a single conversation.

That George Sutton is one of the world's finest bird artists is well known. Many of us agree wholeheartedly with Olin Sewall Pettingill, Jr., who wrote:

"Whether George Sutton's eminence in bird art is greater than in ornithology or popular writing, no one can say. But this I can say: In his life-long devotion to delineating the living bird, he has acquired a singular style that to many of us is sheer perfection" (1966. *Florida Naturalist*, 39:136).

In addition to illustrating his own works, George Sutton has provided many fine illustrations—both color and pen-and-ink—for other books. Examples are "Birds of

Western Pennsylvania," "The Birds of Arizona," "Georgia Birds," Pettingill's two volumes of "Guide to Bird Finding," and "Fundamentals of Ornithology."

Members who attended the annual meeting at Crawford Notch, New Hampshire, in June of 1967 were able to examine his exquisite watercolors of arctic birds, many of which looked as though they were on the very verge of hopping off of the paper to scurry around the room. In the artists' world, as well, George Sutton has been an inveterate teacher. I know a number of the budding bird artists he encouraged and coached (e.g., Robert S. Butsch, William A. Lunk, Robert M. Mengel, David F. Parmelee), but, unfortunately, I have no idea how many there have been over the past 40 years; it surely has been a goodly number. As I surmised, "Doc," as he is known to all of his students, required only two attributes in the potential art student: a genuine interest in bird painting and talent. Given these, his time and patience seemed to be unlimited.

George Sutton has few peers as a lecturer. His apparent effortless delivery is due in large measure to his wide command of appropriate words, his keen sense of story structure, and his flair for the dramatic effect. Only such a truly gifted lecturer can hold an audience spellbound for over an hour without illustrations of any sort. As Dr. Pettingill once expressed it: "Indeed, for Sutton, illustrations hinder his impact whereas for most lecturers illustrations are a necessary crutch."

As an author, George Sutton has his own inimitable style, one filled with enthusiasm, perception, color, and new personal information.

I have often wondered how many readers of "Birds in the Wilderness" soon thereafter woke up in a cold sweat some night after dreaming of struggling to escape from that rotting, hollow log and its Turkey Vultures (vomiting adult, egg, and newly-hatched young), not to mention grand-daddy longlegs and white-footed mice:

"In a panic I tried to back out, only to find myself powerless. It appeared that in my toes, which could push me forward, was my only propellant power. I was doomed to stay, or to go ahead! I breathed hard, spent with exertion. There did not seem to be enough air in the place. My ribs were crowded."

One can visit the arctic regions ("The Exploration of Southampton Island, Hudson Bay," "Eskimo Year," "Iceland Summer") or the jungles of Mexico ("Mexican Birds, First Impressions") with George Sutton and feel as though one were travelling with him, sharing in each new find and facing each emergency. "Iceland Summer" earned him the John Burroughs Medal, which is awarded for excellence in nature writing. "Oklahoma Birds," his latest book, was published by the University of Oklahoma Press in 1967, and represents the fulfillment of a desire born 30 years ago.

Another of George Sutton's conspicuous traits is his interest in people. This is shown, of course, in his skill as a teacher. It also is revealed in his writing, both scientific and popular. He invariably gives credit where credit is due, to all of those who assisted in any way or to those who were merely campanions. This is, in a sense, a matter of intellectual honesty, but with George Sutton it is more than that. It demonstrates his deep sense of the importance of people and friendship, of the drama in life, and of the historic value of people and events. This sense of the value of individuals is just one of the factors that adds color and warmth to his writing.

It has been said that field ornithologists are born and not made. I have never met a better field ornithologist than George Sutton, nor do I ever expect to meet one.

Because of George Sutton's numerous talents, it may seem strange to many readers that perhaps what I have missed most during the past 16 years has been the opportunity to accompany him on field trips. Those that I remember most vividly were field trips at the University of Michigan's Edwin S. George Reserve in Livingston County, Michigan, where Sutton studied for many years. I must admit, however, that he had the unpleasant habit of insisting that the first field trip of the day take place before breakfast. Moreover, he led at a brisk pace, typically outdistancing his companions 18 to 25 years younger. But, he knew every trail, every callnote, and every bird song. He often recognized a distant faint call or a mere fragment of a song which had escaped the rest of us. He stopped frequently, to point out an alarm note or a territorial song, or, at times, to examine tracks in a dusty road: tracks of deer, raccoon, or Vesper Sparrows. He stopped in the Big Woods to listen to the songs of the Acadian Flycatcher and the Cerulean Warbler—and his companions rested. He stopped along the edge of Fishhook Marsh to search for a Brewster's Warbler—and his companions thought mostly about breakfast as they swatted mosquitoes. At breakfast there always was a stimulating discussion of the morning's findings and of the plans for the remainder of the day. I remember driving the Reserve's dirt roads at night, alert for the eye-shine of Whip-poor-wills sitting in the road or at its edge, while Sutton told us of differences in the eye-shine color of Mexican birds.

Few are the ornithologists as gifted as George Sutton in finding birds' nests. So thorough is his knowledge of the breeding behavior of birds that a specific alarm note will let him know at once that a nest is nearby. After scanning the habitat, he often is able to walk directly to the nest, or at least to the tree or bush or tuft of grass containing it.

Because he is an exceptional field ornithologist and author, it might be expected that Sutton keeps meticulous field notes, and this is so. His diligence in writing field notes is exemplary. No matter how strenuous his day has been in the field, and no matter how many skins or sketches are to be prepared near the end of the day, he invariably records in detail his observations and impressions before he thinks of going to sleep. His voluminous notes are, of course, invaluable for his writing at a later time.

George Sutton is an artist in the preparation of bird skins. The size and proportions of his completed skins are perfect; every feather is in proper place; there is no trace of fat, blood, or dirt. One can, almost invariably, pick out a Sutton-made skin from among many skins in a museum drawer, perhaps occasionally being misled by a skin prepared by his most talented student, H. B. Tordoff. A Sutton label contains a wealth of information about the specimen, sometimes including the phrase "no feathers lost." Only someone who has tried to prepare bird skins can fully appreciate that phrase and the pride which must accompany its writing.

George Sutton raised Roadrunners (and other species) and studied their behavior long before most contemporary bird ethologists were born. His "Suggestive Methods of Bird-study: Pet Road-runners" was published in *Bird-Lore* in 1915 (Vol. 17:57–61): this article also contained his first published drawing—that of a pet Roadrunner "in an attitude of fright." Much later he made a thorough study of the molts and plumages of various passerine birds and had his fling as a "sparrow rancher" (1948. *Audubon Magazine*, 50:286–295), again observing the developing behavior patterns as the nestlings grew to become fledglings and then juvenile birds.

I would be remiss, indeed, if I did not call attention to the fact that George Sutton is not only a gourmet but that he is what we may appropriately call a "zoological gourmet." By this I mean that in addition to his Epicurean tastes for the food and drink of "civilized" society, he has a fine appreciation of the foods available on expeditions in the wilderness, particularly when provisions are in short supply. He not infrequently told me of some of his special treats, and I envied him and his field companions. Not wanting to trust my memory, however, I wrote for confirmation. Here is what George Sutton replied (letter of 6 December 1967):

"Are you now delving into the mysteries of the cholesterol content of human blood? You must be. I've eaten white whale (beluga: *kellilughak*) blubber many times, but never Greenland whale (*akvik*) blubber. I've eaten lots and lots of *netchek* seal blubber, some *oogjook* seal blubber, and some *kashigiak* seal blubber. Doesn't all this make your mouth water? But I don't recall ever eating a meal that was *all* blubber. The ideal meal in winter on Southampton Island was some raw caribou plus some cooked caribou and cooked seal blubber. Delicious! Another wonderful meal was fried char plus raw caribou plus cooked seal blubber. I didn't like raw seal blubber. It too often had a 'weaselly' smell.

"I've eaten many kinds of wild duck and goose eggs, of course; tern eggs galore; gull eggs galore; one set of Whistling Swan eggs; and a good many Snowy Owl eggs. All these were good."

Few people probably are aware of the inner struggles faced by a man with so many talents: author, artist, explorer, teacher, lecturer. How does such a man budget his time? Not so much his days, but his weeks and months and years. It is the curse of man that each day has but 24 hours, and that they pass all too fast for the busy creative man. I am not certain that George Sutton feels completely happy about the way he has budgeted his time thus far, but those of us who have read his books, enjoyed his paintings, been stimulated by his lectures, and been inspired by his teaching feel that he has greatly enriched our lives beyond any acknowledgment with mere words. For us his time has been budgeted very well indeed.

Although I have written partly in terms of my own indebtedness and admiration, I also have the privilege here of expressing the sincerest thanks, the deepest admiration, and the very best wishes of countless friends to George Miksch Sutton on the occasion of his 70th birthday.—DEPARTMENT OF ZOOLOGY, UNIVERSITY OF HAWAII, HONOLULU.

NOCTURNAL MIGRATION IN ILLINOIS—DIFFERENT POINTS OF VIEW

Richard R. Graber

Since 1957, with other colleagues of the Illinois Natural History Survey, I have attempted by various means to observe and describe night migration of birds in central Illinois. Our accumulation of data includes more than 3 years of radar observations on film, audio records on magnetic tapes, specimen data from birds killed at television towers, and field censuses of migrants in fall and spring, 1957–1963. From these records, data have been published on the methods of study (Graber and Cochran, 1959; Graber and Hassler, 1962), and on some general characteristics of migration in this region (Hassler et al., 1963; Bellrose and Graber, 1963).

The application of a variety of techniques to the study of migration seems, at times, to confuse rather than clarify the picture. Some of our observations made using different techniques seem even to be contradictory, and yet each method of study probably contributes something to our understanding of the truth.

The objectives of the present paper are to show how different methods of study influence our perception of the truth, and to point out certain consistent traits of night migration in this region, particularly with regard to variation in the volume and direction of migration under various conditions.

METHODS

This paper is based primarily on direct observations of migration, made in central Illinois between 1960 and 1962. The radar and aural methods of study and the equipment used have already been described for the most part (Graber and Cochran, 1959; Graber and Hassler, 1962).

In 1961 I added a mobile radar unit to our equipment. This unit consisted of an APS-42A radar set and portable gasoline generator, mounted in a covered pickup truck (Fig. 1). In the fall, 1961, and spring, 1962, I ran east-west and north-south transects with the mobile unit along highways in the states of Illinois, Indiana and Iowa in order to learn whether the direction of migration varied from place to place. In running transects, the radar was usually operated for periods of 20 to 30 minutes at each stop, and the stops were spaced 20 to 40 miles apart. Because the directional scale on the mobile radar indicators was tied to the truck, accuracy of the directional data from the mobile radar depended on accurate placement of the vehicle. The truck was positioned on the basis of the north star and detailed road maps.

One interpretation which I have made of the radar record needs further

FIG. 1. Mobile radar unit used to observe bird migration at several localities in Illinois.

explanation. An observer watching the radar PPI indicator sees two basic patterns in the display of targets. Most conspicuous are targets moving tangential to the rotating radar beam. Such targets leave a track of spots glowing on the radar scope which mark the progress of the target as it moves through the sky. It is axiomatic that the recording of a track depends upon the target holding its altitude and direction relatively constant through the area covered by the radar beam sweep. Non-tangential targets are usually intercepted by the radar beam only once, if at all. For every tracking bird target observed, usually two to three non-tracking (non-tangential) targets are intercepted (see photo, Graber and Hassler, 1962:372). In working with the radar data, I noticed that the ratio of tracking to non-tracking targets varied from hour to hour, and sometimes from night to night. Feeling that this variation might be related to orientation (or lack of orientation) of migrants, I calculated the "tracking ratio" for each hour of the night for a number of nights (Sept. 1–2, 4–5, 9–10, 11–12, and 13–14, 1960), and found that on clear nights the ratio varied from hour to hour in a consistent pattern. The significance of this pattern and observed deviations from it are discussed below.

To show how widespread are the tracks of the migrant swarm which passes in view of the Champaign radar on a given night, I have extrapolated

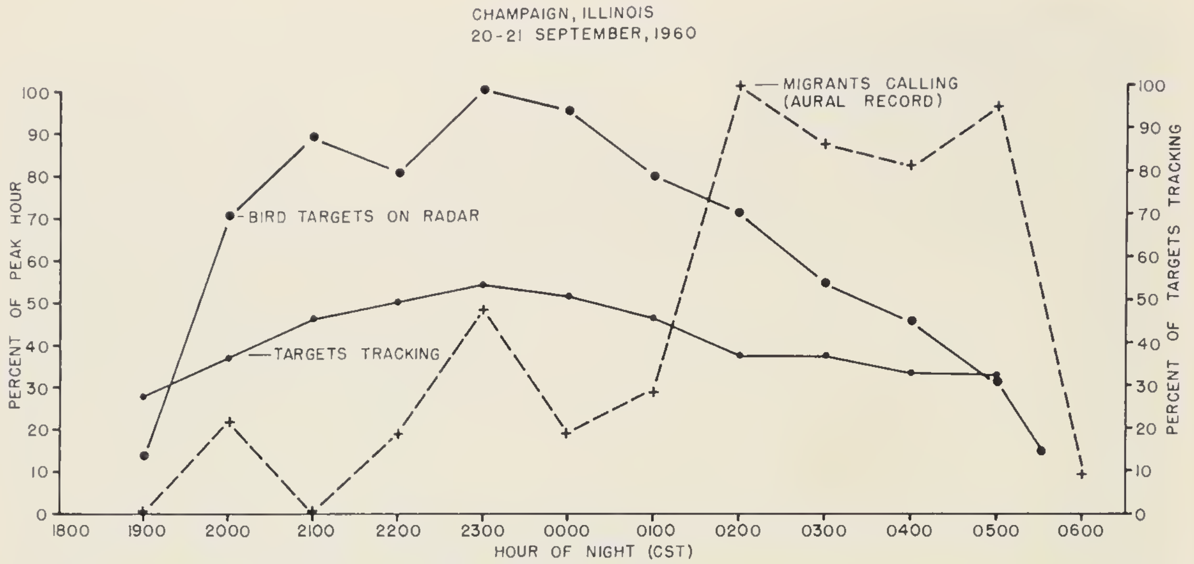

Fig. 2. Comparison of temporal patterns of migration as recorded simultaneously by radar and by aural techniques on a clear night. Also shown is the typical pattern of hour-to-hour variation in the tracking ratio of migrants observed on radar.

from the radar data and projected the flight paths of migrants through a hypothetical night's migration on two typical clear nights, one in fall and one in spring. Data on which this extrapolation is based are the track directions of bird targets and their speeds, and the temporal pattern of migration for the particular night. Two related sets of observations support the validity of such an extrapolation: (1) The wind conditions which night migrants in this region appear to choose for migration are such that the air mass in which the birds are flying is moving (albeit at a slower rate) along with the birds (Graber and Cochran, 1960:260–262; Hassler et al., 1963: 61–63). This circumstance would appear to help the birds maintain their true courses. (2) The telemetered flights of two individual thrushes recorded in spring, 1965 (Anon., 1965; Graber, 1965) showed that birds tended to maintain their initial departure courses throughout the night, though on slightly curving paths.

I have used the term "migrant swarm" to designate the mass of migrating birds passing over a fairly large area. The term does not imply homogeneity in the species composition or uniformity of behavior of the migrating birds. In discussing directional patterns of migration and the composition of the migrant swarm, I have utilized species data from bird kills at television towers, thereby emphasizing the fall data: large kills are much less frequent in spring than in fall in this region.

From field observations reported in the literature I have attempted to determine the major fall migration routes for species of long-range night migrants which pass through east-central Illinois. Some of these data are summarized in Table 2. The principal references used in this summary were: for South Carolina: Sprunt and Chamberlain (1949); Georgia: Burleigh (1958); Florida: Sprunt (1954); West Indies: Bond (1961): Alabama: Imhof (1962); Louisiana: Lowery (1955); Mexico: Blake (1953); and Honduras: Monroe (1964).

Because the radar data for a given night may represent many different populations of birds, references to the mean track and other statistics may be of questionable validity, yet as an indication of the distribution of tracks and their variation from place to place and time to time, statistics (standard deviation, mean and standard error) are presented for most of the data samples included. In this paper statistical correlations or differences are considered significant at the 0.05 level or better.

Scientific names have not been included in this paper: nomenclature follows the A.O.U. Check-List of North American Birds, 5th Ed.. 1957.

COMPARISON OF RADAR AND AURAL RECORDS

Hourly variation.—On clear nights, the typical pattern of migration as seen on radar shows a peak in the number of migrants occurring shortly before midnight; the aural record indicates that the peak in the night's migration comes *after* midnight, usually just before dawn. By recording flight calls and radar targets simultaneously at the same place (Fig. 2), we can demonstrate that the difference in patterns probably reflect something other than the numbers of birds flying. Data for the night of 20–21 September 1960 are exemplary (Fig. 2). The radar showed that most of the migrants passing Champaign were at altitudes between 2.200 and 3.200 feet, well within the range of our audio system (Graber and Cochran, 1959:228). Species which I could identify with certainty from the tape were Swainson's Thrushes, Gray-cheeked Thrushes, and Dickcissels.

Cloud cover has a notable effect on the pattern of calling of night migrants. See Figure 3 for the overcast night of 19–20 September 1960. The record for this night shows the expected pre-dawn peak in calling, but it also shows conspicuously high peaks at other hours. Early in the night, migrants flying under complete overcast were extremely vociferous. As the cloud layer broke, calling declined, but as the overcast closed again about 2200 CST, calling began to increase again, though the radar showed fewer migrants present rather than more (Fig. 3). About midnight when a small number of migrants were under the overcast, the calling rate was high, but by 0200, when migrants appeared to be above the clouds, the calling rate had declined again just before the pre-dawn peak (Fig. 3). Ogden (1960: 65–66) noted the same phenomenon while making flight-call counts at a television tower in Tennessee. When complete overcast came in about mid-

TABLE 1
BIRDS KILLED IN SEPTEMBER (1957–1962) AT A TELEVISION TOWER IN CHAMPAIGN COUNTY, ILLINOIS.

	21–22 Sept. 1957		15–17 Sept. 1958		28–29 Sept. 1959		19–20 Sept. 1960		24–25 Sept. 1962		Totals	
Species	N	%	N	%	N	%	N	%	N	%	N	%
Swainson's Thrush	2	1.7	58	39.5	77	16.6	72	15.0	37	12.5	246	16.4
Ovenbird	32	28.1	4	2.7	66	14.2	85	17.7	31	10.5	218	14.5
Gray-cheeked Thrush	2	1.7	33	22.4	21	4.5	38	7.9	26	8.8	120	8.0
Magnolia Warbler	24	21.0	1	0.7	28	6.0	29	6.0	35	11.8	117	7.8
Red-eyed Vireo	4	3.5	13	8.8	42	9.0	49	10.2	4	1.3	112	7.5
Rose-breasted Grosbeak	1	0.9	2	1.4	39	8.4	29	6.0	21	7.1	92	6.1
Tennessee Warbler	8	7.0	5	3.4	25	5.4	21	4.4	16	5.4	75	5.0
American Redstart	4	3.5	—	—	13	2.8	23	4.8	27	9.1	67	4.5
Catbird	1	0.9	—	—	34	7.3	18	3.8	5	1.7	58	3.9
Bay-breasted Warbler	6	5.3	3	2.0	7	1.5	11	2.3	29	9.8	56	3.7
Chestnut-sided Warbler	4	3.5	1	0.7	17	3.7	12	2.5	7	2.4	41	2.7
Black and white Warbler	4	3.5	—	—	13	2.8	16	3.3	4	1.3	37	2.5
Yellowthroat	2	1.7	—	—	16	3.4	14	2.9	5	1.7	37	2.5
Bobolink	—	—	16	10.9	4	0.9	7	1.5	10	3.4	37	2.5
Scarlet Tanager	1	0.9	1	0.7	13	2.8	10	2.1	9	3.0	34	2.3
Philadelphia Vireo	5	4.4	1	0.7	8	1.7	11	2.3	4	1.3	29	1.9
Palm Warbler	1	0.9	—	—	6	1.3	3	0.6	5	1.7	15	1.0
Black-throated Green Warbler	1	0.9	—	—	3	0.6	5	1.0	4	1.3	13	0.9
Blackpoll Warbler	2	1.7	1	0.7	2	0.4	2	0.4	5	1.7	12	0.8
Northern Waterthrush	—	—	—	—	5	1.1	5	1.0	1	0.3	11	0.7
Wood Thrush	—	—	1	0.7	6	1.3	1	0.2	2	0.7	10	0.7
Blackburnian Warbler	2	1.7	1	0.7	3	0.7	3	0.6	1	0.3	10	0.7
Veery	—	—	4	2.7	3	0.6	1	0.2	—	—	8	0.5
Connecticut Warbler	—	—	—	—	2	0.4	4	0.8	2	0.7	8	0.5
Short-billed Marsh Wren	—	—	—	—	6	1.3	—	—	—	—	6	0.4
Long-billed Marsh Wren	2	1.7	—	—	2	0.4	2	0.4	—	—	6	0.4
Yellow-throated Vireo	—	—	2	1.4	—	—	1	0.2	1	0.3	4	0.3
Cape May Warbler	3	2.6	—	—	—	—	1	0.2	—	—	4	0.3
Black-billed Cuckoo	—	—	—	—	—	—	1	0.2	1	0.3	2	0.1
Eastern Wood Pewee	2	1.7	—	—	—	—	—	—	—	—	2	0.1
Brown Thrasher	—	—	—	—	2	0.4	—	—	—	—	2	0.1
White-throated Sparrow	1	1.7	—	—	1	0.2	—	—	—	—	2	0.1

TABLE 1 (*Cont.*)

	21–22 Sept. 1957		15–17 Sept. 1958		28–29 Sept. 1959		19–20 Sept. 1960		24–25 Sept. 1962		Totals	
Species	N	%	N	%	N	%	N	%	N	%	N	%
Virginia Rail	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Sora	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Yellow-bellied Sapsucker	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Traill's Flycatcher	—	—	—	—	1	0.2	—	—	—	—	1	0.1
House Wren	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Nashville Warbler	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Yellow Warbler	—	—	—	—	—	—	—	—	1	0.3	1	0.1
Myrtle Warbler	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Savannah Sparrow	—	—	—	—	—	—	1	0.2	—	—	1	0.1
Totals	114	100.5	147	100.1	465	99.9	478	99.3	296	99.6	1,500	100.1

night his call count increased greatly but as the cloud layer broke the count declined again. Inherent in the observation that calling rate of migrants appears to vary with cloud conditions, is the question of whether the rate of calling is related to disorientation.

At Champaign on the overcast night, as on the clear night, *Hylocichla* thrushes accounted for about 80 per cent of the calls heard, yet that night 32 species of birds were killed at a TV tower just 11 miles from the radar-audio station and *Hylocichla* thrushes accounted for only about 23 per cent of the 478 birds killed (Table 1). The radar showed no migrants under 1,500 feet at any hour of the night (Fig. 3), despite the large number of birds killed at the 983-ft. tower.

The Tracking Ratio.—The hourly measure of the tracking ratio of migrants observed by radar may help to indicate what the birds are doing at a particular time of the night. In Figures 2 and 3, the tracking ratio is expressed as the per cent of bird targets making a track. This percentage rarely falls below 15 or reaches above 55. The tracking ratio pattern shown in Figure 1 is typical for a clear night. Early in the night the number of birds tracking is relatively low (about 28 per cent). The percentage climbs progressively until about the middle of the night, when nearly half the bird targets are tracking, and then progressively declines until at dawn the percentage is back to the low of around 30. Presumably the low figures at the beginning and end of the night reflect the fact that large numbers of migrants are changing altitude at these hours, ascending early in the night, descending late. It is in the middle of the night that the largest numbers of migrants maintain constant altitude. What I have interpreted to be altitudinal changes

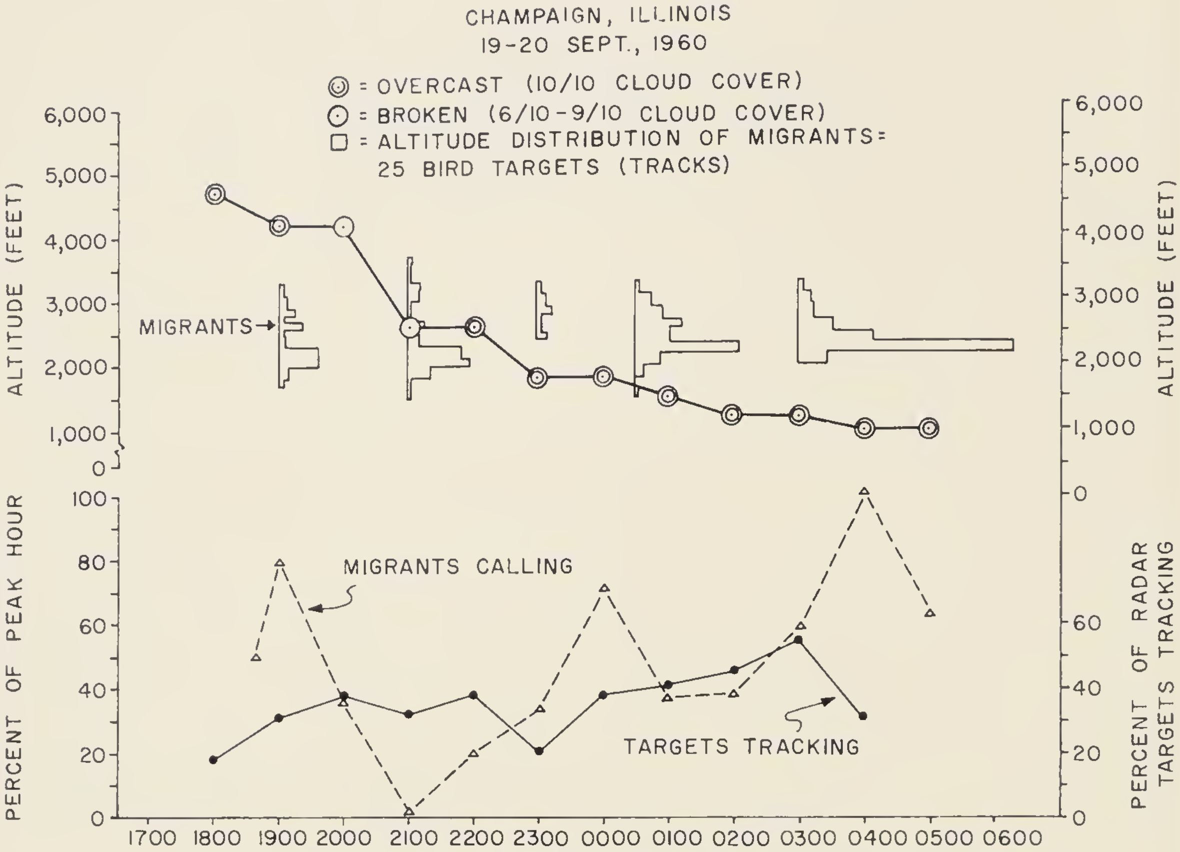

Fig. 3. Hour-to-hour variation in patterns of calling and tracking by migrants on an overcast night. Circle symbols and heavy line show altitude of cloud cover. Open square symbols show altitude and number of migrants.

could also be directional changes, for if migrants were changing their flight directions erratically early in the night and again late, the effect on the tracking ratio curve would be the same. For a clear night at least, it seems more reasonable to interpret the curve in terms of altitudinal, rather than directional shifts.

Under overcast on the night of 19–20 September 1960, birds departing from the Champaign area showed an exceptionally low tracking ratio (about 18 per cent, Fig. 3), and the hourly variation did not show the characteristic pattern seen on clear nights. As the cloud layer broke, the tracking ratio improved, but declined sharply when overcast reformed and lowered to 1,700 feet. As large numbers of migrants appeared above the overcast, the tracking ratio again improved before falling off about dawn, apparently as migrants started to land (Fig. 3). On this night birds were apparently shifting altitude, direction, or both, in response to changing cloud conditions.

There is also a possible non-ornithological explanation for the variation in the tracking pattern. If false echoes were particularly numerous early in the night and again late, the tracking pattern would be similar to that shown in Figure 2, because false echoes never make a track. This explanation does

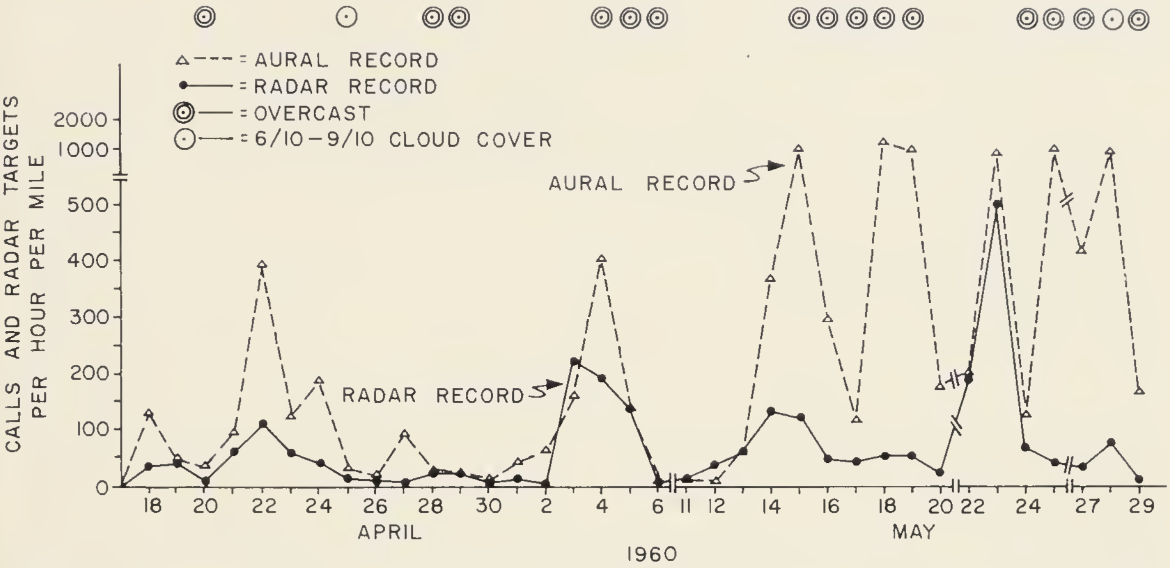

FIG. 4. Comparison of radar and aural records of migration at Champaign, Illinois, Spring, 1960.

not hold up under closer scrutiny however, because it is the number of tracking targets which actually effect the curve, while the number of non-tracking targets tends to remain more constant from hour to hour.

Nightly variation.—Because both radar and flight call counting are methods commonly used for the study of migration, it is worthwhile to directly compare seasonal radar and audio records made at the same time and place (see Fig. 4). There is no significant statistical correlation between the radar and aural readings from night to night ($r = 0.373$), though there is some coincidence of peaks in the graph (Fig. 4). As expected the aural record is more variable than the radar record. Because migrants are especially vociferous on overcast nights, it is not surprising that the disparity in results from the two techniques is particularly great on nights with cloud cover (Fig. 4).

SPECIES COMPOSITION OF THE MIGRANT SWARM

In the ensuing discussion tower kill data are used to indicate the species composition of the migrant swarm. It is, therefore, essential to ask how well the kills reflect the migrant fauna which we observe in the field. As a basis for comparison we have the results of field censuses conducted almost daily in Champaign County by Jean Graber and the author in forest and shrubby forest edge habitat during fall (14 August–15 October), 1957–1962, and spring (15 March–1 June), 1958 to 1963. A comparison of field count and tower kill figures for forest and forest edge species is presented in Figure 5. The data shown are the summed counts of birds killed, and birds seen in the field during the period (15–30 September, 1957–1962) when kills occurred.

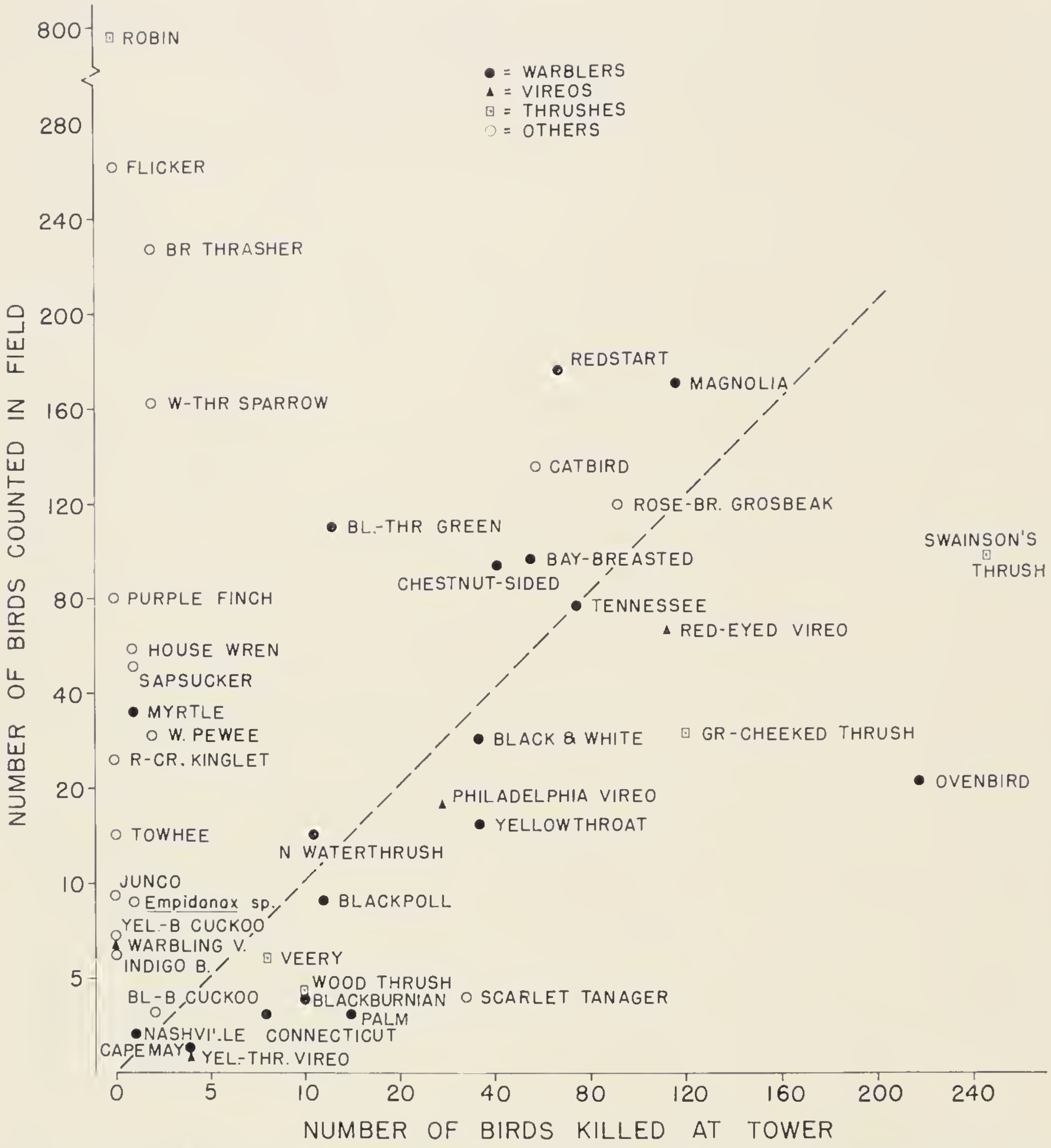

Fig. 5. Comparative data on the numbers of migrants killed at a television tower and the numbers observed in the field near Champaign, Illinois during the period (15–30 September 1957–1962) when kills occurred.

In general, species which were seen commonly in the field were also common tower victims, though there were notable exceptions. If we compare the number of birds of each forest species killed on a given night with the numbers of the same species counted in nearby woods the following morning, we find no significant correlation (r = 0.350) between the two counts. Further analysis shows that this lack of correlation largely reflects the field observer's varying ability to see different species in their natural habitat. Inconspicuous species (Ovenbird, Gray-cheeked Thrush) are killed in numbers out of proportion to the numbers seen, while conspicuous species (flycatchers. Myrtle Warbler) *seem* to be less frequent victims. If we choose closely related species and compare the numbers killed with the numbers seen. we usually find a high degree of correlation between the counts. For example. correlation coefficients between field counts and kill counts for species of vireos ($r = 0.993$). *Hylocichla* thrushes ($r = 0.983$), and *Dendroica* warblers ($r = 0.828$) are all significant. Some of the discrepancies are inexplicable. One *Dendroica*, the Black-throated Green Warbler, appears to be much less susceptible to the tower peril than its congeners (Fig. 5). The Robin. seen in greater numbers than any other species during the kill period. has not been recorded as a casualty. The Robin is widely known as a diurnal migrant, though in east-central Illinois arriving flocks often seem to appear during the night or very early morning. Yellow-shafted Flickers were more numerous during the September kill period than at any other time. yet the few flickers we have found at the tower were killed in early October. Does this imply that some flicker populations are more susceptible to kill than others?

The September tower kills at Champaign include relatively few open field species (Table 1): most of the open field passerine migrants pass through the area after September. Stoddard's (1962) study showed that the open field fringillids and other passerines are also common tower victims during their late fall migrations. Shorebirds and waterfowl pass mainly either before or after September. though shorebirds and waterfowl appear to be relatively rare casualties at any U. S. tower at any season.

While this analysis provides justification for using kill data to interpret the September directional patterns of migration observed at Champaign. it should be remembered that the altitude range covered by the tower is entirely different from that covered by radar; this discrepancy could represent important faunal differences.

DIRECTIONAL PATTERNS OF MIGRATION

Investigators who use radar in migration studies often average their directional data to obtain a generalized picture (Bellrose and Graber. 1963: 366; Drury and Nisbet. 1964:70. and others). This procedure is useful. and is applied in the present study also. but it presents an overly simplified picture. On any given night during the migration seasons. many species of birds are flying (Table 1; see also Brewer and Ellis. 1958). and each species may represent a number of distinct populations (Raveling. 1965:91). Thus. the great spread of track directions recorded by Champaign radar during one night (Figs. 6 and 7) is not surprising. As yet there is no way to ascribe the various tracks observed on our radar to particular species or populations of birds, though this is probably an attainable goal.

Fig. 6. Flight directions of migrants recorded by radar on a typical clear Spring night. Heavy arrows show the per cent of migrants on a given 5-degree track. Dash lines extend the radar tracks through a full night's migration, the extrapolation based on each track direction, its speed in knots (K), and the temporal pattern observed at Champaign.

As observed by radar, there is a typical pattern of flight directions for the long-range passerine migrants which pass through central Illinois in large numbers particularly in May (Fig. 6) and September (Fig. 7). On an exemplar spring night (22–23 May 1960) about 75 per cent of the migrants were tracking east of 355 degrees (Fig. 6). Projected, the majority of these tracks intersect the belt of coniferous forest between the Great Lakes and Hudson Bay, the center of the breeding range for many of the northern migrants which pass Champaign at this season. The audio record for this night showed the presence of Swainson's and Gray-cheeked thrushes, cuckoos, Dickcissels, and Solitary Sandpipers, plus other species, probably mainly northern warblers, whose call notes I could not identify specifically. Because most of the species of long-distance migrants which are common in the Champaign area in spring, also appear there commonly in fall, we might expect that the spring and fall directional patterns detected by Champaign radar would simply be reversed in the two seasons, i.e., with the dominant vectors northeast in spring and southwest in fall. In fact, the dominant vectors are east of the north-south line in *both* spring and fall (Figs. 6, 7 and 9).

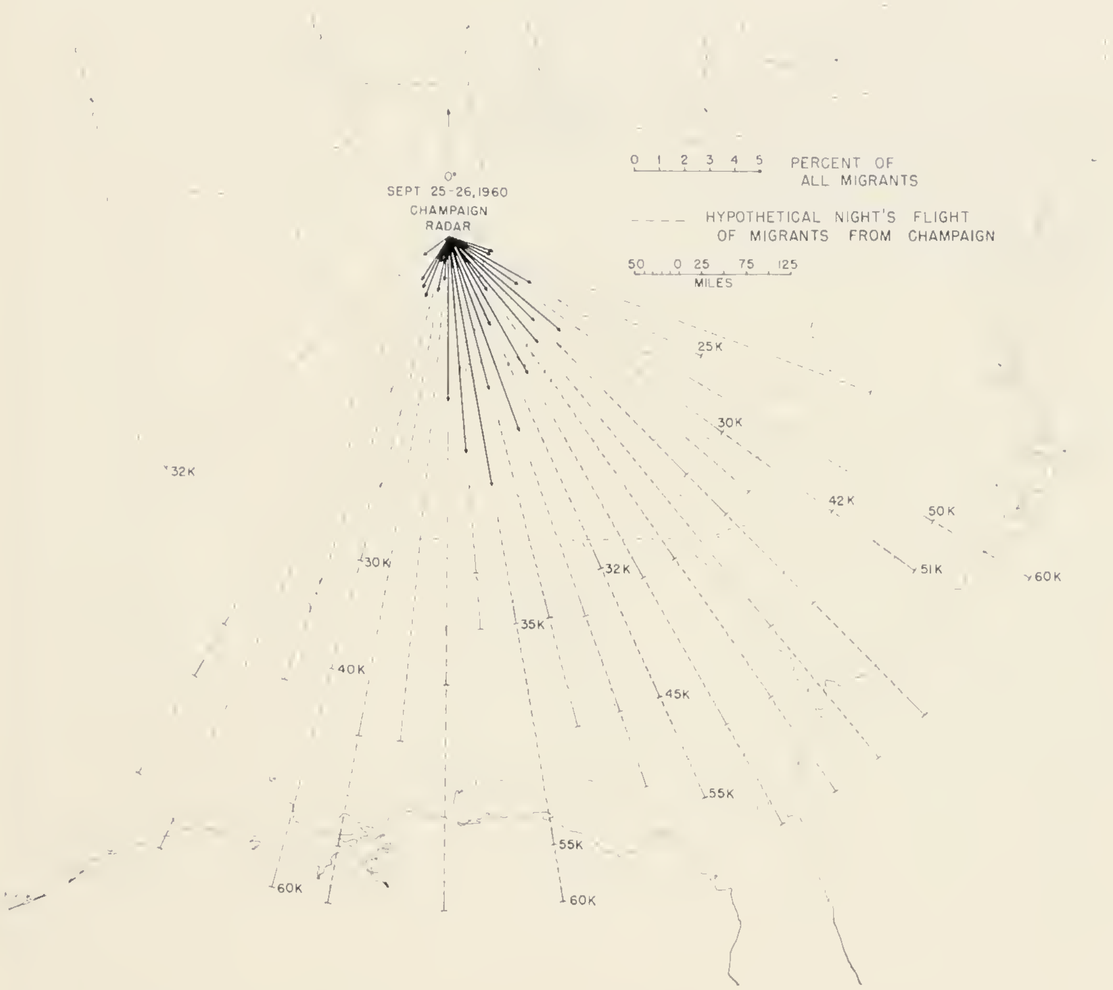

FIG. 7. Flight directions of migrants recorded by radar on a typical clear Fall night. Heavy arrows show the per cent of migrants on a given 5-degree track. Dash lines extend the radar tracks through a full night's migration, the extrapolation based on each track direction, its speed in knots (K), and the temporal pattern observed at Champaign.

Characteristically for fall, on the exemplar night of 25–26 September 1960 about 75 per cent of the bird targets detected by Champaign radar were tracking east of south (180 degrees), with only 18 per cent west of south, and only 6 per cent aimed west of the Gulf of Mexico (Fig. 7). Thus, nearly all of the long-distance migrants which pass Champaign at this season appear to be en route either to a trans-Gulf or a Florida-Antillean (West Indies) migration, or some combination of the two. Most of these night migrants are of species which winter in Central or South America or the West Indies. Their probable fall migration routes can be ascertained from data presented in various regional studies (Table 2). Migrants tracking east of 165 degrees from Champaign would intercept either the Florida peninsula or the southern U. S. Atlantic coast (Fig. 7), and would appear to

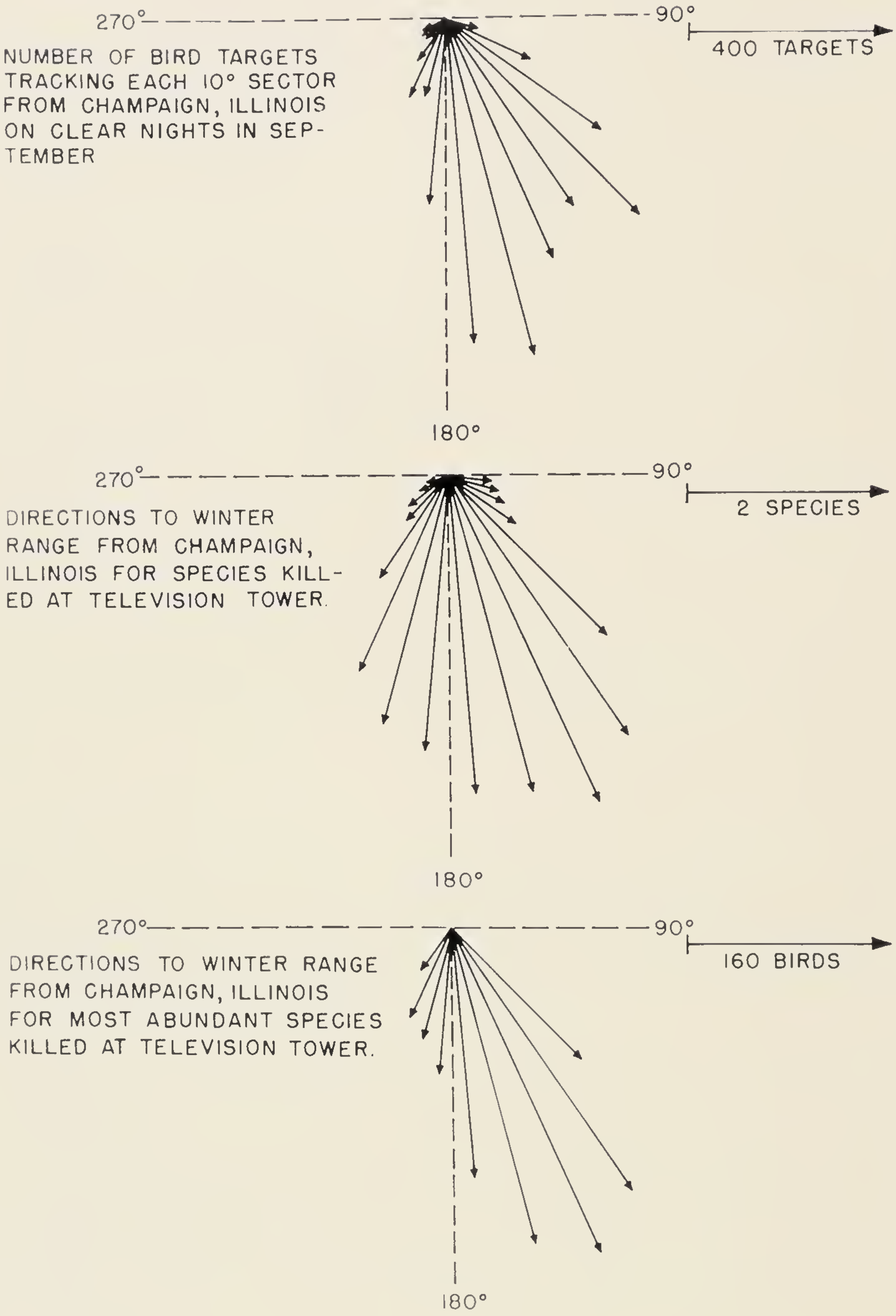

Fig. 8. Comparative data on the number of bird targets tracking each direction from Champaign radar (top), the directions to the winter ranges from Champaign for species of night migrants killed at Champaign (middle), and the directions of the winter ranges for the most abundant species of migrants killed at Champaign (bottom).

TABLE 2

DATA ON PROBABLE FALL MIGRATION ROUTES OF SPECIES OF LONG RANGE MIGRANTS KILLED AT CHAMPAIGN, ILLINOIS.

Species	South Carolina	Georgia	Florida	West Indies	Alabama	Louisiana	East-Central Mexico	Honduras	Kill Ratio 1 Bird Ill. : N Florida	Primary Route(s)
Gray-cheeked Thrush	+	+	0	0	+	+	0	0	0.4	Tr.-Gulf
Veery	+	0	0	0	0	+	0	0	52	"
Philadelphia Vireo	0	0	0	0	0	+	0	+	0.1	"
Chestnut-sided Warbler	+	+	0	0	+	+	0	+	4	"
Scarlet Tanager	0	+	+	0	+	+	0	0	1	"
Traill's Flycatcher	0	0	0	0	0	+	+	+	5	Tr.-Gulf & Mexico
Wood Thrush	+	+	0	0	+	+	+	+	9	
Swainson's Thrush	+	+	0	0	+	+	+	+	0.5	"
Yellow-throated Vireo	+	+	+	0	+	+	+	+	14	"
Red-eyed Vireo	+	+	+	0	+	+	+	+	14	"
Blackburnian Warbler	+	+	0	0	+	+	+	+	4	"
Nashville Warbler	0	0	0	0	0	+	+	0	1	"
Bay-breasted Warbler	0	+	0	+	+	+	0	+	1	W. Ind.-Tr.-G
Cape May Warbler	+	0	+	+	0	0	0	0	0.5	W. Indies
Blackpoll Warbler	+	0	+	+	0	0	0	0	0.1	"
Palm Warbler	+	+	+	+	0	0	0	+	18	"
Bobolink	+	0	+	+	0	0	0	0	2	"
Black-billed Cuckoo	0	0	0	+	0	+	+	+	3	All Routes
Wood Pewee	+	+	0	+	+	+	+	+	5	"
Catbird	+	+	+	+	+	+	+	+	6	"
Black and white Warbler	+	+	+	+	+	+	+	+	4	"
Tennessee Warbler	0	+	0	+	+	+	+	+	1	"
Yellow Warbler	+	+	+	+	+	+	+	+	23	"
Magnolia Warbler	+	+	0	+	+	+	+	+	1	"
Myrtle Warbler	+	+	+	+	+	+	+	+	4	"
Black-throated Green Warbler	0	+	0	+	+	+	+	+	0.7	"
Ovenbird	+	+	+	+	+	+	+	+	0.8	"
Northern Waterthrush	0	+	+	+	+	+	+	+	11	"
Yellowthroat	+	+	+	+	+	+	+	+	8	"
American Redstart	+	+	+	+	+	+	+	+	4	"
Rose-breasted Grosbeak	0	0	0	+	+	+	+	+	0.1	"

Sources of data are given in the text. Symbol + indicates the species is fairly common to abundant as a transient or winter bird; symbol 0 indicates uncommon, rare or absent at the particular locality.

be en route to an Antillean migration. Tracks which fall in this sector comprise about 60 per cent of the tracks detected by Champaign radar in mid- to late September. Coincidentally, about 60 per cent of the migrants killed at Champaign tower in this period are of species which appear commonly in the Antilles either as transients or winter birds (Tables 1 and 2). Other species of migrants which are frequent tower victims in September rarely appear in the Antilles (Table 2); they comprise about 40 per cent of the birds killed at Champaign, and coincidentally, about 40 per cent of the tracks picked up by Champaign radar are aimed at the Gulf of Mexico west of the Antilles.

The directional pattern of migrants at Champaign could also be expected to have a direct relationship to the destinations (winter ranges) of the

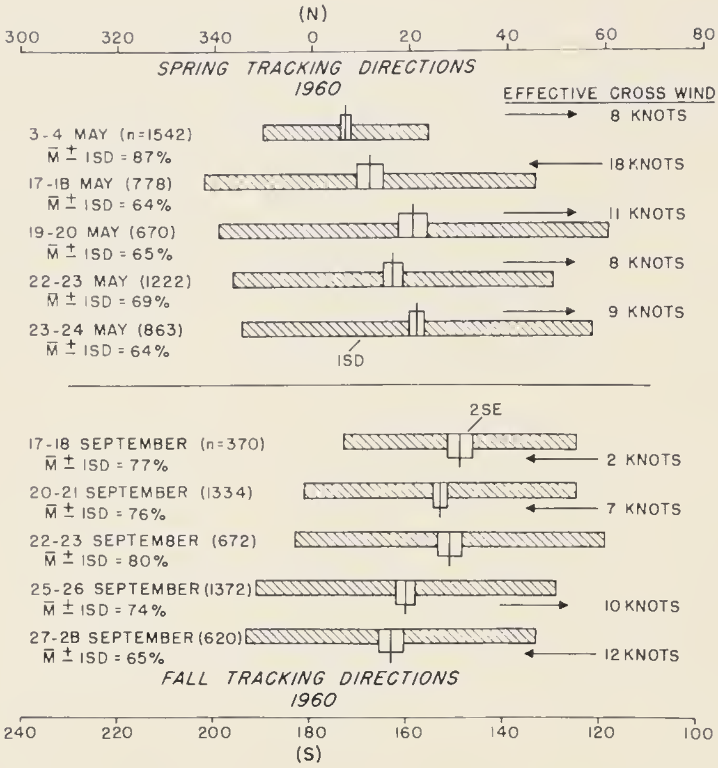

Fig. 9. Distribution of tracking directions (in degrees) of migrants from Champaign, Illinois on clear nights in spring and fall. The vertical line represents the mean track, the center box represents 2 standard errors on each side of the mean, and the lateral shaded boxes represent 1 standard deviation on each side of the mean. The effective crosswind was calculated for the group of migrants representing the mean track and speed, using winds aloft data for central Illinois.

migrants involved. The longitudinal breadth of the winter range varies greatly between different species of migrants. For example, the known winter range of the Red-eyed Vireo lies between eastern Ecuador on the west and southwestern Venezuela on the east (A.O.U. Check-list, 1957). To reach this area in the shortest flight distance (Great Circle Route) from Champaign, vireos should fly a course between 163 and 148 degrees from Champaign, an arc of 15 degrees. The winter range of the Ovenbird is much broader, lying between 219 and 131 degrees from Champaign, an arc of 88 degrees. By plotting the tracking arcs that represent the Great Circle Route to the wintering grounds of common night migrants in this area, we can determine precisely where the winter ranges for these species are in relation to Champaign, and compare the winter range directions with the flight directions recorded by radar (Fig. 8). From this analysis, it is clear that the winter ranges of the species killed at the Champaign television tower lie predominantly east of the Champaign meridian (88 deg. 15 min.), and that there is a high degree of correlation (r = 0.895) between the directions to the winter ranges and the radar directional pattern (Fig. 8). The winter ranges

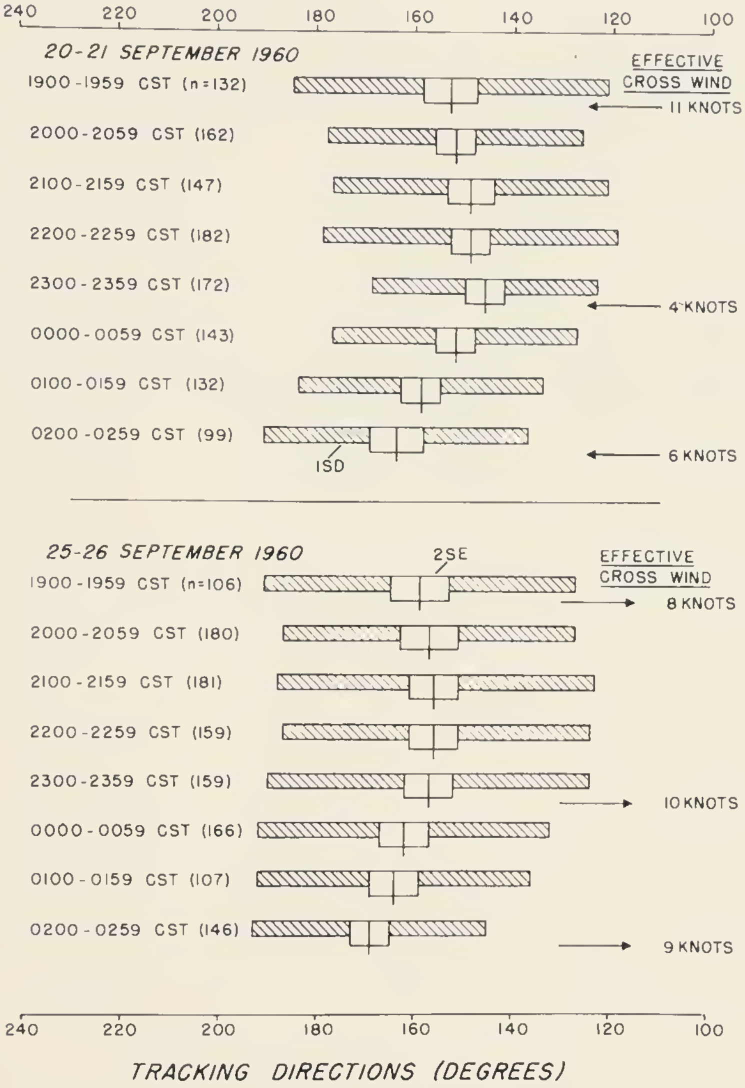

Fig. 10. Variation in tracking directions of migrants from hour to hour on two clear Fall nights, as observed by radar at Champaign, Illinois. The vertical line represents the mean track, the center box represents 2 standard errors on each side of the mean, and the lateral shaded boxes represent 1 standard deviation on each side of the mean.

of the most common species killed (Table 1) are even more decidedly easterly (Fig. 8).

NIGHTLY, HOURLY AND LOCAL VARIATION IN THE DIRECTION OF MIGRATION

The concept of a typical directional pattern of migration for an area, though useful as a generalization, is still an oversimplification. Even on clear nights the recorded flight directions actually showed significant variation from night to night (Fig. 9, Table 3), and even from hour to hour (Fig. 10, Table 3). There was no consistent relationship between variation in the directional pattern and variation in wind direction or speed (Figs. 9 and 10).

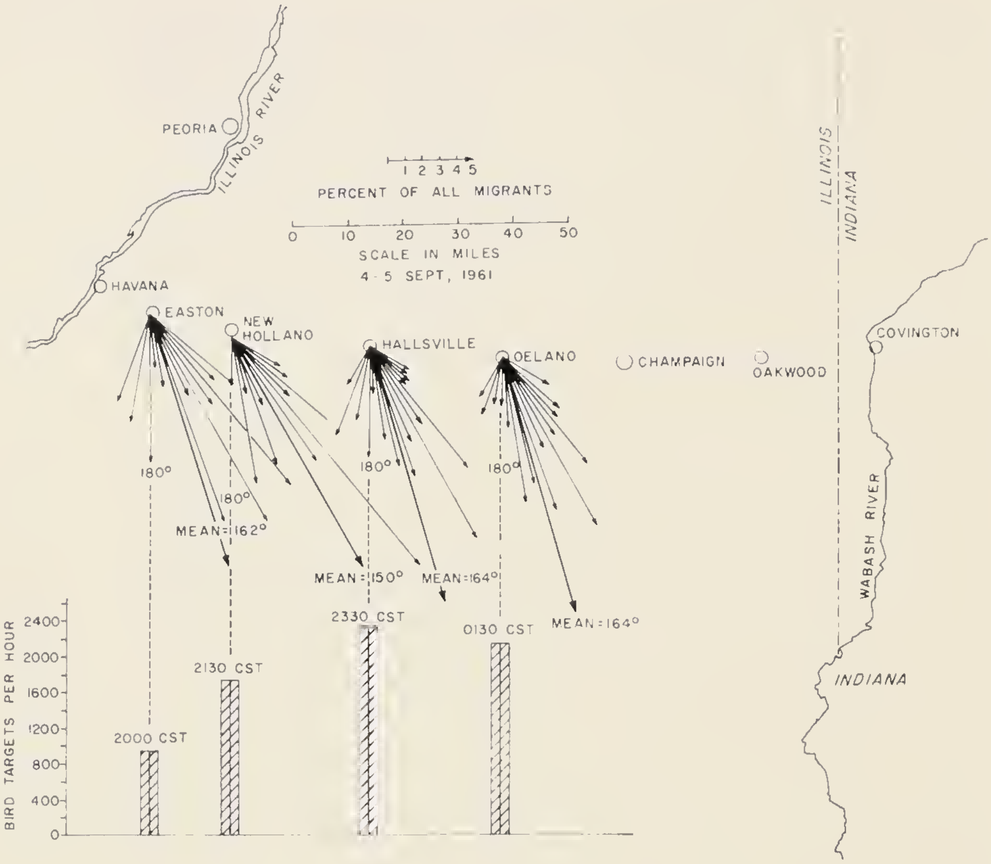

Fig. 11. Flight directions and numbers of night migrants at four localities in central Illinois on the night of 4–5 September 1961, as observed with a mobile radar unit.

Both in spring and fall there was also conspicuous variation in the spread of tracks. On most clear nights in spring about 65 per cent of the tracks fall within the range of the mean plus and minus 1 SD (Fig. 9), the track distribution in this respect resembling a normal distribution. A notable exception was the night of 3–4 May, when tracks were closely bunched around the mean (Fig. 9). Only a few of the calls recorded that night were identifiable (Dickcissels); the field censuses indicated a large flight of Palm Warblers and White-throated Sparrows, but little else. The mean flight direction on this night was less decidedly eastward than on other clear May nights, a fact probably relating to the position of the breeding range of the Palm Warbler (nominate race) which lies mainly west of the Champaign meridian. In general, tracks of migrants were more tightly bunched around the mean in fall than in spring (Fig. 9). This greater spread of tracks in spring is not surprising for the breeding grounds of most of the long distance migrants are only about 10 degrees of latitude north of Champaign, and have a broader longitudinal spread than the wintering grounds which lie about 25 degrees south from Champaign.

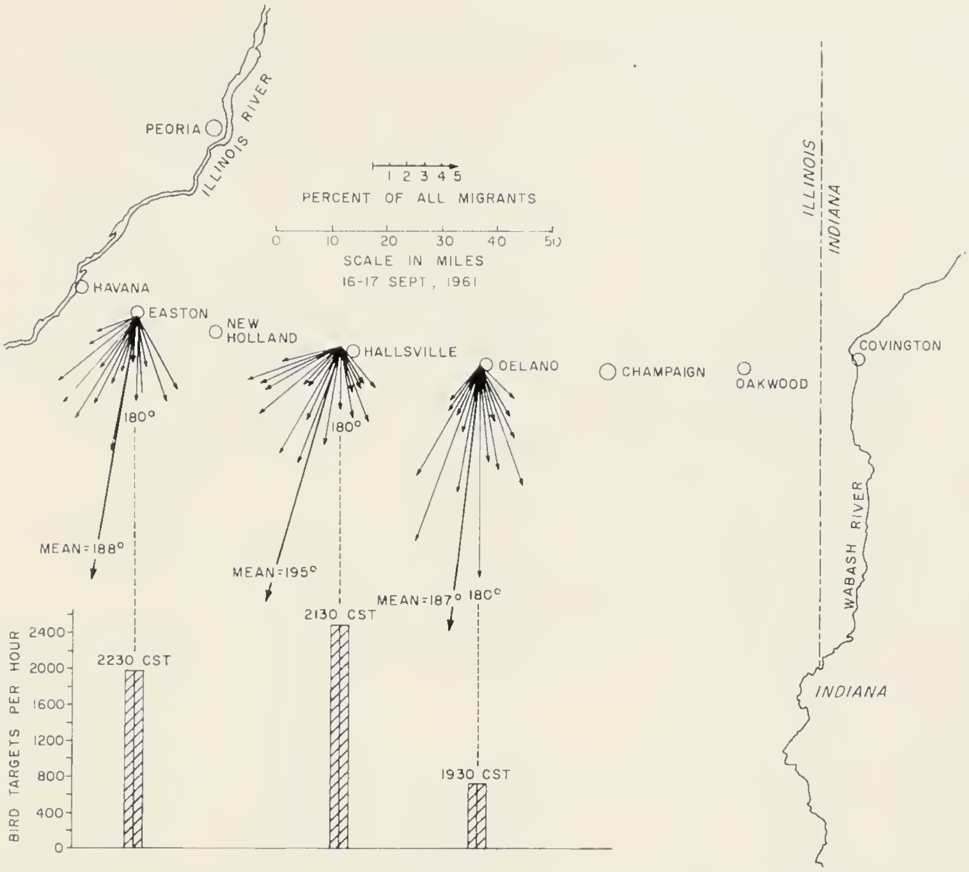

Fig. 12. Flight directions and numbers of night migrants at three localities in central Illinois on the night of 16–17 September 1961, as observed with a mobile radar unit.

Hour-to-hour variation in the September tracking pattern is generally insignificant in the hours before midnight, but significant changes occur after midnight, with the mean track often, but not invariably, turning westward (Fig. 10, Table 3). The cause and significance of this post-midnight change in the mean flight direction are unknown, but are not apparently related to wind variation, for on the nights examined, the winds aloft varied more before midnight than after (Fig. 10).

Having observed the flight directions of long-distance migrants at Champaign, I was interested in learning whether the flight patterns varied from one locality to another in central Illinois. The flight directions observed with the mobile radar unit at a few central Illinois localities on clear nights in September are shown in Figs. 11–13. The mobile radar is satisfactory for making rough comparisons of the flight *directions* of migrants at different localities, but the time difference in the data from any two or more stations complicates the comparison of flight *densities* between stations, because flight densities almost invariably change from hour to hour. Note in Figure 11 the flight densities at different stations seem to show the typical temporal pattern seen at a single station (see Fig. 2).

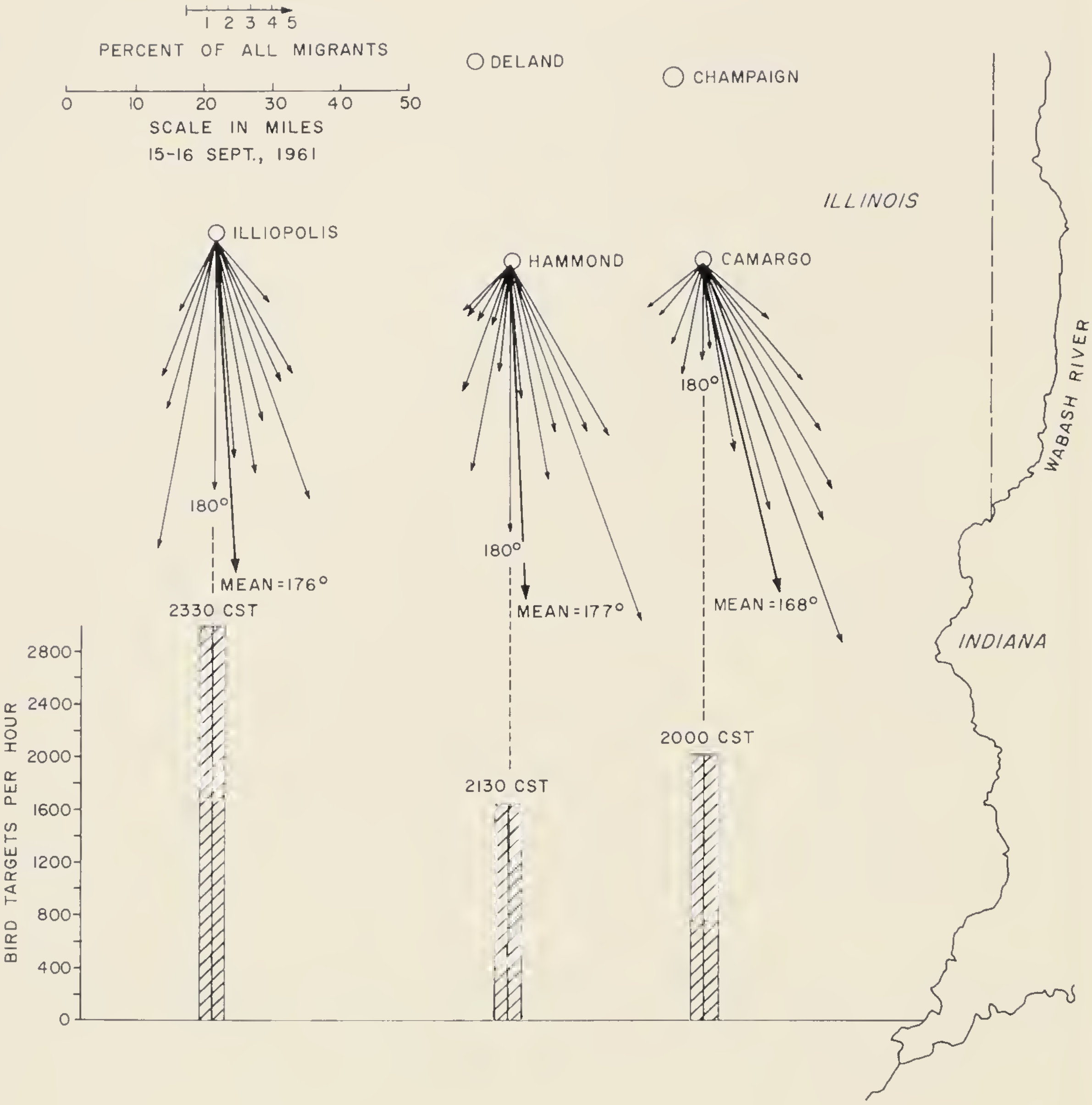

Fig. 13. Flight directions and numbers of night migrants at three localities in central Illinois on the night of 15–16 September 1961, as observed with a mobile radar unit.

On the night of 4–5 September 1961, the dominant flight directions showed the typical east-of-south pattern at all stations spanning a transect of about 80 miles (Fig. 11). The mean track at different stations varied from 150 to 164 degrees, more than the usual hourly variation (pre-midnight) at Champaign, but less than the variation observed between nights. Over the same region on the night of 16–17 September 1961 the dominant flight directions were *west* of south (the means: 187 to 195 degrees), but again the basic directional pattern was the same at all stations (Fig. 12). This west of south movement, exceptional for central Illinois, actually began the night before (15–16 September), and the mobile radar transect for that night shows its development (Fig. 13). As the mobile unit moved west, the tracks of migrants appeared to shift increasingly westward. This shift was not related to geography but to time, for the radar had detected a great influx of southwestward-oriented migrants whose numbers increased greatly after 2130 CST. This change in the flight direction pattern was *not* related to changing winds, for the wind conditions in central Illinois were almost identical (about 300 degrees at 10–15 knots for altitudes between 150 and 2,000 meters) on the two nights during which the change occurred. The southwestward direction of this flight, then, almost certainly related to the species composition of the migrant swarm. Field observations made on the morning of 17 September across central Illinois shed light on the species which were probably involved in the flight. Conspicuous among the arriving migrants were Black-crowned Night Herons, Common Nighthawks, American Coots, Yellow-shafted Flickers, Yellow-bellied Sapsuckers, Wood Pewees, *Empidonax* flycatchers, Catbirds, and Warbling Vireos. All but the flicker are common transients in Mexico, and all are likely candidates for a southwest migration from Champaign.

In general, the flight directions of September migrants as observed by radar over the Illinois River at Havana are similar to those observed at Champaign, though the mean nightly track at the two stations may differ significantly (Table 3). Weather may have a pronounced effect on the directional pattern of migration in central Illinois, as on the night of 24–25 September 1962. On this night the tracking pattern of migrants at Havana was the typical September pattern for central Illinois localities (Figs. 14 and 15). The mean track was 155 degrees (SD = 32 degrees); the range of mean ± one SD included about 75 per cent of all tracks observed. Early in the night (until 2130 CST) there was fog at Havana and visibility was poor, but there was no sustained overcast in the area. Most of the migrants that passed Havana were coming from the northwest where clearer weather conditions prevailed. No large scale bird kills occurred at high TV towers in Peoria and Moline (north and west of Havana radar). South and east of Havana, weather deteriorated and sizeable kills of migrants occurred at Springfield and Champaign (Figs. 14 and 16), where low overcast (under 3,000 feet) and fog persisted with low visibilities (under 4 miles) nearly all night. This weather accompanied a slow-moving cold front that reached Springfield and Champaign at about the same time (2130 CST). By midnight the front had moved only a few miles beyond Champaign. This is the typical combination of weather and migration patterns (large numbers of migrants overtaking a front) which precipitate kills in this region (Graber and Cochran, 1960:268). The flight direction pattern of migrants at Champaign was very different from the "normal" and from the pattern at Havana

TABLE 3

PROBABILITIES OF SIGNIFICANT DIFFERENCES IN THE TRACKING PATTERNS OF NIGHT MIGRANTS IN CENTRAL ILLINOIS FROM STATION TO STATION, FROM NIGHT TO NIGHT, AND FROM HOUR TO HOUR.

Localities–Dates–Hours	Probability of Significant Difference: Between Stations	Between Dates	Between Hours
Champaign			
20–21 Sept. 1960 (1900–2300 CST; 4 hours)			0.500
(2300–0300 CST; 4 hours)			0.999
22–23 Sept. 1960 (2000–2300 CST: 3 hours)			0.999
(2300–0300 CST; 4 hours)			0.500
25–26 Sept. 1960 (1900–0000 CST; 5 hours)			0.500
(0000–0300 CST; 3 hours)			0.900
Champaign			
19–20, 22–23, 23–24 May 1960 (3 nights)		0.990	
17–18, 20–21, 22–23 Sept. 1960 (3 nights)		0.950	
Easton Hallsville–Deland			
4–5 Sept. 1961	0.500		
16–17 Sept. 1961	0.800		
4–5, 16–17 Sept. 1961		0.995	
Champaign–Havana			
24–25 Sept. 1962	0.995		
25–26 Sept. 1962	0.800		
26–27 Sept. 1962	0.995		

(Figs. 14 and 15). The mean track at Champaign was 175 degrees (SD = 48 degrees), with nearly as many birds tracking west of south as east of south. The mean ± one SD included 63 per cent of the tracks observed. The high standard deviation, indicating a wide spread in the tracks, reflects a mass disorientation in the migrant swarm.

In numbers, the kills at Springfield (218 specimens) and Champaign (296 specimens) were not unusual for late September. The species composition of the kill was also typical for Champaign (Table 1). The kills at Champaign and Springfield were remarkably similar, even to the numbers of each species killed (Fig. 16). The most noteworthy differences in the kills at the two stations were in the larger numbers of *Hylocichla* thrushes, Magnolia Warblers, and Rose-breasted Grosbeaks killed at Champaign (Fig. 16). Data from another simultaneous kill (16–17 September 1958) at the two towers indicates that the species differences were not due merely to chance. The 1958 kill was much greater at Springfield (827 specimens) than at Champaign (117 specimens), possibly because visibility in the Springfield

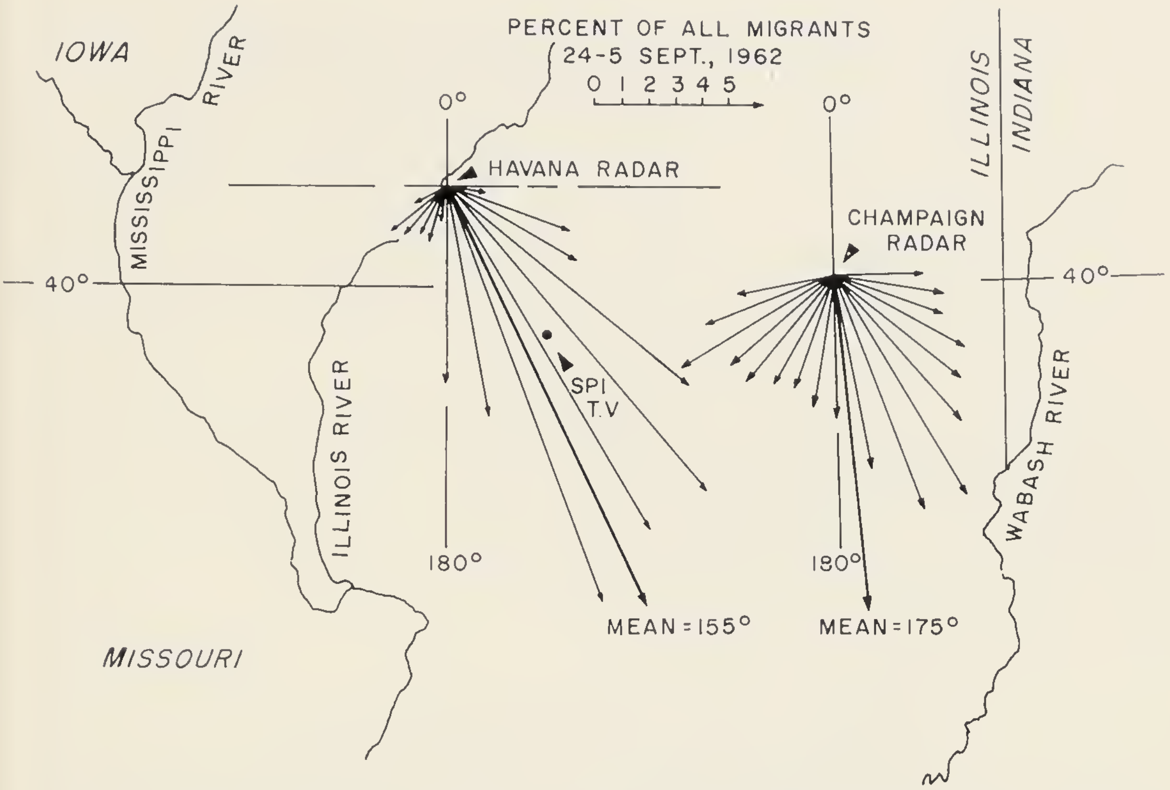

FIG. 14. Flight directions of migrants at Havana and Champaign, Illinois on night of 24-25 September 1962. Note the wide spread of tracks indicating deterioration of orientation at Champaign. Kills of migrants occurred at towers near Springfield (SPI) and Champaign.

area remained poor most of the night after midnight, while at Champaign visibility was poor only for about 1 hour (2300–0000 CST) during the night. Despite the disparity in total numbers of birds killed, the 1958 and 1962 kills at Champaign and Springfield showed the same general ties between species and locality (Fig. 17). On both dates, more thrushes and grosbeaks were killed at Champaign, while the Springfield tower claimed more Ovenbirds, Tennessee Warblers, Chestnut-sided Warblers, Bay-breasted Warblers, Northern Waterthrushes and Yellowthroats. Of the thirteen most numerous species killed (87 per cent of the total kill), only two (Magnolia Warbler and Bobolink) were not consistently more numerous at one tower than the other (Fig. 17). The probability of such a coincidence by chance is less than 0.02 ($\chi^2 = 6.23$, 1 df). These data indicate that each locality has its own characteristic fauna of passing migrants. In this observation there is also an implication that each population of migrants follows precisely the same migration route year after year.

DISCUSSION

An observer's impressions of night migration may vary considerably, depending upon the technique of study he uses. Vleugel (1960) discussed

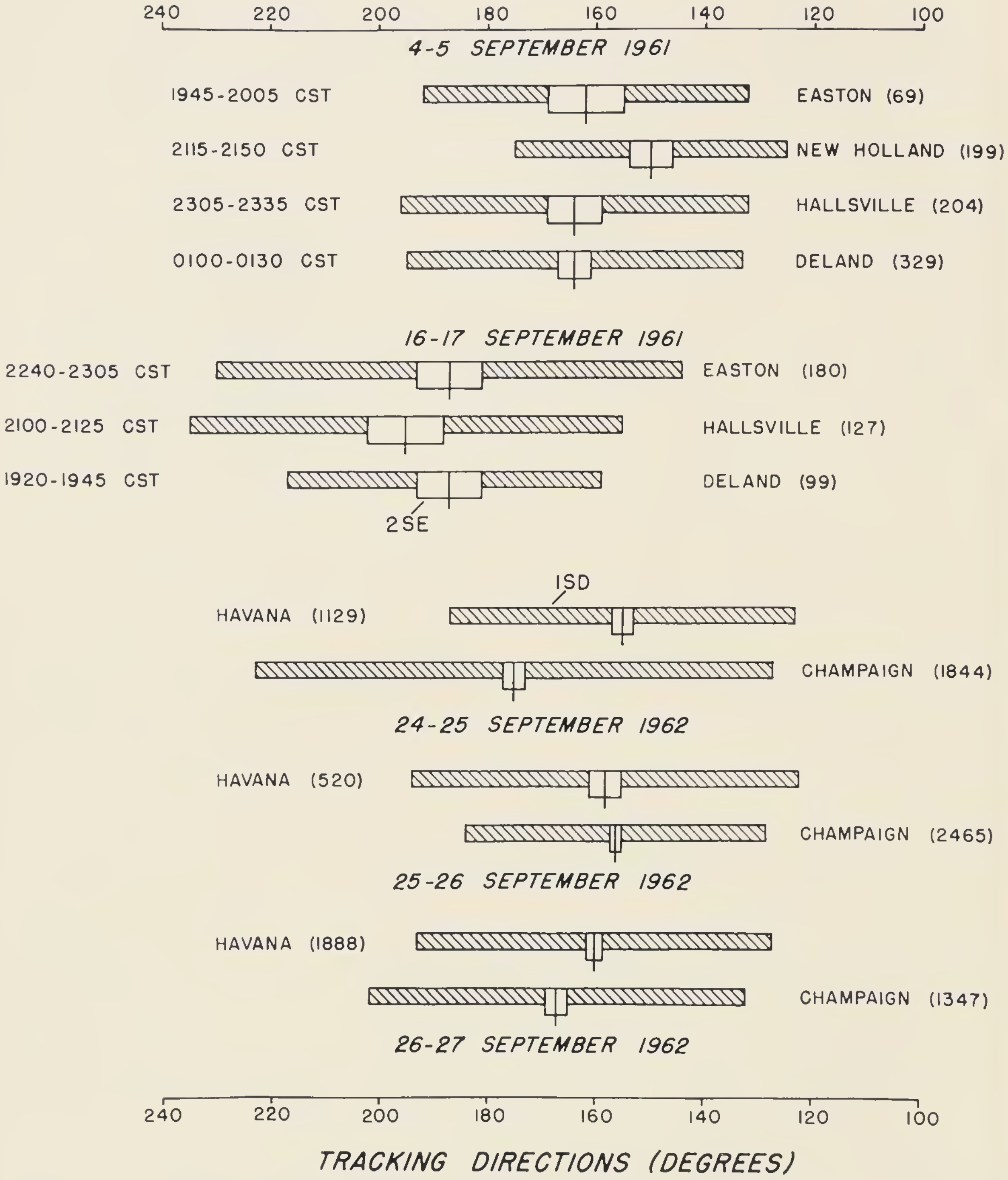

FIG. 15. Comparative data on the variation in flight directions of night migrants at various localities in central Illinois. Numerals in parentheses are the numbers of tracks recorded in each sample.

the contradictory findings from lunar and aural studies on the nightly temporal pattern of migration. Dwelling particularly on Ball's (1952) study of thrush migration on Gaspe. Vleugel (p. 15) hypothesized that the aural temporal pattern reported by Ball could be explained on the basis of geography (the sizable water barrier around Gaspe). In the flat farmlands of central Illinois, the pattern of migrant calling is the same as that which Ball

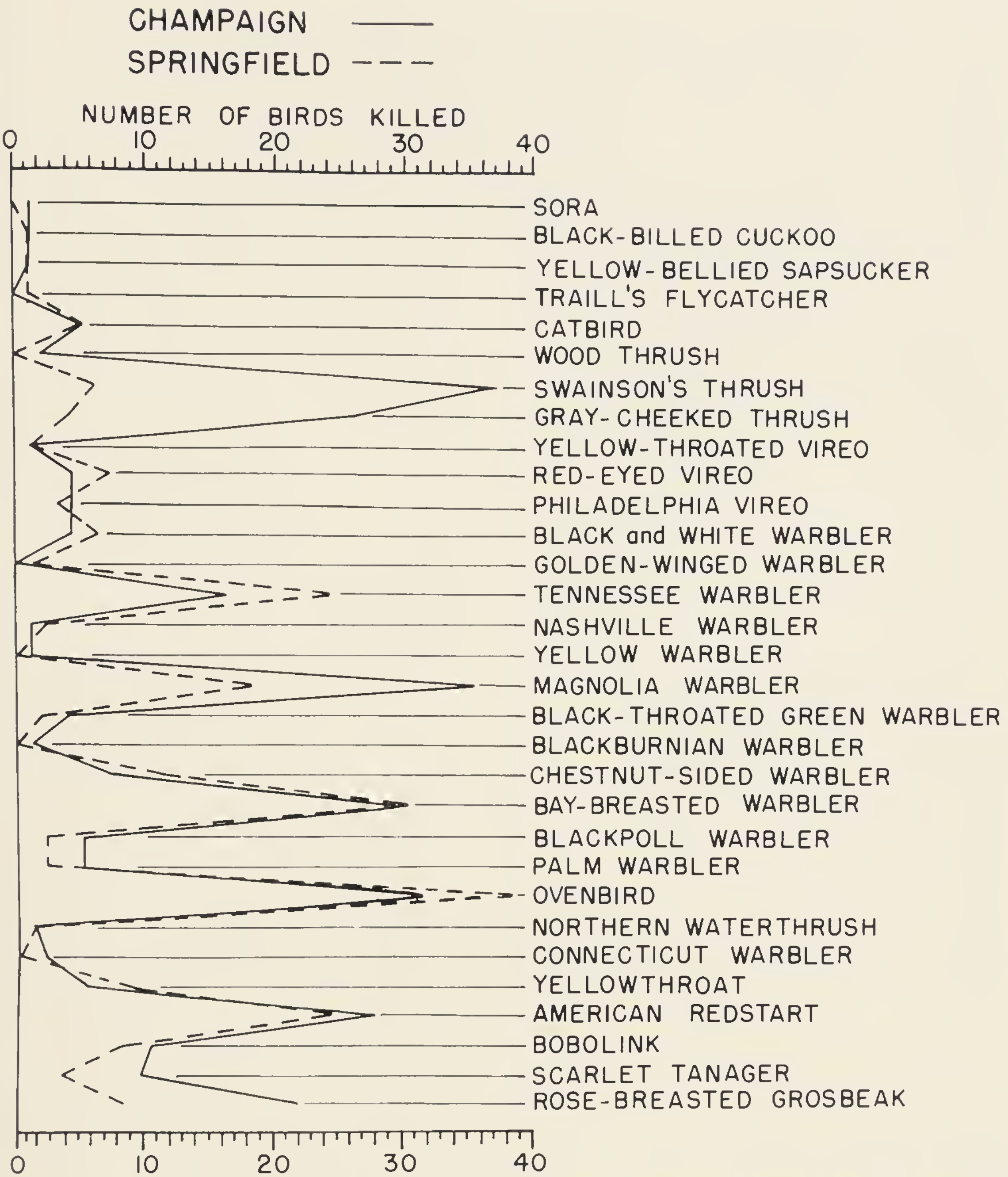

FIG. 16. Comparative numbers of migrants killed at television towers near Springfield and Champaign, Illinois on the night of 24–25 September 1962.

recorded in Quebec. Furthermore, the consistent nightly temporal pattern of migration as observed on radar in central Illinois is similar to the pattern recorded through lunar observations in many areas (Lowery, 1951:116; Hassler et al., 1963:57). Obviously, then, these typical patterns do not reflect topography or geography, but something that the birds themselves are doing. One technique seems to belie the other. When radar shows the number of migrants to be declining in the early morning, the audio system suggests that more migrants are calling. Radar shows that migrants are *not* flying at

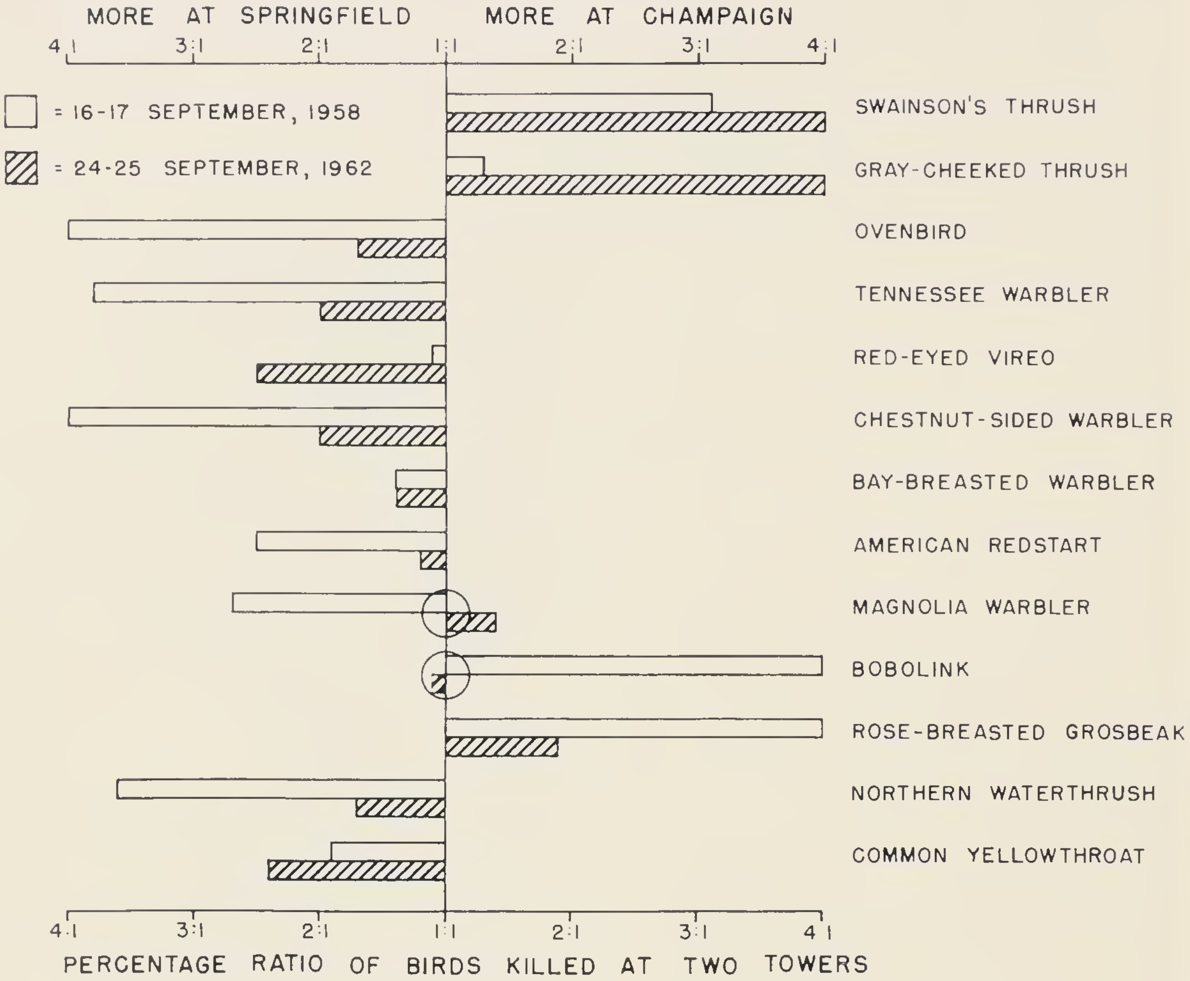

Fig. 17. Comparative numbers of birds of the most common species killed on two nights (different years) at two central Illinois television towers. Note that in most cases if the species was more numerous at Champaign in the first kill, it was also more numerous there the second kill (exceptions encircled).

altitudes above the effective range of the audio system. The behavior pattern that seems best to explain this apparent paradox is that migrants must continue their flight until daylight, but reduce their flight altitude to 1,500 feet or less after midnight, and increase their rate of calling as dawn approaches. Because of the inherent "blindness" of the radar at short range, large numbers of migrants pass at low altitude without being detected. This is clearly shown on nights when migrants are killed at the Champaign tower (981 feet high), though Champaign radar shows no migrants below 1,500 feet. Mascher et al. (1962:215) also concluded that radar missed the low altitude migration in Sweden.

Changes in the rate of calling by migrants tend to coincide with changes in the tracking ratio of the migrant swarm (Fig. 3). The tracking ratio, in turn, reflects either a directional or an altitudinal shift by the migrants.

Thus, both the increased calling rate of migrants after midnight, and the declining numbers of bird targets seen on radar after midnight (Fig. 2) are probably measures of the same phenomenon, i.e., the descending of migrants to lower altitudes.

Though the available data from all points of view seem clearly to indicate that the migrant swarm reduces its altitude after midnight, the shift itself seems inexplicable. It could be interpreted as an intention to land, but there are no data to show that migrants land at night. In populations of long-distance migrants which regularly cross large stretches of open water such as the Gulf of Mexico or the Great Lakes, any tendency to land in the dark would seem to be a liability. The post-midnight altitudinal shift coincides with a directional shift (Fig. 10). The significance of both remains to be discovered.

Why would birds increase their rate of calling after reducing altitude? Calling by migrants increases under an overcast (Fig. 3) and when the birds are changing altitude and/or direction, indicating that the phenomenon is related in some way to orientation or perhaps disorientation of the birds. Hamilton (1962) hypothesized that the night calls of migrants serve to maintain flocks and to convey flight direction information from one member of the flock to another. This hypothesis fits the observation that increased calling coincides with the post-midnight directional shift. It could also be argued that the calls function in spacing or spreading the migrants as an anti-collision system. High calling rate is often sustained following the midnight altitudinal shift even on clear nights, which supports the view that calling is related to spacing, for the reduction in altitude must compress the migrant swarm and increase the flight density. From flight call counts made in the vicinity of a television tower, Cochran and Graber (1958) concluded that migrants were attracted to the structure and its lights. This attraction may exist, but it is now clear that calling rate is an unreliable index to flight density, and that the high calling rate near the tower, like that occurring with overcast skies, reflects a situation of potential peril for the migrants and not necessarily a high flight density. The night calling behavior so prominent among *Hylocichla* thrushes is also well developed in certain Old World species of *Turdus* (Siivonen, 1936), and Vleugel (1951:19) incidentally recorded an instance of increased calling among disoriented thrushes "attracted" to the lights of a city in the Netherlands. The recording of call notes is valuable to indicate the presence of various species of unseen migrants, but as a quantitative record such data may be greatly misleading without some behavioral interpretation.

Estimates of flight densities of migrants have been made on the basis of various techniques of study, including lunar observations (Lowery, 1951), tower kills (Tordoff and Mengel, 1956), and audio and radar studies (Graber and Cochran, 1960; Graber and Hassler, 1962). Data from three of these sources (tower kill, audio and radar) are available for the night of 19–20 September 1960 at Champaign. Flight density estimates from these sources are widely divergent (radar: 70 bird echoes per hour crossing a mile of terrain; audio: 1,300 calls per hour; tower kill: 93,000 birds per hour). Disparity in the estimates is not surprising. Radar misses that part of the migration which occurs at altitudes under 1,500 feet, while the calling rate is exceptionally high on kill nights. The number of calls recorded is almost invariably greater than the number of bird targets detected by radar (Fig. 4). Though the radar is capable of detecting individual birds (Graber and Hassler, 1962), each echo could represent more than one migrant, depending upon their spatial arrangement. The extremely high estimate of flight density from tower kill data is probably a gross distortion because it is based on the assumption that the tower merely cuts a slice out of a uniform migrant swarm as the birds pass. This assumption does not take into account the actual manner in which the kills occur. Migrants approaching the tower enter a lighted area from which they are reluctant to leave. Lovie Whitaker (pers. comm.) pointed out to me that the situation could be compared to that of free-flying birds in a lighted room at night. Even if the doors and windows are open, the birds will not leave the lighted area to fly out into the dark. This is precisely the behavior I have observed at the Champaign tower. On the night of a kill, migrants often fly right through the tower framework and on out toward the edge of the lighted "room" around the tower, only to turn back again toward the light. Circling in this fashion some of them will inevitably strike the dark guys which support the tower.

The kills probably do provide an accurate picture of the night migrant fauna for the place and time they occur. Species commonly killed are also observed commonly in the field (Fig. 5), and for species of comparable conspicuousness, there is significant correlation between the numbers of birds killed and the numbers seen in the field. The tower kill data thus provide at least a tentative base on which to interpret the directional patterns of migration observed by radar.

Despite the gross differences in measurements of the *volume* of migration from different techniques, the audio system, radar, the tower kills all detect the same night-to-night periodicity or *timing* of migration in this area. Consequently we have drawn essentially the same conclusions about the influence of weather on migration from different methods of observation (Graber and Cochran, 1960:254; Hassler, et al., 1963). Earlier Bennett (1952) perceived the same weather-migration relationships from daily field censuses in Chicago. Apparently many populations of night migrants respond to weather factors in much the same way. Mass flights in September characteristically follow closely a wind shift to northerly, usually to northwesterly, with the passage of a cold front. In fact, the close association of the birds with the front leads to the kill (Graber and Cochran, 1960). The mobile radar shows that the phenomenon is occurring over a broad front and that the directional pattern of the migration is essentially the same along the front across central Illinois. Even the major river valleys, the Mississippi and Illinois, have no obvious effect on the pattern. Night-to-night variation in flight directions of migrants definitely exceeds variation related to locality (Table 3). When the flight directions shift conspicuously, they shift on a broad front (Figs. 11–13). Such marked shifts in flight direction are probably related primarily to changes in the species composition of the migrant swarm rather than to wind shifts or other physical changes. While there may be subtle or even significant variations in the flight directions of migrants from night to night, and even from hour to hour particularly after midnight, and from place to place in central Illinois (Table 3), the consistent east of north pattern in spring and east of south pattern in fall is a dominant characteristic of the migration in this region. Considering the many potential sources of variation in the flight directions, the similarities of the pattern at different times and places are more impressive than the differences (Figs. 6–9; Table 3).

Why is the fall migration direction southeast? Apropos of the constancy of the fall directional pattern is the consistent nature of the species composition of kills at television towers from year to year and place to place in the north-central states (Table 1; Kemper et. al., 1964). The winter ranges of most of these species lie well east of the Champaign meridian (Fig. 8), and the predominantly westerly winds of this latitude tend to carry any air-borne object eastward. In fact the general direction of fall migration, following as it does in the wake of cold fronts, is downwind. Also, based on the geography of the breeding ranges of tower-kill species, more (about 60 per cent) of the population of September migrants nests west of the Champaign meridian than east of it, and the breeding ranges of virtually all of the species extend west of Champaign. Many of the species involved in the September flights are probably of (south) eastern origin (see Mengel, 1961, on the Parulidae).

Lincoln (1950:56) suggested that Bobolinks, in the course of their migration, adhere to ancestral flyways, western populations moving eastward in fall rather than directly toward the wintering grounds. The same pattern of fall migration may be seen in the western race of the Palm Warbler. The migration route of this population is somewhat triangular or perhaps elliptical. In fall much of the population moves eastward (not directly southeast toward the winter range), approaching the Appalachians before turning south toward the South Carolina coast and the Florida Peninsula. That this route greatly concentrates the population during migration is shown by the magnitude of the fall tower kills of western Palm Warblers in northern Florida (Table 2; Stoddard, 1962:75). Like the Bobolink, northeastern populations of the Palm Warbler (the eastern race) move south and southeast down the Atlantic coast in their Fall migration. This flight direction is still downwind, for in fall the postfrontal winds along the Alleghenies are predominantly northeasterly. Do the western populations of these species intentionally move toward the ancestral range, or is the fall flight direction merely a consequence of the temperate zone westerly circulation? To pursue the question further it is worthwhile to examine the migration route of a species such as the Nashville Warbler, which is probably of western origin (see Mengel, 1964:25). In fall, the race of the Nashville Warbler must move southwest, for it is rare in the southeastern U. S., becoming increasingly common along the direct line route between the breeding grounds (eastern Canada and northeastern U. S.) and northern Mexico. Though relatively uncommon at Champaign in fall, Nashville Warblers (eastern race) are occasionally victims of the Champaign tower. They are much more common victims to the north in Wisconsin, and even more common in Minnesota (Kemper et al., 1964:166) and in northeastern Kansas (Tordoff and Mengel, 1956:9). The association of Nashville Warblers (eastern race) with east-oriented species in tower-kill samples shows that Nashvilles migrate behind frontal systems, as the *east*-oriented migrants do. The magnitude of Nashville Warbler mortality at the different towers also indicates that this population does not travel to its wintering grounds (central and southern Mexico) by the most direct route, but stays north of the direct-line route, as western Palm Warblers do on their east-oriented flights. To accomplish their west and southwest migration, Nashville Warblers must compensate for displacement from the northwesterly winds to a much greater extent than do east-oriented populations, which fly more nearly downwind. Thus, a Nashville Warbler going from the center of the breeding range to the center of the winter range would fly a heading aimed well north of the winter range toward Arizona, the center of distribution for this particular complex of *Vermivora* warblers (Mengel, 1964:25). The migration routes of the Nashville Warbler are roughly a mirror image of the Palm Warbler's routes. Just as the *eastern* race of the Palm Warbler has only to fly southward or southwestward to reach its winter range, the *western* race of the Nashville Warbler also has a simpler route (south or southeast) than its eastern counterpart. In both species, the migration routes of the ancestral populations are little affected by the primary westerly circulation.

For east-oriented fall migrants it could be argued that east-orientation has survival value through conservation of energy from "riding the wind" and that the flight direction is unrelated to the ancestral range, but the migration of the Nashville Warbler shows that some populations at least migrate toward the ancestral range in spite of the winds, and at an energy *cost*: the survival value in such a migration is not apparent. The example also suggests that postfrontal "pressure pattern" migration may have some significance to migrants other than that related to energy conservation. The feature of the air mass which would appear to have greatest value to a bird attempting to duplicate the same flight year after year would be constancy (dependability). The more variable the movements of the air, the less favorable would be the bird's chances of duplicating its route. This factor of constancy characterizes the air mass behind the fall cold fronts, and whether or not the airflow is favorable (as it is for east-oriented migrants), it provides a fairly constant and dependable set of conditions in which to migrate. Furthermore, the primary seasonal patterns of the general circulation of the earth's atmosphere have probably not changed significantly in North America since the beginning of the Pleistocene though the temperate zone westerlies may have expanded and intensified during periods of glacial maxima (Willet, 1953:51–54). By responding to the frontal cues migrants can hold a given heading and arrive on the wintering grounds even though the winds are not helpful in reducing the flight time. We might conclude from the example of the Nashville Warbler's migration, that migration routes evolve from the accidental resultant of (1) the bird's heading toward its ancestral range, and (2) the force exerted upon it from the primary patterns of atmospheric circulation over the route. The overwhelming majority of migrants which pass Champaign in fall are east-oriented and *do* benefit from favorable winds. They are probably also mainly of (south) eastern origin.

Clearly, the radar record indicates that the populations of migrants which pass Champaign in spring are different from those which pass in fall. Fall migrants are coming largely from the northwest; the spring birds are moving to the northeast. On the surface, these directional patterns seem to conflict with the accumulating evidence that a given passerine migrant abides in or near the same nesting territory (Nice, 1937:73; Graber, 1961:322) and the same winter "territory" (Robertson, 1961:123; Schwartz, 1963; Nickell, 1962:54; Mewaldt, 1964) year after year, but there is no information on how consistently a migrant retraces its path between its summer and winter home. Mewaldt's (1964) study of displaced White-crowned Sparrows shows that some migrants, at least, need not follow a particular migration route to reach their prescribed destination. In view of this precision in homing, the disparity in the spring and fall flight directions at Champaign seem to indicate that most of the night migrants detected by radar have an elliptical migration route.

For east-oriented trans-Gulf or Antillean migrants, an elliptical migration route fits the general pattern of atmospheric circulation and the positive response of migrants to favorable wind cues both in spring and fall (Graber and Cochran, 1960: Hassler et. al., 1963). Whereas the postfrontal airflow in fall at latitude 40 degrees N is predominantly northwesterly, and in spring, southerly (with a warm front or on the back edge of a high pressure area), winds over the Gulf of Mexico are consistently easterly or southeasterly, except immediately in the wake of cold front passage, when spring migration is halted. Thus, a migrant flying downwind (southeastward) from Champaign in fall, would be moved back westward over the Gulf on its northward passage. Most of the species of long-distance migrants which pass Champaign are trans-Gulf migrants in spring (see Stevenson, 1957). At times the easterly circulation over the Gulf brings large numbers of migrants to the south Texas coast. These flights become especially evident when they meet adverse flying conditions near the coast, as in the dramatic example of a kill reported by James (1956). Most of the 39 species represented in this large kill (2,421 specimens examined) at Padre Island on 6–7 May 1951 are common mid- and late-May migrants at Champaign. Included were 165 Bay-breasted Warblers, 64 Chestnut-sided Warblers, 16 Acadian Flycatchers, 6 Cerulean Warblers, and 4 Golden-winged Warblers. At Padre Island these species were far west of their winter ranges, and near the extreme western meridian of their breeding ranges. Furthermore, the breeding ranges of virtually *all* of the species killed lie mainly (north) east of Texas, so to reach their nesting areas, many of them would almost certainly have had to fly east of north. At the latitude of Texas they were leaving the influence of the easterly winds. At higher latitudes deviations from the south flow become increasingly westerly again, thus completing the elliptical circuit. The bulk of the transients which pass Champaign in May must pass well east of Champaign on their fall flight, while the September migrants must, on their northward flight, pass west of the station.

Field observations at Champaign also tend to support the concept of an elliptical migration, for some populations of transients show marked disparity in the numbers passing between spring and fall: examples are: the Veery (2 in spring to 1 in fall), Solitary Vireo (2 to 1), Blue-winged Warbler (10 + to 1), Nashville Warbler (4 to 1), Parula Warbler (12 to 1), Magnolia Warbler (1 to 12), Cape May Warbler (7 to 1), and Palm Warbler (30 + to 1). The most classic example is the Golden Plover, of which hundreds are seen in spring for every fall record. Much the same trends have been reported for the same species in southeastern Michigan (Kelley et al., 1963).

yet if the same populations passed these areas in both spring and fall, the spring populations would probably be lower, reflecting winter's attrition. Marked differences in the spring-fall ratios for a given species probably reflect primarily a change in the migration route between spring and fall.

The elliptical migration route seems to apply to west-oriented as well as to east-oriented populations. The spring migration of the Palm Warbler fits the general pattern for east-oriented populations, since much of its population comes under the influence of the low latitude easterlies on the northward flight. This westward displacement would definitely bring many more Palm Warblers to Champaign in spring (vs. fall), as our field observations show. But why do more Nashville Warblers pass Champaign in spring than in fall? Such a difference would result only if the Nashville's spring route passed well east of the fall route, reversing the pattern for east-oriented species.

Nashville Warblers, which winter in Mexico, do not come much under the influence of the easterlies: but migrate northward with southerly or southwesterly winds. Given these wind conditions, the Nashville's spring migration route would be east of the fall route if the birds merely reversed their heading from fall to spring. Because most of the long-distance migrants are ultimately of southern origin, we might assume that the spring migration routes would have at least as much zoogeographic significance as the fall routes, if not more. The migration of the Nashville and Palm Warblers does not bear out this supposition. The spring migration of both appears to bear less relationship to the ancestral range than the fall route. It was hypothesized above that the fall migration route evolved from the accidental resultant of the migrant's heading toward its ancestral range and the predominant pattern of postfrontal circulation, and that the complete elliptical migration circuit was greatly influenced by this circulation. It is axiomatic that the spring and fall routes are necessarily interdependent since the end of one is the beginning of the other. The spring route is no less an accident than the fall route, but the relationship of the spring heading to the ancestral range is less apparent because of the displacement which has already occurred in the southward flight. As in the case of the Nashville Warbler, the spring heading for east-oriented populations is probably merely a reversal of the fall heading. The appearance of large numbers of trans-Gulf migrants on the northwest shore of the Gulf (some far west of their winter range and probably west of their destination) is ample evidence of the wind's influence on the migration route, yet by holding a constant southeast heading in fall and reversing that heading in spring a northern migrant will complete an ellipse by timing its flights with the postfrontal circulation. The system is not navigation as observed in species of Old World warblers by Sauer

(1958), but is more like the unidirectional orientation observed in displaced waterfowl by Bellrose (1963) and others. The system could involve various methods of orientation, including the use of celestial (Vleugel, 1954; Sauer, 1958), wind (Vleugel, 1952), and/or even topographic cues. The method which best seems to fit the available data is that the migrants orient on a single point observable over a vast part of the entire route, i.e., most probably celestial orientation. The repeated observation of oriented flight under overcast skies (see Bellrose and Graber, 1963:387) indicates that another effective orientation method may be used by migrants, though at times with poor results (see Fig. 14). The failure, at times, of this auxiliary method of orientation provides a clue to its nature. The system appears to fail when migrants overtake a slow-moving front and pass into an area of variable or calm winds (see Graber and Cochran, 1960:268). Thus, the success of the system seems to depend upon a sustained wind flow: when this condition is lost, the migrants revert to positive phototropic response and orient on any artificial lights near their altitude. This response becomes apparent in the massive kills of birds at TV towers.

Better understanding of the population shifts and migration routes of the many populations passing any locality will come mainly from banding and telemetric studies, but better coverage of more television towers, following the fine example of Stoddard (1962), can greatly augment other types of observations. A comparison of the kills at Champaign with those for the tower in northern Florida studied by Stoddard (1962) during the same span of years (1955–1960) supplements field observations on the migration routes of many species of night migrants. The Florida tower yielded far more specimens, partly because of the superior coverage which Stoddard provided. The average ratio of fall specimens for species killed at both towers was 1 at Champaign to 3.5 in Florida. For some species the numbers of birds killed at the two towers depart greatly from this ratio (Table 2). Aside from the better coverage given the Florida tower, we would expect a greater kill in Florida in view of the southeast directional pattern of migration at Champaign and the fact that most of the species involved are (south) east-oriented in fall. This orientation produces a "funnel effect" (a concentration of the swarm at lower latitudes) along the migration route, which is clearly observable in the kills of some species. Veeries, for example, are killed in a ratio of 52 in Florida to 1 in Illinois. Other species which may show the funnel effect are: the Yellow Warbler, Palm Warbler, Yellow-throated Vireo, Red-eyed Vireo, Northern Waterthrush, Wood Thrush and Yellowthroat (Table 2). A low ratio may indicate either a widely spread migration route for the species or a narrow route which completely misses the Florida tower. It is not surprising that the Florida tower kills only one-tenth as many

Philadelphia Vireos as the Illinois tower, because field observations in general indicate that this species funnels down to the *center* of the Gulf coast so that most of the population passes west of the Florida tower. The low kill of Blackpoll Warblers at the Florida tower supports the view that this species migrates to a large extent off the eastern seaboard (Nisbet et al., 1963), thus east of the Florida tower; the Cape May Warbler may use much the same route (Table 2). The low kills of Scarlet Tanagers, Swainson's and Gray-cheeked thrushes in Florida may indicate that these species pass mainly west of the Florida station over the Gulf; all are uncommon in the Antilles (Table 2).

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SINGING BEHAVIOR OF THE SWAINSON'S WARBLER

BROOKE MEANLEY

The Swainson's Warbler (*Limnothlypis swainsonii*), relatively common in some areas, is a difficult bird to locate because of the character of its habitat, its neutral color, and its habit of spending much time close to or on the ground in the shade. Thus, it would rarely be observed were it not for its song.

Its song, one of the outstanding of warbler songs, has been analyzed by Gunn (in Griscom and Sprunt, 1957:26–27). Brewster's (1885:72–74) description of its singing behavior has been cited in most of the later writings on this species.

As part of a life history study of this species, I obtained information on its singing behavior, particularly during the springs of 1965 and 1966. Most observations were made in the Ocmulgee River floodplain forest a few miles south of Macon, Bibb County, Georgia, and in the Dismal Swamp, Nansemond County, Virginia. Observations from other years and localities also are included.

Methods of study involved listening to and observing birds on their territories. As a guide for the conduct of this study, I have made use of Harold Mayfield's report of his study of the Kirtland's Warbler (*Dendroica kirtlandii*) (1960). Time used in this study is Eastern Standard Time, unless otherwise indicated.

SINGING BEHAVIOR ON GROUND AND IN TREES

The Swainson's Warbler sings from the ground, and from trees, shrubs, and vines, usually below 30 feet. Singing from the ground usually is more sporadic since it is done while hunting for food. After a male has spent some time on the ground foraging and intermittently singing, it may fly to the limb of a tree to rest, preen, or continue singing.

During the first few days after they arrive on the breeding grounds, birds in the Ocmulgee River floodplain forest canebrakes sing considerably more often from the ground than from trees or shrubs. In 40 hours of observations, three of four individuals were observed to sing only from the ground during their first week, 12–19 April 1965. In April 1966, during the first few days on the breeding grounds, a male sang only from the ground when under observation 10 hours during parts of 4 days (12–15 April). When I next observed this bird, on 28 April, it was also singing from trees. Another male sang 135 songs from the ground and 65 from a tree when under observation for 90 minutes on 15 April.

When singing in a tree one of the Swainson's Warbler's favorite perches is a dead branch well out from the trunk in the lower part of a tree.

It sings from a stationary position when perched in a tree or shrub, as pointed out by Brewster (1885:73–74): "While singing he takes an easier posture, but rarely moves on his perch. If desirous of changing his position he flies from branch to branch instead of hopping through the twigs in the manner of most warblers." However, a singing bird may reverse its position on the same perch and resume singing while faced in the opposite direction.

In the course of one hour, a Charleston, West Virginia male sang from 18 perches, once only from each of 17, and 5 times from 1. The shifting from perch to perch by a Swainson's Warbler during the first half hour (plus) of morning song was noted in the Dismal Swamp, Virginia, on 3 June 1966. The bird started singing at 4:27 AM. It sang from the first location for 11 minutes, from the second for 10 minutes, from the third for 10 minutes, from the fourth for 4 minutes, from the fifth for 1 minute, and from the sixth for 1 minute. It began feeding at 5:15 (for the first time that morning) and singing from the ground.

SECONDARY, FLIGHT, AND INCOMPLETE SONGS

Secondary Songs (whisper and subsong) have been defined by Berger (1961:169) as follows: the whisper song "as the soft inward rendering of the primary advertising song, with or without variations." "Subsong differs from whisper song in that it is unlike the primary advertising song." Secondary songs of the Swainson's Warbler were sung mainly from the ground, but occasionally from trees, shrubs, and logs. They were given throughout the breeding season. The bird's head was not tilted upward when singing the secondary songs as when singing the primary advertising song.

Mayfield (1960:127) thought that the Kirtland's Warbler sang whisper songs mainly when other males were nearby. Most males that I heard were in isolated territories, and to my knowledge, other males were not nearby. Secondary songs were seldom audible beyond 30 feet. They were often repeated continuously for as long as 3 minutes.

Flight Songs that I heard had no resemblance to the primary advertising song or secondary songs. A bird that had just chased another out of its territory took off from the ground and flew in a spiralling flight to a height of about 35 feet, continuously singing as it flew upward.

Incomplete Songs or songs without endings and songs consisting of only the first, second, or third notes may be heard at any time throughout the breeding season. They are sometimes given when a bird is startled, and often at the beginning of a course of songs. They are more often heard in the latter part of the breeding season than in the earlier part.

SEASONAL SONG CYCLE

The Swainson's Warbler sings vigorously from the time it arrives on its breeding grounds in April, until the nesting season is over, which is usually by the latter part of June. Thereafter singing becomes more sporadic.

On 16 June, in the Dismal Swamp, a male whose mate was incubating sang several songs during each half hour of the day from 5:30 AM to 4:40 PM (when I left its territory). On 30 June, the same male was singing almost as frequently as on the 16th, although the nest of the pair had been destroyed.

In floodplain forests of the Ocmulgee River, Georgia, and Arkansas River, Arkansas, I heard a few individuals singing during each day in July and August. On 6 August 1966, during a 2 hour period (11:00 AM to 1:00 PM C.S.T.) that I was in a canebrake near Pendleton Ferry, Arkansas, a male sang 93 songs.

Mayfield (1960:128–129) had the impression that Kirtland's Warbler males "sang more when not in close company with the female—that is if unmated, or if the mate is incubating eggs or brooding young—and less while the pair are in close companionship during pre-incubation." I observed the same behavior in the Swainson's Warbler at Alexandria, Louisiana, and at Macon, Georgia. At Macon, 25 to 28 April 1963, I observed the singing behavior of four territorial males in a 7.5 acre tract of cane. Only one of the four males was mated. The three unmated males sang vigorously through most of the day, while the mated male sang only in the early morning up to about 7:30 AM. But when the female began nest building the male resumed his schedule of singing during almost every hour of the day. While the female builds the nest, incubates, and broods the young, the male sings up to within about 30 feet of the nest, but usually at greater distances.

BEGINNING AND END OF DAILY SONG

The daily singing schedules of the Swainson's Warbler and other woodland passerine birds are rather similar. The first singing of the Swainson's Warbler and other woodland birds was noted on a mild cloudy morning in the Ocmulgee River floodplain forest, 14 April 1966. Sunrise was at 6:07. The first bird that sang was a Cardinal (*Richmondena cardinalis*), at 5:25 AM; followed by a Rufous-sided Towhee (*Pipilo erythrophthalmus*), at 5:32 AM; White-throated Sparrow (*Zonotrichia albicollis*), at 5:33; Wood Thrush (*Hylocichla mustelina*), at 5:35; and then two Swainson's Warblers, at 5:47. The Swainson's was the first Warbler to sing, followed by the Prothonotary Warbler (*Protonotaria citrea*), at 5:55; and Hooded Warbler (*Wilsonia citrina*), at 5:57. Almost all species of woodland birds were singing by 6:00 AM.

Table 1

Songs per Minute in Courses by a Territorial Male Swainson's Warbler: 4:15–6:43 pm*

Length of course	Songs/minute
4:15–4:20	8, 5, 5, 3, 2
4:27–4:32	8, 6, 5, 2, 4
4:40–4:46	7, 7, 7, 4, 4, 4
4:50–5:03	8, 6, 4, 5, 5, 4, 5, 6, 6, 5, 5, 4, 1
5:13–5:25	9, 6, 5, 4, 5, 4, 4, 4, 3, 4, 4, 2
5:26–5:31	5, 5, 5, 6, 5
5:48–5:51	8, 4, 1
6:14–6:16	5, 5
6:33–6:38	7, 5, 3, 4, 2
6:40–6:43	5, 6, 4

* Dismal Swamp, Virginia—15 June 1966.

In the Dismal Swamp, Virginia, in a section of swamp forest, 3 June 1966, the first Swainson's Warbler sang at 4:27 am, following a Cardinal, Wood Thrush, Wood Pewee (*Contopus virens*), Crested Flycatcher (*Myiarchus crinitus*), Hooded Warbler, and Tufted Titmouse (*Parus bicolor*) all of which began singing after 4:05. Sunrise was at about 4:44 am.

On 14 April, in the Ocmulgee forest, two Swainson's Warblers with adjoining territories sang up to 7:00 pm and 7:14 pm, respectively. Sunset on that date was at about 7:00 pm. On 2 June, in the Dismal Swamp, a Swainson's sang until 6:45 pm. Only the Wood Thrush, Cardinal, and Wood Pewee sang later in that section of the woods. Sunset was at about 7:28 pm.

RATE OF SINGING

Songs are given in courses or series, that is, periods of steady singing for several minutes at a time. Sometimes in the early morning the pause between courses is so brief that they seem to run for one-half hour or more. The rate of singing is usually faster at the beginning of a course of songs (see Table 1).

During the first hour of morning song on 2 June, a Dismal Swamp male sang at a fast but gradually diminishing rate of speed: 9 songs per minute for the first eight minutes, 5–6 per minute thereafter. Norris and Hopkins (1947:8) noted that the average time interval between songs of a male at Tifton, Georgia was 10.7 seconds.

The rate of singing is sometimes relatively constant over long periods of time. A male in the Ocmulgee floodplain forest, 19 April, sang between

TABLE 2

NUMBER OF SONGS PER 15 MINUTE INTERVAL OF A TERRITORIAL MALE SWAINSON'S WARBLER*

Period ending:	Minutes					Temperature degrees F (in woods)
	15	30	45	60	Total	
Hour	Songs (N)					
4:00 AM	0	27	84	75	186	42
5:00	61	33	50	48	192	47
6:00	52	51	44	47	194	51
7:00	54	53	48	43	198	52
8:00	38	47	35	35	155	59
9:00	24	23	29	0	76	61
10:00	0	0	0	0	0	67
11:00	0	0	0	0	0	67
12:00	0	0	0	0	0	69
1:00 PM	0	0	1	0	1	68
2:00	0	25	7	3	35	70
3:00	8	21	12	31	72	70
4:00	21	1	20	17	59	69
5:00	0	0	0	0	0	62
6:00	0	0	0	0	0	60
7:00	0	0	0	0	0	55
				Total	1168	

* Observation made 2 June 1966, at Dismal Swamp, Nansemond County, Virginia.
Sunrise about 4:44 AM, sunset about 7:28 PM. Sunny most of day.
First song at 4:27 AM, sang until 6:45 PM previous evening.

40 and 46 songs (40. 42. 46. 43. 42) each 15 minute period from 8:00 to 9:15 AM. See Table 2 for songs per 15 minute interval by a Dismal Swamp male.

DISCUSSION

On hot June days in the Dismal Swamp, I found the Swainson's Warbler to be one of the most frequent singers in the woods if birds still had active territories. The Red-eyed Vireo (*Vireo olivaceus*) sang more continuously. but its song did not stand out like the Swainson's. In the early afternoon when song activity is generally at a minimum for most birds. the Swainson's Warbler was often the most persistent singer in the swamp.

The frequency of singing depends upon the time of day. stage of the breeding cycle, proximity of territories, territorial conflict. weather, the singing of other species, and perhaps other factors. With the exception of the song of another Swainson's Warbler. the comparatively loud song of the Carolina Wren (*Thryothorus ludovicianus*) seems to be more effective in initiating singing activity by the Swainson's Warbler than any other song in the Coastal Plain.

Brewster (1885:72) says that the Swainson's Warbler is "ventriloquial to such a degree that there is often great difficulty in tracing it to its source." I have not had that impression after listening to this species sing each spring for the past 22 years, but a friend who recently spent the day with me in the Dismal Swamp listening to the Swainson's Warbler for the first time, thought that birds he heard were singing from high in the trees, when actually they were singing from the ground or at a height of 20 feet or less.

SUMMARY

Studies of the singing behavior of the Swainson's Warbler were conducted mainly near Macon, Bibb County, Georgia, and in the Dismal Swamp, Nansemond County, Virginia, during the springs of 1965 and 1966. Singing behavior on the ground and in trees is discussed. Swainson's Warblers sing vigorously from the time they arrive on the breeding ground until the latter part of June, when the singing of most birds becomes more sporadic. At Macon, Georgia, in mid-April, morning song of one bird began about 20 minutes before sunrise; and evening song of the same bird ceased about 15 minutes after sunset. Songs were delivered at the rate of about 8–9 per minute for the first few minutes of morning song, decreasing to 5–6 per minute for most of the morning. Songs are given in courses or series. The rate of singing is usually faster at the beginning of a course. The number of songs sung by a territorial male in 1 day in the Dismal Swamp, Virginia, 2 June, was 1168. It produced 280 songs the first hour, and sang at a fairly constant rate from 5:00 to 8:00 AM, 192, 194, 198 songs per hour.

ACKNOWLEDGMENT

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U. S. DEPARTMENT OF THE INTERIOR, PATUXENT WILDLIFE RESEARCH CENTER, LAUREL, MARYLAND, 27 AUGUST 1966.

ECOLOGICAL ASPECTS OF DUCKS NESTING IN HIGH DENSITIES AMONG LARIDS

Kees Vermeer

Very little work has been done on ducks nesting among larids. During a study on the ecological interactions between two sympatric gull species, *Larus californicus* and *L. delawarensis*, on two islands, A and B, in Miquelon Lake, located at 53° 15′ N and 112° 55′ W in Alberta, data were collected of ducks nesting among these gulls in 1964 and 1965. The two islands carried dense populations of both California and Ring-billed gulls. The islands A and B were composed of boulders, sand and clay and consisted of six and five acres, respectively. Their highest points were six feet above the lake level. A few small trees and shrubs grew on them such as *Populus tremuloides*, *Salix* sp., *Cornus stolonifera*, *Ribes oxyacanthoides* and *Rosa woodsii*. The most common herbs were *Sonchus arvensis*, *Cirsium arvense*, *Artemisia absinthium*, *Chenopodium album*, *Urtica gracilis*, *Descurainea richardsonii*, *Scirpus americanus*, *Scirpus validus*, *Carex rostrata*, *Axyris amaranthoides*, *Amaranthus retroflexus*, *Glyceria striata*, *Hordeum jubatum*, *Taraxacum officinale* and *Juncus balticus*.

The number of duck clutches initiated on islands A and B in 1964 and 1965 are shown in Table 1.

On 23 April 1965, an observation cabin was occupied on island A. At that time the island was covered with snow, and the ice in the lake was thick and solid. Two pairs of Mallards (*Anas platyrhynchos*) were already present on the island and were observed to set out for exploration on the snow cover.

Table 1

Number of Duck Clutches Initiated on Islands A and B in 1964 and 1965

	No. of clutches				
	Island A		Island B		
Duck species	1964	1965	1964	1965	Total
Mallard	9	3	3	3	18
Pintail	2	4	4	6	16
American Widgeon	3	1	2	1	7
Gadwall	26	15	3	10	54
Lesser Scaup	41	44	26	32	143
White-winged Scoter	9	2	2	7	20
Total	90	69	40	59	258

Mallards and Pintails (*A. acuta*) were first observed to arrive in the Miquelon Lake region in the spring of 1964 and 1965 in the first week of April. Two pairs of Pintails were first seen on island A on 26 April, one pair of American Widgeon (*Mareca americana*) on 29 April. one pair of Gadwalls (*Anas*

TABLE 2

CLUTCH COMMENCEMENT FOR FIVE SPECIES OF DUCKS AT MIQUELON LAKE IN 1964 AND 1965

Date of clutch initiation	No. of clutches started				
	Mallard	Pintail	Gadwall	Lesser Scaup	White-winged Scoter
27–28 April	3				
29–30	1	3			
1–2 May	2	1			
3–4	1				
5–6	2	2			
7–8		1			
9–10		1			
11–12	1	1			
13–14					
15–16					
17–18				1	
19–20					
21–22					
23–24			3		
25–26		2	1		
27–28			2	1	
29–30		1	2		
31 May–1 June		1		2	
2–3 June			1	7	
4–5			2	7	
6–7	2		3	4	1
8–9		1	2	5	1
10–11		1	6	14	2
12–13			5	8	2
14–15			1	5	
16–17			4	7	1
18–19	1		5	9	2
20–21	2		1	20	2
22–23			1	9	1
24–25			5	8	2
26–27			4	5	2
28–29			3	9	2
30 June–1 July			1	3	1
2–3 July			1	3	1
Total	15	15	53	127	20

TABLE 3
INCUBATION PERIOD, CLUTCH SIZE, HATCHING AND FLEDGING SUCCESS OF GADWALL AND LESSER SCAUP ON ISLANDS A AND B IN 1964

	No. of clutches studied	Gadwall	No. of clutches studied	Lesser Scaup
Average incubation period	10	25.1 (22–27) days	18	24.8 (21–27) days
Average clutch size	26	9.9 eggs	59	10.5 eggs
No. of clutches hatched	29	26 (90%)	67	60 (89.5%)
No. of clutches preyed upon by gulls		(0%)		4 (6%)
No. of clutches deserted by hen		3 (10%)		2 (3%)
Unknown loss		(0%)		1 (1.5%)
Fledging success	26	Nil	60	Nil
Cause of duckling mortality		Mostly gull predation		Mostly gull predation

strepera) and eleven pairs of Lesser Scaup (*Aythya affinis*) on 1 May. and six pairs of White-winged Scoters (*Melanitta deglandi*) on 6 May in 1965.

Table 2 shows the commencement of egg-laying of five species of ducks nesting on islands A and B. The 1964 and 1965 laying data of ducks were grouped together. since the laying periods of each species were similar for both years.

The majority of clutches shown in Table 2 were found during the laying period. A few which had been completed when located were backdated from the time of hatching to obtain the date of clutch initiation.

Gull predation on eggs of late-nesting ducks was less than for early nesters. This was partly due to the development of nesting cover with the advance of the season and partly the result of Lesser Scaup and Gadwalls having more time to become used to my checking the gull nests. The incubation period. clutch size. hatching and fledging success of the Lesser Scaup and Gadwall in 1964 are recorded in Table 3. These two duck species in 1964 were selected because the situation for late nesters was most normal that year and also because these species were the most numerous nesting ducks (see Table 1).

The 59 Lesser Scaup clutches, with known clutch size and which hatched. produced 619 eggs of which 91 percent hatched. The eggs which were addled and those which disappeared made up 6.6 percent and 2.4 percent. respectively. Of the 259 eggs produced by 26 Gadwall clutches, 95.4 percent hatched. The eggs which were addled and disappeared made up 3.1 percent and 1.5 percent. respectively. Table 4 compares the hatching success of Gadwalls and Lesser Scaup nesting on islands with and without gulls.

It can be seen that the hatching success of insular nesting Gadwalls and Lesser Scaup is high. whether or not nesting gulls are present.

TABLE 4
COMPARISON OF HATCHING SUCCESS OF GADWALL AND LESSER SCAUP
NESTING ON ISLANDS

		Hatching success			
Authority	Locality, year	No. of clutches studied	Gadwall	No. of clutches studied	Lesser Scaup
Duebbert, 1966	North Dakota, 1956	70	85.7%		
"	" " , 1957	109	92.7%		
Keith, 1961	S.E. Alberta, 1953–57			18	83.3%
†This study	Central Alberta, 1964	29	90.0%	67	89.5%

† = occupied by gulls.

The high mortality of ducklings at Miquelon Lake was caused by California Gull predation. Since the island shores were devoid of emerging aquatic vegetation, the ducklings lacked protective cover against this type of predation. As soon as the ducklings entered the water, they were swallowed by the California Gulls.

European observers reported that certain duck species exhibited a strong social attraction for larids (Hildén, 1964). Evidence was gained at Miquelon Lake that Pintail and Lesser Scaup strongly associate with larids. The association was not the result of nesting on islands free from mammalian predation. In 1964, 21 Common Tern (*Sterna hirundo*) clutches were initiated within an area of 30 × 20 feet at one tip of another island on Miquelon Lake. After the establishment of the first Common Tern clutches, two nesting pairs of Lesser Scaup and two pairs of Pintails associated themselves with the terns. No other duck nests were found on the island in that year. In 1965, the terns did not nest on the tip of this island, except for one clutch which was started approximately 300 feet from where the tern colony was located in the previous year. As soon as the Common Tern clutch in 1965 was completed, two Lesser Scaup and two Pintail clutches were initiated within a 15-foot radius of the tern nest. No other duck nests were found that year on any part of the island.

The mechanism which leads to ducks selecting breeding sites in larid colonies may be imprinting of ducklings to these particular circumstances. Birds nesting among larids may benefit from the association. They are warned at an early stage by the larids' alarm at the approach of a predator. Certain avian predators such as crows and predaceous gulls may be driven away from the nesting colony (Kruuk, 1964). Where ducks nest in association with larids such as Common Terns, Black Terns (*Chlidonias niger*), Franklin Gulls (*Larus pipixcan*) and pure Ring-billed Gull colonies, a high fledging success for ducks may result. Hildén (loc. cit.) observed "social

TABLE 5

EGG PARASITISM OF DUCKS ON ISLANDS A AND B IN 1964 AND 1965

Parasitizing ducks	Parasitized ducks—No. of nests parasitized				
	Lesser Scaup	Gadwall	White-winged Scoter	Pintail	Mallard
Lesser Scaup	12	8	1		
White-winged Scoter	5	3	1		
Gadwall	1				
Redhead				4	1
Total	18	11	2	4	1

attraction" of ducks to gulls such as the Black-headed Gull (*Larus ridibundus*), the Common Gull (*Larus canus*) and the Lesser Black-backed Gull (*Larus fuscus*). However when ducks nest among one of the larid species predaceous upon them, the result may be disastrous. This occurred in 1964 when fledging success was nil among ducks which nested on islands A and B occupied by California Gulls (Table 3).

Not much is known about the anatid-larid relations in North America. The Lesser Scaup was also a numerous nesting duck in some of the other mixed California and Ring-billed Gull colonies which were visited in Alberta. Most of the Gadwall nests were located in dense herbaceous cover, i.e., in nettles on islands A and B at Miquelon Lake. Duebbert (1966) found 121 nests of the Gadwall on a seven-acre island in the Lower Souris Refuge, North Dakota, in 1957. No larids nested there. Not far from the island where Duebbert did his study, there was a 0.8-acre island. Henry (1948) reported 160 pairs of Gadwalls nesting on the latter in 1947. A colony of Common Terns also nested on the 0.8-acre island that year. It is possible that the higher concentration of Gadwalls breeding on the 0.8-acre island was due to the presence of nesting Common Terns.

EGG PARASITISM

As a result of the high density of nesting ducks on islands A and B, several duck nests were parasitized accidentally. Foreign eggs in parasitized clutches could be recognized by either shape, colour and size. Table 5 shows the egg parasitism of ducks.

Some nests were parasitized by more than one hen. One Gadwall nest, e.g., was parasitized by a Lesser Scaup and White-winged Scoter. In two Lesser Scaup nests the clutches increased by three eggs per day, indicating that more than one hen parasitized these nests. A two-egg increase per day in one nest and none in the other was observed in two closely located Lesser Scaup nests. In one of these, a double clutch resulted while the neighboring clutch never advanced beyond two eggs. The clutch with two eggs was probably not found again by the hen which initiated it, since it was not incubated. These examples show that at least in the Lesser Scaup, egg parasitism resulted as a consequence of the high density of nesting ducks. That egg parasitism is related to the nesting density of ducks can also be indirectly seen by comparing Tables 1 and 5. The Lesser Scaup and Gadwall were the most numerous nesting ducks on islands A and B. The Redhead (*Aythya americana*) did not nest on the islands, hence egg parasitism was deliberate. The relatively high number of Pintail nests parasitized by Redheads is probably a consequence of Pintails having on the average the most exposed duck nests on the islands at Miquelon Lake.

Since most egg parasitism was observed during the process of laying, no eggs of the late nesting Lesser Scaup and White-winged Scoters were found in clutches of early nesting Mallards and Pintails. Of the three late nesting ducks, the Gadwall parasitized nests of other ducks least. Gadwalls and White-winged Scoters nested in more dense cover, i.e., nettles, than the Lesser Scaup. The Gadwall appears more adept in finding its own nest than the White-winged Scoter in this type of cover.

SUMMARY

A high density of ducks was observed nesting among California and Ring-billed gulls at Miquelon Lake, Alberta. The most numerous ducks, the Lesser Scaup and Gadwall, had a hatching success of 90 percent and 89.5 percent, respectively, but the fledging success of both species was nil due to gull predation.

Evidence was gained that Pintail and Lesser Scaup strongly associated with Common Terns.

Due to the high density of nesting ducks, egg parasitism occurred frequently.

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CANADIAN WILDLIFE SERVICE, 10015 - 3 AVENUE, EDMONTON, ALBERTA. 4 OCTOBER 1966.

THE COWBIRDS OF OTTER LAKE[1]

DANIEL S. MCGEEN AND JEAN J. MCGEEN

DURING a study of the nesting birds on 55 acres just west of Pontiac, Michigan, data on the Brown-headed Cowbird (*Molothrus ater*) parasitism were collected. This paper is a report on findings and inferences as to number of female cowbirds present, size of clutches, number of eggs laid, length and peaks of egg laying seasons, hosts used, and area covered by the birds.

The study area consisted of unused, hilly pasture in the early successional stages of reforestation and low, wet thicket bordering a canal connecting Cass and Otter Lakes. The host species studied primarily was the Yellow Warbler (*Dendroica petechia*). Approximately 50 pairs and their nests were found in the area in 1950. Complete seasonal censuses of breeding species have already been reported. (O'Reilly et al., 1951*a*:71; 1951*b*:66; 1954:93).

Nice (pers. comm.) has confirmed our feeling that, though unproven, most investigators believe that different cowbird egg types indicate different females laying them.

Since we desired to know how many cowbirds were laying on the area we decided to use this generally accepted, though unproven, approach to cross-check on actual counts of females on the area. In 1950, therefore, a reference collection of unblown cowbird eggs were started as soon as possible so that accepted eggs could be compared at the nest without collecting them. (Blowing eggs changes color values for comparison with those left in nests when accepted by hosts.) Only deserted, covered, or broken eggs were collected from the warbler host, but five accepted eggs were taken, one at a time, from Song Sparrow (*Melospiza melodia*) nests to build up the collection. Broken eggs were repaired into usable specimens by means of plaster of Paris. This reference collection was carried on daily rounds and comparisons were made at nests containing accepted eggs. A Boley millimeter caliper was used to measure eggs when compared.

NUMBER AND IDENTIFICATION OF FEMALES ON AREA

We believe that five females were responsible for the 34 eggs collected and the 56 eggs recorded during this one season for the following reasons: First, repeated censuses counted five females on the area and never more. Second, ground color and marking comparisons divided these eggs into five types (Table 1). Third, only two of these types were not found deposited on the same day at least once (Table 3). These types, B and E, were widely dissimilar in coloration, markings, and measurements (Table 1). Since passerines lay but once a day, eggs found laid the same day are almost certainly from different females.

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[1] Presented at the XIII International Ornithological Congress, Ithaca, N.Y., 1962.

TABLE 1

COWBIRD EGG CHARACTERISTICS—1950

Female	Mean size (mm)	Description
B	20.3 × 15.8	Smallest; usually fine brown and light purple markings
D	21.3 × 16.5	Marbled type; chocolate brown and light purple markings
A	21.2 × 16.7	Light glossy brown and faint purple traces of markings
C	22 × 16.9	Dark brown, minute markings covering the whole egg densely
E	22.2 × 16.7	Marbled type: light greenish hue to the base white, markings brown in bold splotches, much less purple

The most interesting series, Type E. showed a remarkable similarity in length measurements. A statistical analysis was made of these lengths on the 18 eggs and on a sampling of 24 unselected cowbird eggs. therefore, presumably from different females (Mayfield. 1960:167). The F and t tests proved the variances and means of the lengths of the E type to be significantly different from those of the Mayfield sample at the 5 per cent confidence level (Table 2). This supports the hypothesis of the single origin for the E type eggs.

The similarity in lengths of the smaller type D series of eggs was not great enough to support this hypothesis. Inadequate sampling prevents valid analysis in the other three types.

Walkinshaw (1949:82) had a remarkable series of 25 cowbird eggs found in Field Sparrow (*Spizella pusilla*) nests (with two exceptions) in a very restricted area, which from color, markings, and similarities of length measurements, also supported by statistical analysis, he believed to be the production of one female.

Both Friedmann (1929) and Nice (1937) believed different females to be responsible for their different egg types, but had smaller series to work with and statistical support was thus denied them.

Perhaps organic dyes or radioactive tracers (phosphorus or calcium salts for shell components) fed or injected into captured breeding female cowbirds prior to color banding and release would help answer some of these questions in the field since eggs and their source female could thus be indisputably matched.

The study of captive females would undoubtedly be of value if they could be induced to lay. This has apparently been done by F. L. Rand (Friedmann. 1929:184) with a hand-raised bird. He merely supplied this young bird of the previous year with nests containing candy eggs. It laid 13 eggs in 14 days and frequently removed the pseudo-host eggs as they were often found on the floor.

TABLE 2
EGG LENGTHS

Type	No. eggs	Extremes (mm)	Range	Median	Mode	Mean	Std. dev.
D	11	20.7–21.8	1.1	21.1	21.0	21.2	0.336
E	18	21.4–23.2	1.8	22.1	22.1	22.2	0.417
Walkinshaw (1949:82)	11	21.4–22.1	0.7			21.8	0.20
Mayfield (1960:167)	24 unselected	20.0–23.6	3.6	20.65	20.6	20.9	0.859

COWBIRD EGG LAYING SEASON

Table 3 is a condensation of laying data from three seasons. Since nests were checked daily in 1950, exact dates of laying were known in most instances or the date could be ascertained easily within a day or two by knowledge of the host's cycle. In these few cases eggs usually fitted into an empty day in a clutch like a piece into a jigsaw puzzle. As less time was spent in the field in 1948 and 1949, and as less attention was directed to this phase of the problem at that time, we may indicate those dates as probable ones for the depositions in those years. However, the actual date of laying for a reasonable number of them is known, with ample justification for dating the others as we have. The maximum error possible would be one or two days.

The peak for the 1949 season appears to be nine days earlier than the 1950 peak. This correlates with the lateness of the latter season as a whole, and with the beginning of the Yellow Warbler cycle for both years. In 1950 at least four female cowbirds were laying at the time when the warblers were finishing nest construction.

SUMMARY OF LAYINGS

Female A laid six eggs in two clutches of five and one, with a four-day nonlaying period between. The total observed laying period was 11 days. Female B also had six eggs in two clutches of four and two, with a four-day interval noted and a known laying period of 10 days. Female C had seven eggs in two clutches of four and three with an interval of 20 days and a 30-day laying period. Female D had 19 eggs in six clutches of six, five, one, two, four, and one, with intervals of three, five, six, four, and four days, with a known laying period of 41 days. Female E had 18 eggs in five clutches of three, seven, five, one, and two with intervals of five, two, thirteen, and two days, and a known laying period of 40 days. Perhaps the last three eggs belonged to one clutch instead of two, making a total of only four

Table 3

Laying Dates, Clutches, and Hosts of Different Type Cowbird Eggs at Pontiac, Michigan

	x*	May	9	D*							June	5	D*	E	
z			10	D*								6		E	
z (3)			11	D*					z			7			
z (2)			12	D*								8			
			13	D*								9		E	
			14	D*								10	D‡	E	
z			15									11	D‡	E	
			16									12	D*	E	
z			17									13	D	E	
			18	D			A	B				14			C
			19	D				B				15			
			20	D		C	A	B		x		16			
			21	D*		C	A	B				17			C*
z	x		22	D			A					18	D*		C*
z			23		E	C	A*					19			
z			24		E	C						20			
z			25		E							21			
			26					B				22			
	x		27					B				23			
			28	D			A					24			
z			29									25			
			30									26			
	x		31		E							27		E	
		June	1		E							28			
			2		E							29			
z			3		E							30		E	
			4	D*	E						July	1		E	

x = 1948 Season Eggs 5 Total
z = 1949 Season Eggs 15 Total
A, B, C, D, E Types = 1950 Season Eggs 56 Total
Three Year Total = 76 Eggs

* = Song Sparrow host; ‡ = Traill's Flycatcher host; All others = Yellow Warbler host.

clutches. This would eliminate the last two-day interval, but the other one is between two full-sized clutches of seven and five eggs, respectively.

DISCUSSION OF INDIVIDUAL CLUTCHES

Judging from known egg depositions, Females A, B, and C apparently laid only two clutches apiece, although this is uncertain for it will be noted later that they may have covered some territory not under observation.

The incompleteness of known second clutches for Females A and B seems apparent. Probably the gaps in the first clutches of Females A and C and in the second of C did not actually exist. Also, another clutch may have been missed entirely in the 20-day interval between the two known clutches of Female C.

Female D had the earliest cycle of all the females, being synchronized with the earliest known Song Sparrow nestings on the area. In one instance, its nonlaying interval appeared to be only three days with 11 eggs apparently deposited in 14 days.

Female E had the latest start for her cycle, or possibly we missed finding evidence of an entire previous clutch. It is more likely that we only missed the first few eggs of its first clutch, however, since from a glance at the hosts (Table 3) we suspect this female was a "specialist" on Yellow Warblers. If it did have an earlier first clutch, like Female D, it would have had to impose upon the Song Sparrows, since the first warbler nests were not available until 17 and 18 May that year. The first four eggs we attributed to this female showed a progressive increase in width which would seem to be more indicative of a first clutch than a later one. The first known egg of this bird was found 23 May. We had located only the nests of 32 pairs of warblers, up to that time, out of the complete population of 50 pairs. The possibility exists that a few earlier eggs were missed, therefore.

This female, like Female D, presents a very interesting picture, in that 12 eggs apparently are laid in 14 days with only a two-day nonlaying interval between the two clutches. This is reminiscent, too, of Rand's captive female.

In the case of Female D, the short three-day interval was following the first clutch on the Song Sparrows when the majority of the warbler population started nesting practically simultaneously on the area, which apparently was covered most thoroughly by this female. Female E's short interval was between the second and third clutches, however, when only warbler pairs engaged in second or third nesting attempts (due to cowbird or predator interference) were available to her.

LENGTH OF EGG LAYING SEASONS

Table 4 summarizes material on length of laying for apparent individual birds, as well as for the species in single seasons. It will be noted that Walkinshaw's (1949) female had a season one month longer than either of the two Pontiac birds. Its season was only 24 days less than the longest cycle (94 days) noted for a group of females in one season.

About two-thirds of the depositions in this study were found in May (47 eggs) and one-third in June (27 eggs). Only one was found in July. Berger (1951) found two in August. If several or more seasons are counted the

Table 4

Cowbird Egg Laying Seasons

Individuals	Eggs	Dates	Days	Clutches	Source
Female D	19	9 May–18 June	41	6	This work
Female E	18	23 May–1 July	40	4 or 5	This work
Female Battle Creek	25	15 May–20 July	70	7[1]	Walkinshaw (1949:82)
1932 A	9[2]	27 April–24 May	29	3	Nice (1937:156)

The species

Location	Eggs	Dates	Days	Area	Source
Butler, Penna.	81	10 April–12 July	94	90 Acres	Norris (1947:86)
Ann Arbor, Mich.	67	25 April–26 July	92	Washtenaw County	Berger (1951:27)
Cleveland, Ohio		13 May–26 July	75	Cleveland area	Williams (1950:153)
Buckeye Lake, Ohio		19 April–30 June	72	44 Sq. Mi.	Trautman (1940)
Pontiac, Mich.	56	9 May–1 July	53	55 Acres	This work
Madison, Wis.		20 May–3 July	44	5 Acres	Young (1949) and pers. comm.

[1] Nice's analysis—Nice 1949:232.

[2] Assuming gaps in clutches were off area depositions, not skipped days in laying, the eggs would total 17.

length of total egg laying cycle can be extended, but this is misleading since no single seasonal cycle would approach in size such a compound overall cycle.

HOSTS

Examination of Table 3 reveals that Females A and C parasitized both the warblers and the Song Sparrows. Female D included the Traill's Flycatcher (*Empidonax traillii*) in its host group as well as the above two species. But Females B and E were only known to parasitize the warblers. The small number of eggs in the case of Female B makes the classification of it as a specialist highly problematical. (It had the smallest eggs and these most closely resembled the warbler's in coloration and markings.) Female E is the second example of a female cowbird that has been identified circumstantially to be host specific on the basis of a fair-sized series of eggs. In the case of Female E no variation from choice of the warblers as host for 18 eggs was uncovered, while Walkinshaw (1949) found that only the first two eggs of the 25 he attributed to one female were laid in the nest of a host other than the Field Sparrows he was studying. Since no Field Sparrow nests were yet available, the cowbird used an earlier nesting towhee for these first two depositions.

Friedmann (1929) cited several records wherein there was a suggestion of specialization involving as host species the Lark Bunting (*Calamospiza melanocorys*), the Red-winged Blackbird (*Agelaius phoeniceus*), and the Prothonotary Warbler (*Protonotaria citrea*). He also believed a seasonal type specialization to be evident due to lack of other hosts, as in the case of the parasitized early nesting Eastern Phoebes (*Sayornis phoebe*) in the Ithaca, New York region. (This may also be inferred from the manner in which Female D, the "opportunist" of this Pontiac group of females, switched to using the Yellow Warblers when this host's cycle began.) The three females Friedmann studied at Ithaca were not specialists, however, since his Females A and C used three host species, and Female B, two, for the 14 eggs noted for all three females (1929:183).

Several interesting questions are brought up by these results. If a female does specialize, what is the determining factor in her host choice? Would she choose the host which reared her, due to imprinting? Obviously a great deal of work remains to be done before we can hope to answer these questions satisfactorily.

AREA USED

Eggs of Females A, B, and C were found only in a narrow strip along the western edge of the area involving about 15 acres or less. Female D covered nearly the whole area (40 acres of 55) judging from actual egg locations, and may have covered more. Female E covered slightly less (35 acres) according to egg finds, but again may have covered more.

The three females for whom the lesser numbers of eggs were found were confined to the smaller areas as might be expected on a numerical basis. They may have ranged beyond the bounds of our study area, to the north. However at least 20 acres of cultivated field just across the road from the western boundary cut down the number of nests available to them in that direction. This would not prevent such ranging, of course.

Since cowbirds apparently do not defend an area (Laskey, 1950), the home acreage covered by a single cowbird female may best be called her range. There can be an extensive overlapping where cowbirds are abundant. For instance three of four nesting attempts of one pair of Yellow Warblers on the Pontiac area were parasitized with all five cowbirds participating. Any acreage-per-female figure derived by dividing total acreage by number of females present must be a minimum figure because of this overlapping.

Walkinshaw's (1949) female confined herself to a small range of 12.5 acres according to his egg finds. Nice (1937:154) believed 18–20 acres to be the ordinary range with occasional birds covering 30 acres.

From the above we may deduce that cowbird females may regularly cover ranges of 12–40 acres depending upon, presumably, choice of host, host density or spacing, and perhaps fecundity of the cowbird. The mean figure would be 26 acres derived from these two extremes, close to the 24-acre mean observed for the five Pontiac females.

It would seem likely that the density of hosts on an area is the controlling factor in range size rather than area *per se* and cowbird range ought to be reckoned in units of host-pairs as well as units of area measurement.

The number of hosts available per female on the Pontiac area was 20 pairs (99 pairs per five cowbirds), counting only the three species actually noted to be parasitized on the area in the 1950 season. If we consider other commonly used hosts as available even though we observed no parasitism on them we could extend the list to over 25 pairs of hosts per female.

Nice's (1937) figures varied from 14–15 pairs available per female to only eight pairs of hosts per parasite female during the later years of her study when adverse conditions, mostly caused by man, had decimated the Song Sparrow population especially. The average figure on that area was 11.5 pairs per female, making it close to another Ohio report (Hicks, 1934) of 12.5 pairs per female. The female studied by Walkinshaw (1949) had about 19 pairs of Field Sparrows to utilize, but chose only 15. A study of the Ovenbird (*Seiurus aurocapillus*) (Hann, 1937) indicates about four pairs of Ovenbirds per female, but no figures are given on other hosts, so the picture is obviously incomplete.

DISCUSSION

The tendency toward indeterminate laying as exhibited by Females D and E with 11 and 12 eggs in 14 days, respectively, with intervals of 3 and 2 days between the clutches may corroborate Rand's observation cited above. Friedmann (1929) mentioned L. J. Cole's theory that the cowbird could be in a transitional state from a determinate layer to an indeterminate layer where laying may continue daily for longer periods of time. This obviously would be advantageous for a parasite.

Both Cole and Hamerstrom found a tendency towards indeterminate laying in the House Wren (*Troglodytes aedon*) (Kendeigh et al., 1956:50). Cole's wren laid 30 eggs in 43 days with the first group having 13 eggs in 13 days, then a 4-day interval. Apparently 13 eggs in a series is about the limit for passerines. Hamerstrom's banded female laid 14 eggs in 17 days and 12 eggs in 15 days at the beginning and end of its season.

Davis (1942:12) believed that the Brown-headed Cowbird lays no more than 5 eggs in a clutch. From our records they may lay 6 or 7 in a clutch. Nice (1949:234) assumed intervals of at least 5 days, while our two birds seemed to have intervals of 4, 4, 4, 4, 3, and 2 days. Davis (1942:11) believed from histological evidence that a female Shiny Cowbird (*M. bonariensis*) had only a two- to three-day interval between clutches.

Payne reports (1965:57) an average of 10 to 12 eggs. with 15 a maximum per season for the Brown-headed Cowbird on histological evidence: clutches of one to six with 3.1 eggs average, and time between clutches to vary from a few days to a few weeks. These were northern Michigan birds. with a breeding season a month shorter than in lower Michigan. He also reported three of 33 females laid 10 eggs or more by the date of collection and might have laid twice that number by the end of the season.

SUMMARY

Brown-headed Cowbird parasitism observations were made at Otter Lake, Pontiac. Michigan while working on a colony of 50 pairs of Yellow Warblers on a 55-acre area.

It is believed on the basis of the appearance and size of eggs plus dates of laying and female censuses that in 1950 five females deposited the 56 parasite eggs found on the area.

The laying cycle varied from year to year with host cycles. Probable single female cycles of 18, 19, and 25 eggs in four or five, six, and seven clutches, covering 40, 41, and 70 days, respectively, are suggested from the Otter Lake E and D types and Walkinshaw's data. Single year egg laying seasons of 75, 92, and 94 days have been reported in the literature for the species. Possible non-laying intervals between clutches of only two or three days are reported. The number of eggs laid on and off the area was undoubtedly greater than observed.

If our inferences are correct, some cowbird females appear to specialize on certain hosts. Others do not. We believe one female laid 18 eggs all in Yellow Warbler nests in a 35-acre area. Statistical analysis on the 18 egg lengths supports this conclusion. The 19 eggs of another presumed single female, by contrast, were found in the nests of three hosts.

From 12 to 40 acres may be covered by a single female with about 25 acres being a likely mean. A great amount of overlapping of ranges occurred. The number of hosts available per female is important in determining the density of parasites.

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NOTES ON THE RED RAIL (*LATERALLUS RUBER*)

Robert W. Dickerman

The Red Rail (*Laterallus ruber*) has been mentioned in nearly every major regional list of birds compiled from an area within its range, Mexico to Nicaragua. It is probably the most abundant species of its family over much of its range in Mexico, and probably elsewhere, and in the past 10 years has become well represented by specimens in ornithological collections. However, as recently as 1941 Friedmann (*in* Ridgway and Friedmann, 1941) could find no specimens in the downy or juvenal plumages and still more recently Paynter (1955) considered the species to be known from very few specimens. During the course of this study, I have examined about 100 specimens with complete data without searching for every available individual. It is interesting to note that well over half of these specimens were collected during the period since 1955.

A number of authors have contributed to our knowledge of the species. Brodkorb (1943:34) gave the colors of the soft-parts of a "good-sized" young, the first known downy chick, but he did not describe the down. The bill in the dried specimen was black except for the extreme tips of the mandibles which were whitish. Land (1963) mentioned, apparently for the first time, the juvenal plumage, but only that it was "gray-brown." Dickey and van Rossem (1938:162) described in detail a nest of the species as open at the top, and noted in the field that the eggs, collected but later lost, were similar to those of the Clapper Rail (*Rallus longirostris*) in color and shape although smaller in size. Smithe (1966) presented descriptions of the nest and eggs made by Alexander Skutch.

FIELD NOTES

On the Atlantic Coastal Lowlands of Mexico, one can hardly drive through the marsh regions of Veracruz and Tabasco without hearing, from the moving car, the explosive downward trill of the Red Rail. During the spring of the year (April) the species is most vociferous, although individuals are regularly to be heard calling at any time of the year. Red Rails are in my opinion more diurnal than other small rails in their calling activity and it is not uncommon to hear them calling into mid-day in the spring season.

I have repeatedly found the species to be abundant, and the experience of other collectors has confirmed this. In Chiapas, four birds were collected by Warren Rook with a single shot. Allan R. Phillips and I have stood without moving in a tall saw-grass swale 43 miles south of Acayucan, Veracruz, barely 8 feet from one another, and by "squeaking" collected 5

FIG. 1. The nest and eggs (inset) of the Red Rail.

Red Rails. At Ingenio San Cristobal, Veracruz, with a field assistant, I collected nine of the species within a few feet of the railroad track running through the edge of the marsh. At the latter locality in April 1962, rails were calling constantly throughout the morning. At that time males were collected with gonads measuring, in millimeters, 5.5 × 2 and 3 × 2; 1 × 4.5 and 3 × 5.5; 5 × 5 and 9 × 5; and 2 × 7 and 3 × 2.5.

On 30 July 1967, in a small cattail marsh 3.3 miles southeast of Choloma, Cortez Province, Honduras, I flushed a Red Rail from a nest containing four eggs. I returned on 3 August, photographed the nest (Fig. 1), and collected the eggs. An adult male was collected a few feet from the nest, but I was unable to collect its mate, although it called almost constantly, at times within a few feet of me. Once it gave a "churring," wren-like scolding note.

The nest was a relatively tightly woven, globular one, with a side entrance.

much like a very large, loosely woven nest of a Long-billed Marsh Wren (*Telmatodytes palustris*). It was made entirely of dried leaves of grasses and cattail, and was placed with its entrance about ten inches above the water level. The base of the nest was moist and contained a nest of ants of the genus *Anochetus* (subfamily Ponerinae). The ants were kindly identified by D. H. Janzen. The eggs were cream-colored with reddish-brown fleckings at the larger end (inset, Fig. 1). They measured 29.9 × 23.4, 29.5 × 23.1, 28.8 × 23.6 and 28.5 × 23.7 mm.

Through the cooperation of Eugene Ostmark, of the United Fruit Company at La Lima, Honduras, the eggs were placed in a cell culture incubator in the company's research laboratories. On 8 August two of the eggs were pipped, but one of the chicks was dead. It was preserved in formalin. The following day the second egg was opened slightly to assist the young in hatching. On the morning of the 10th the chick was out of the egg but was dead. The other two eggs contained fully developed but dead embryos. The soft part colors of the two chicks were similar, and differed from the description presented by Brodkorb (op. cit.), in that the entire bills were pink, slightly paler along the culmen, and slightly darker basally. The egg teeth were white. The tarsi and toes were medium gray. The down was a flat black with virtually no irridescence.

MOLTS AND PLUMAGES

The juvenal plumage is essentially a dark "gray-brown" as mentioned by Land (1963). I have examined a number of juvenile Red Rails ranging in age from birds still retaining some down on the head to others in all stages of the first prebasic molt. The youngest of these, taken at Putla, Oaxaca on 21 October 1965, are sooty gray, nearly black on the rump, crown and tail, with a brownish cast in the interscapular region, and richer about the shoulders. Ventrally they are dark gray on the flanks and across the breast. The throat is whitish, and the mid-belly area is near pale gray to cream, with a pinkish cast in some individuals, uniform gray in others. The prebasic molt apparently starts in the mid-ventral region giving a strong pink appearance to this area even as the wing feathers are barely breaking from their sheaths! The thighs and lower abdomen are medium gray; undertail coverts are dark gray with a slightly brown cast. The coloration of the soft parts of two juveniles collected 18 July 1962 by William J. Schaldach 3 mi E of Sarabia, Oaxaca, and recorded by him in the field were: "iris grayish-white, bill pinkish to dusky horn basally, dusky distally. Bare orbital skin grayish with faint greenish tones. Tarsi greenish gray, dusky at elbows, feet same but soles duller in tone." The first basic plumage is an "adult-type" plumage, gained directly by molt from the juvenal plumage. The first basic differs from the definitive plumage in averaging somewhat paler on the belly and possibly the breast and in lacking sexual dimorphism. Specimens in all stages of the first prebasic molt show no indication of molt in the wings, and I believe the juvenal remiges are retained through this molt. Two males from Putla, Oaxaca still largely in the gray juvenal plumage have wings measuring 82 and 83 mm, near the upper limit of this measurement. In spite of the large size of the series examined, no specimens have been seen in any stage of a later molt.

In the Red Rail, there is a generally unrecognized yet distinct sexual dimorphism in the extent of chestnut on the upperparts, especially the rump. Although Hellmayr and Conover (1942:380) described this based on four specimens from Putla, Oaxaca, subsequent authors have failed to take it into account in their discussions of the species. Males generally have the lower back and rump brownish to dusky, whereas in adult females the lower back, rump and upper tail coverts are considerably richer, more chestnut in coloration. Immature females have a dusky rump as do males. Apparently this dimorphism led Miller and Griscom (1921) astray in characterizing the subspecies *L. r. ruberrimus* as having a chestnut rump. The type of *ruberrimus* is of course a female. Dickey and van Rossem (1938) in discussing a mated pair of Red Rails wrote "The female is typical *ruberrimus* in color while the male is only slightly redder than *ruber*." They apparently did not realize the significance of the observed differences. There is some individual variation in this character. Five of 48 *supposed* males examined for this character had a chestnut rump. Two of these are probably males as indicated by their longer bills, two have equivocal measurements, and one is probably missexed. Seven immature females all had dark rumps, while 21 out of 24 females whose age was not obviously immature had chestnut colored rumps. There is a slight sexual dimorphism in size with males averaging larger than females, especially in the length of the culmen.

SYSTEMATICS

Three subspecies have been described for the Red Rail. The two in addition to the nominate form (type locality: Verapaz, Guatemala) are:

L. r. ruberrimus (Miller and Griscom)—bill shorter and stouter than *ruber*, and with chestnut of upperparts extending over the entire upperparts including the wing coverts. Type locality: Jinotega, Nicaragua.

L. r. tamaulipensis (Nelson)—bill longer and heavier, chestnut reduced to a collar which is paler and less rufous than in *ruber*. Type locality: Alta Mira, Tamaulipas.

It is evident from the extent of sexual dimorphism described above that the color characters used in the descriptions of both forms were based largely or entirely on this variation. The types are of the sexes that one would predict based on the characters used to separate the two forms. There are no color characters that are of value in distinguishing subspecies in the Red Rail.

This leaves the mensural character of the bill as the only possible means of maintaining the named forms. Mean culmen lengths (from anterior edge of nostril) of males are as follows: Tamaulipas, Veracruz, and the Atlantic slope of Oaxaca 11.1–12.6 (ave. 12.0, n = 10); southern Mexico, Yucatan, British Honduras, and Guatemala 10.7–12.4 (ave. 11.5, n = 26); Nicaragua and Honduras 11.4–12.2 (ave. 11.7, n = 5). Measurements for females from these same respective areas are: 10.6–11.4 (ave. 11.0, n = 9); 9.2–11.3 (ave. 10.7, n = 19) and 9.9–11.1 (ave. 10.5, n = 4).

It is clear that there are no significant differences between these populations, and I fully endorse the views of Brodkorb (1943) and Paynter (1955) that neither of the named forms should be recognized and the Red Rail should be considered monotypic.

In Mexico the Red Rail is widely distributed on the Atlantic coastal lowlands north to Alta Mira in Tamaulipas, being abundant from at least central Veracruz southward. It is more restricted on the Pacific slopes, reaching at least as far north as Laguna Tres Palos, just south of Acapulco, Guerrero, and being locally abundant at Putla, Oaxaca. It is locally common in the interior of Chiapas and apparently relatively so, where suitable habitats exist, in Yucatan and on Isla Cozumel, Quintana Roo.

Specimens examined: *Mexico*: Total: 63 (Tamaulipas 2; Veracruz 17; Tabasco 2; Guerrero 1; Oaxaca 16; Campeche 1; Yucatan 10; Quintana Roo 2; Chiapas 12); *British Honduras*: 13; *Guatemala*: 10; *Honduras*: 14; *Nicaragua*: 1.

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I wish to express my appreciation to the curators of the following collections for permitting me to examine specimens under their care: Museum of Comparative Zoology, Harvard; United States National Museum; American Museum of Natural History; Carnegie Museum; University of Louisiana Museum of Zoology; Chicago Natural History Museum; University of Minnesota Museum of Natural History; Robert T. Moore Laboratory of Zoology; University of Kansas Museum of Natural History, and the Western Foundation of Vertebrate Zoology, Los Angeles. I have had the pleasure of the company of Allan R. Phillips on several Red Rail hunts; and I particularly wish to express my gratitude to the following field assistants and collectors who have provided a number of the most critical specimens: Abrahan Ramirez A., Sostonez Romero H., Juan Nava S., Santos Farfan B., and Inocensio Salamon. Scientific collecting permits were provided by the Departmento de Forestal y Casa of the Mexican Government. Field work in coastal Veracruz was supported in part by the United States Public Health Service Training Grant No. 5-T1-A1-231 from the National Institute of Allergy and Infectious Diseases.

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DEPARTMENT OF MICROBIOLOGY, CORNELL UNIVERSITY MEDICAL COLLEGE, NEW YORK, NEW YORK 10021, 10 OCTOBER 1966.

GENERAL NOTES

Some bird records from western Pennsylvania.—Four recently collected specimens, now in the collection of Carnegie Museum, constitute records of distributional interest. Three of these were mist-netted at the Museum's Powdermill Nature Reserve, in eastern Westmoreland County, Pennsylvania, 3 miles south of Rector (the locality is shown as "Crisp" on many maps).

Yellow Warbler (*Dendroica petechia*).—A first-year male (cranium incompletely ossified) was taken on 25 September 1966, about a month later than the normal last departure date for this species in western Pennsylvania. It was seen to be an exceptionally dull and dark bird, and was therefore preserved as a specimen. Comparison with material at the United States National Museum showed that this specimen belongs to the Alaskan subspecies *D. p. rubiginosa* (Pallas). It is a good match for USNM 106,666, unsexed immature, Koowak River, Alaska, 10 August 1885, and for USNM 115,799, unsexed immature, Middleton Island, Alaska, 26 August 1888. The A.O.U. Check-list (1957) lists this distinctive subspecies as casual on migration only as far east as Mississippi. John W. Aldrich, however, has identified (initials on label) USNM 221,472, Washington, D.C., 12 October 1910, as *rubiginosa,* undoubtedly correctly. This record is listed as the "extreme departure date" for the District of Columbia by Stewart and Robbins (1958. *North American Fauna* No. 62:282). Any exceptionally late Yellow Warbler in the northeastern states should obviously be examined carefully. Several Florida specimens in the U. S. National Museum have also been labeled "*rubiginosa*" and at least one of these birds has been correctly identified. The Pennsylvania specimen appears to be the northeasternmost known record of *rubiginosa.* Griscom and Snyder (1955. "The birds of Massachusetts," Peabody Museum. Salem) listed four Massachusetts specimens as "*rubiginosa,*" but these were matched not with western Alaskan birds but with specimens from the Arctic Red River, Northwest Territories. Yellow Warblers from the latter area are not *rubiginosa*; they are currently assigned to *D. p. amnicola* Batchelder, but represent an apparently undescribed subspecies inhabiting the area from the west coast of Hudson Bay to the interior of Alaska.

Rose-breasted × Black-headed Grosbeak (*Pheucticus ludovicianus* × *P. melanocephalus*).—On 20 May 1966, a schoolboy, David Mertens, found a grosbeak, obviously ill or wounded, in Fox Chapel, Allegheny County, Pennsylvania. He took it to his teacher, Miss Beulah Frey of Fox Chapel High School. Miss Frey knew it to be an unusual bird, and arranged for its donation to Carnegie Museum. Upon autopsy it was found to have a subcutaneous tumor on the right side under the wing. The tumor has been preserved, but has not yet been studied. The bird appears in all ways to be a normal adult male Rose-breasted Grosbeak (testes enlarged, 9 × 14 mm), except that the normal rose color of the breast, axillars, and under wing coverts is replaced by a color nearest the Capucine Yellow of Ridgway (1912. "Color standards and color nomenclature."). It is quite possible that this represents simply an abnormal pigment condition. Examination of long series of Rose-breasted Grosbeaks from the eastern United States and Canada in several museums, however, failed to reveal a similar specimen. On the other hand, Dr. Lester L. Short, Jr., then of the Bird and Mammal Laboratories, U. S. Fish and Wildlife Service, showed me specimens he had collected in Nebraska indicating this "yellow-breasted grosbeak" pattern to be one of the phenotypes appearing in the area of hybridization between the Rose-breasted and Black-headed grosbeaks. Two of his specimens from this hybrid zone matched the Pennsylvania specimen quite well. There are several records of the Black-headed Grosbeak from the eastern United States, and it does not seem unlikely that birds from the overlap zone might as readily stray eastward as those from within the range of typical *melanocephalus*. The Pennsylvania bird, therefore, in the absence of evidence to the contrary, is identified as a member of the mixed Rose-breasted × Black-headed grosbeak population of the Great Plains region. West (1962. *Auk*, 79:399–424) has described this hybridization in some detail, and argues plausibly that these two forms should be considered conspecific, a viewpoint shared by several other recent authors.

Rufous-sided Towhee (*Pipilo erythrophthalmus*).—On 12 November 1966, a towhee, obviously of one of the western subspecies, was mist-netted at Powdermill. It proved to be a first-year male, with large skull "windows." It was compared at the U. S. National Museum with young males taken on the breeding grounds of the two easternmost, migratory subspecies of the "spotted" group, *P. e. arcticus* (Swainson) and *P. e. montanus* Swarth, both of which have been known to stray east of their normal migration routes. Females of these two subspecies are easy to distinguish, but identification of males, according to Phillips, Marshall, and Monson (1964. "The birds of Arizona"), is "risky." Careful study of young males in their first prebasic molt indicates that the head feathers of *montanus*, when fresh, show little or no brown edging, whereas such edging is present and conspicuous in *arcticus*. The flank color averages richer in *montanus*, and the latter race also generally has less white on the inner web of the outer rectrices than does *arcticus*. The rumps of young males of *arcticus* average browner, less gray than *montanus*. and there are more extensive brown edgings on the upper tail coverts of *arcticus*. The white stripes of the dorsum and the white wing-bars are usually more extensively washed with brown in *arcticus*. The Pennsylvania specimen has wing-bars that are purer white than those of most *arcticus*, but matches that subspecies in all other characters that distinguish it from *montanus*. The A.O.U. Check-list (1957) gave no records of *arcticus* east of Illinois, but Buckley (1959. *Auk*, 76:517–518) listed two specimens from New York and one from New Jersey, all females, as *arcticus*. It is noteworthy that all of the specimens mentioned by Buckley were collected in December, and that collected at Powdermill was taken two to three weeks after the last of the eastern *P. e. erythrophthalmus* have normally left the area.

Brown-eyed Junco (*Junco hyemalis*).—This English name is used in preference to "Slate-colored Junco," since the writer is one of those who believes that the *hyemalis* and *oreganus* subspecies groups belong to a single biological species. Individuals of the *oreganus* group are now seen and reliably identified almost annually in western Pennsylvania and adjacent areas during the period from late October through mid-March. One was banded at Powdermill by Robert C. Leberman on 20 March 1963. There are relatively few definite eastern records, however, for the population, intermediate in appearance between the two subspecies groups, to which Miller (1941. *Univ. California Publ. Zool.*, 44:329–345) applied the name *cismontanus* Dwight. The A.O.U. Check-list (1957) adopted Miller's concept of this subspecies, retaining it as a subspecies of *hyemalis* while calling *oreganus* (with which it admittedly interbreeds) a separate species. The first indication that *cismontanus* occurred in western Pennsylvania was a net-casualty taken at Powdermill on 28 October 1962. The true identity of the bird was not suspected until the specimen was being prepared. As is well known, first-year females of *J. h. hyemalis* are often extensively brownish, and the Powdermill bird was at first thought to be an individual of this type. Its cranium, however, was completely ossified, and its ovary compatible in appearance with that of an adult bird. Comparisons were then made with specimens in Carnegie Museum from the western Alberta portion of the breeding range of *cismontanus*, and the Powdermill bird was quickly seen to be referable to that form. Several other individuals assignable to *cismontanus* have since been seen at Powdermill; one was banded by the writer and A. C. Lloyd on 11 December 1966. Although *hyemalis* and *cismontanus* vary greatly in color in the fall, one character serves very well to identify females of *cismontanus* such as that collected at Powdermill. In *hyemalis* the gray of the breast continues (even if mixed with brownish) onto the flanks, giving a concave or horseshoe-shaped outline to the pigmented portion. In *cismontanus* the edge of the gray breast is convex, with pinkish-buff (sometimes mixed with gray) flanks contrasting abruptly with the edge of the gray breast area. There is usually more brown on the dorsal areas of adult females of *cismontanus* than of *hyemalis*, and it tends to contrast with adjacent gray areas rather than to blend with them. An excellent color photograph by Karl Maslowski of a junco showing *cismontanus* characters was published in the magazine *National Wildlife* (vol. 5, no. 1, December–January 1966–1967, p. 14).

Preservation of the specimens described above was made possible through the alertness and assistance of Robert C. Leberman, Albert C. Lloyd, Mary A. Heimerdinger, and Beulah Frey. The warbler and the grosbeak were prepared as study skins by Otto Epping, the towhee and the junco by the writer.—KENNETH C. PARKES, *Carnegie Museum, Pittsburgh, Pennsylvania, 16 January 1967.*

Two female Mallards incubating on one nest.—On 1 June 1956, I flushed two Mallard hens *(Anas platyrhynchos)* simultaneously from one nest site on an island in Unit 320 of the Lower Souris National Wildlife Refuge near Upham, McHenry County, North Dakota. At this time, I suspected that both hens may have been sharing a single nest. Upon investigation of the nearby nesting cover, I discovered a well formed nest containing 20 mallard eggs.

Additional confirming observations were made on 8 June and 12 June, and on the latter visit the nest contained only 17 eggs. On 17 June, I returned to the island and crawled within 6 feet of the nest enabling me to see both females sitting side by side in incubation before they flushed. The nest contained 5 hatched ducklings and 3 pipped eggs; the other 9 eggs were intact. Within 5 minutes after this visit, both hens returned to the nest.

The final fate of this nest was determined on 24 June: 9 eggs remained in the nest, five with 18–20 day embryos, three with undeveloped embryos and one with a full term embryo. Apparently when one clutch of eggs hatched, both hens departed with the brood leaving one clutch of eggs in the nest. During the next week, I observed a brood of 8 mallard ducklings near the island with two hens in attendance.

Factors leading to the expression of this unusual reproductive behavior are unknown. The dual nest occupancy may have originated from parasitic egg laying by one hen with mutual tolerance developing in incubation. Remarkable cooperation was required for these two hens to complete the many complex behavioral rhythms involved in egg laying and incubation on one nest.—HAROLD F. DUEBBERT, *U. S. Bureau of Sport Fisheries and Wildlife, Northern Prairie Wildlife Research Center, Jamestown, North Dakota 58401, 21 December 1966.*

A Swallow-tailed Kite in trans-Pecos Texas.—Due to rapid decline in numbers and decrease in range of the Swallow-tailed Kite (*Elanoides forficatus*) in recent years (Austin, 1961. "Birds of the world." p. 76; and Oberholser, 1938. "The bird life of Louisiana." La. Dept. of Conserv. Bull. No. 28:156) the following record is noteworthy. On 26 August 1966, we observed a Swallow-tailed Kite slowly cruising over downtown

Fort Davis, Jeff Davis County, Texas, just above the tree tops. According to Col. L. R. Wolfe (pers. comm.), the westernmost record of this species in Texas is from near Rockport, more than 400 air miles southeast of Fort Davis. The rarity of this species excluded the possibility of securing the bird as a specimen. We thank Dr. George M. Sutton, University of Oklahoma, for permitting examination of a specimen of the Swallow-tailed Kite.—R. ROY JOHNSON, *Department of Biology, University of Texas at El Paso* AND JANET E. JOHNSON, *308 Crane, El Paso, 30 January 1967.*

Osprey carrying bird. On 11 October 1966 while watching a hawk migration near the shore of Lake Michigan, about 30 miles north of Milwaukee, Wisconsin, we saw an Osprey (*Pandion haliaetus*) approaching from the north which appeared to be carrying something bright red. As the bird passed us it was at an altitude of about 60 feet and was about 150 feet west of us. With favorable light and with the aid of binoculars we were able to determine definitely that the object being carried was a red bird, presumably a male Cardinal (*Richmondena cardinalis*).—CHARLES SINDELAR, *1865 S. West Avenue, Apt. 5, Waukesha, Wisconsin,* AND ERROL SCHLUTER, *3701 S. Center Road, Waukesha, Wisconsin, 2 March 1967.*

Turkey nesting behavior.—Between 23 May and 4 June 1962, observations were made on a nesting Turkey hen (*Meleagris gallopavo*) in Vinton Township, Section 22, Vinton County, Ohio. The Turkeys in this area are presumed to be wild birds reintroduced in 1956 and 1957 by the Division of Wildlife (Sickels, 1959. Proc. First Natl. Wild Turkey Management Symposium, Memphis, Tenn.).

The nest, well concealed under a greenbrier (*Smilax* sp.) thicket at the base of a redbud (*Cercis canadensis*) tree, was discovered on 14 May 1962. The Turkey hen flushed directly from the nest when observed, knocked two eggs out, and flew out of sight to the south. The nest had 13 eggs in it.

On 23 May, at 6:30 AM, the hen was again flushed (she flew directly from the nest), and one egg was taken to determine the age of the embryo by comparing it with a known-age Turkey embryo series at the Waterloo Wildlife Experiment Station. The embryo was approximately 18 days old, which would place the start of egg laying on 23 April and the expected hatching on 2 June.

A pop tent blind was placed facing south 54 feet from the nest on 23 May. A total of 55 hours was spent in the blind during which time detailed notes were taken on nesting behavior and on the newly hatched poults.

The hen sat attentively on the nest, occasionally stood up in the nest, and apparently fed very little during the latter part of incubation. At one point in our observations (2 June), the hen was on the nest at 4:53 AM. She left the nest at 3:10 PM and returned one hour and 17 minutes later. If we assume she was on the nest at dark the previous day, this would make a total of at least 19½ hours of uninterrupted incubation.

The human disturbance factor should be mentioned, for the hen was flushed on three separate occasions. In addition, the blind undoubtedly influenced her behavior to some extent for she appeared to be aware of its presence by facing it during the observation period. When first discovered she was facing in the opposite direction. These disturbances, coupled with a jet plane breaking the sound barrier, a noisy vehicle passing on a nearby forest road on 2 June, and someone's shooting a shotgun five times one-half mile from the nest on 3 June, did not cause desertion. It was apparent that the hen under observation had a strong tendency to remain on her eggs. This is in agreement with Audubon's account (Bent, 1932. *U. S. Natl. Mus. Bull.* 162).

The blind was entered at 10:00 AM on 3 June. The first poult was observed at 11:00 AM, one day after the estimated hatching date. The hen raised her body slightly, and the poult walked out of the nest from underneath her. It appeared to be dry, and stayed close to the nest. The hen fed the poult for four minutes by picking up material she could reach from a sitting position, and placing it in the poult's mouth. The poult then returned to the nest.

Subsequent poult observations on 3 June were at 11:45 AM (three observed for 10 minutes), 2:20 PM (five observed for 15 minutes. and 2:45 PM (two observed for 15 minutes). In each of these cases the poults stayed close to the nest. During the 11:45 AM observation, the hen picked at her body and then the poults picked at the hen's mouth.

We left the blind at 4:10 PM. The hen was on the nest and showed no indication of leaving.

When we entered the blind at 5:15 AM on 4 June the hen was on the nest. At 8:00 AM a poult walked out of the nest from underneath the hen, followed by another poult. They picked at material around the nest and appeared to be more active, sometimes running four or five feet from the nest and returning. These poults were replaced by two more poults that exhibited the same behavior pattern. A crow (*Corvus brachyrhynchos)* flew over the nest area, called, and the poults immediately ran for cover under the hen.

On 4 June, at 9:15 AM, the hen without hesitation walked off the nest followed by four poults, and disappeared in the cover to the southwest. We left the blind at 9:45 AM to examine the nest. Two dead poults and six infertile eggs were found. The poults had apparently been stepped on by the hen.

This paper is a contribution from Ohio Pittman-Robertson Project W-105-R.—ROBERT W. DONOHOE, CHARLEY E. MCKIBBEN, AND CHARLES B. LOWRY, *Waterloo Wildlife Experiment Station, Ohio Division of Wildlife, New Marshfield, Ohio 45766, 23 January 1967.*

Incubation period of the Spotted Sandpiper.—A. C. Bent (1927, *U.S. Natl. Mus. Bull.* 142, Part I, 84) reports the incubation period of the Spotted Sandpiper (*Actitis macularia)* to be 15 days. Although Bent mentions no variations, I found the incubation period to vary normally from 14 to 16 days. In one case the incubation period was 18 days.

In the summers of 1959 through 1961 observations were made on Spotted Sandpiper nests on the farm of E. M. Burger, Niskayuna, New York. All nests were within 1,000 feet of the Mohawk River. Eleven nests were studied throughout the entire incubation period and were checked daily. In 10 of the nests both parents were often observed on or near the nest. In two nests the incubation period lasted 14 days, in one nest the incubation period lasted 16 days; and in the remaining seven nests the incubation period was 15 days.

On 16 June 1961 a nest was found 160 feet from the river under a squash plant. Three eggs were in the nest and both parents were nearby. The next day the nest contained four eggs. Thereafter only one parent was observed at the nest. This bird was marked with paint applied with a squirt gun. Although the nest was checked at least three times daily, the marked adult was the only bird observed on the nest. The lone parent was away from the nest in 22 out of 61 observations and it stayed away from the nest for up to 180 minutes at a time. The incubation period was 18 days for this nest. It is assumed that this increased time was due to the lack of normal incubation because of the presence of only one parent.—JOANNA BURGER, *Biology Department, State University College, 1300 Elmwood Avenue, Buffalo, New York, 12 December 1966.*

Reaction of Mourning Doves to cowbird eggs.—Friedmann (1963. *U. S. Natl. Mus. Bull.* 223:46–47.) reported that Mourning Doves (*Zenaidura macroura*) are occasionally parasitized by the Brown-headed Cowbird (*Molothrus ater*) but that there is no positive record of a fledgling being produced. In 1966 at Fremont, Nebraska, cowbird parasitism on several species was found to be heavy. The absence of parasitism in 110 Mourning Dove nests was very conspicuous. Therefore, eggs of cowbirds and Red-winged Blackbirds (*Agelaius phoeniceus*) were removed from Redwing nests and placed in Mourning Dove nests.

The following results were obtained:

M-31—On day eight of incubation I put in two Redwing eggs. They were there for three days. On the fourth day they were both broken on the ground directly under the nest.

M-21—A cowbird egg was added on day 15 of incubation. The Mourning Dove eggs both hatched, the cowbird egg remained on the nest for four days with three dove young. All were taken by a predator.

M-24—I put in a cowbird egg (incubated one day) between the laying of the first and second dove egg. The eggs were all taken by a predator on about the day when the cowbird should have hatched, 11 days later.

M-23—Two cowbird eggs were added on the fifth day of incubation. On the day when they should have hatched (11 to 12 days), one cowbird egg disappeared. The other was still present seven days later when the doves hatched and eventually was pushed off the nest by the growing young.

M-26—A cowbird egg was put in on day three of incubation; seven days later (day 11 of cowbird egg incubation) the cowbird egg was gone.

M-45—Two cowbird eggs were put in on day four of incubation; all eggs were gone on the following day.

From these few experiments it appears that Mourning Doves are tolerant to other eggs in their nests. In M-23 and M-26, cowbird eggs disappeared on the day when they should have hatched. It may be that these eggs hatched and the nestling cowbird was removed from the nest by the Mourning Dove.

I would like to hypothesize why cowbirds do not parasitize Mourning Dove nests more often, and if they do, why eggs and young are not found often in the nests. If eggs are laid in a nest, they may be knocked off accidentally from the frail platform nest of the dove. When doves leave the nests, they do so very quickly, and I have known them to knock their own eggs or young off the nest. The quick, fluttering take-off from the nest by the adult dove may knock off the cowbird eggs which are much lighter than dove eggs. I suspect this is what happened to the Redwing eggs in M-31. Mourning Doves stay at the nest site and leave for only short periods of time. I have very infrequently found an adult dove away from the nest in the morning hours when the cowbird would be laying her eggs. Friedmann (op. cit.) discusses reasons why a dove would have difficulty in raising a cowbird, the major reason being a difference in behavior of feeding young.—LARRY C. HOLCOMB, *Department of Biology, Creighton University, Omaha, Nebraska, 27 September 1966.*

Age of a female *Amazona festiva* at sexual maturity.—The age until sexual maturity for most species of Amazon parrots (genus *Amazona*) is unknown due to the difficulty in making relevant field observations, in acquiring young birds whose age is known, and in successfully breeding adults in captivity.

Some information is available for a few species. Boosey (1956. "Parrots, Cockatoos and Macaws," Camelot Press, London, pp. 38, 46) noted that he had to wait four years for newly acquired, "young," *Amazona aestiva,* and *Amazona leucocephala,* to show interest in breeding. Vane (1957. *Aviculture,* 63:183–188) kept a pair of *Amazona autumnalis* which started laying when they were "about three years old." The following observations were made on a captive female Festive Amazon (*Amazona festiva*).

The parrot was six months old when obtained by the author in Iquitos, Peru. It was 3.5 years old in January 1967. Since September 1965, the bird has been caged in a windowless room which varies from 21–24 C, and is usually dark from 000 to 0700 hours. It is fed a variety of seeds and fruits and appears healthy.

The bird is handled daily, and for the first time, on 5 December 1966, it demonstrated female soliciting behavior while perched on the author's hand. When stroked near the base of the tail under the wings, or around the cloaca, the bird crouched low pressing its breast against the palm of the hand, raised its tail exposing its cloaca which began to pulsate, rapidly fluttered its wings, and issued a previously unheard sound, like the "whimpering" of a dog. If stroked occasionally, this behavior was continued for up to 15 minutes, after which the bird 'lost interest.' This behavior was evoked almost daily, but became more difficult to elicit by early February 1967. After 12 February 1967, the bird no longer responded and did not tolerate the stroking.

Although the time until sexual maturity may be somewhat different for wild birds, this activity indicates that *A. festiva* females become sexually mature in their third year, not unlike closely related species. It should be pointed out that this breeding behavior was observed only during months which correspond to part of the rainy season in the Peruvian Amazon basin (November–March), the time when much avian breeding activity occurs (G. Cetraro (pers. comm.), and personal observation).—Lawrence E. Licht, *Department of Zoology, University of Texas, Austin, Texas 78712. (Present address: Department of Zoology, University of British Columbia, Vancouver, B.C.). 1 March 1967.*

Budgerigars are not determinate egg-layers.—Possible factors regulating the species-typical clutch sizes of determinate and indeterminate egg-layers are extensively reviewed by Lehrman (1961. *In* "Sex and Internal Secretions," Vol. 2, W. C. Young, ed.; Williams and Wilkins Co., Baltimore, Md.: pp. 1268–1382) and by van Tienhoven (ibid., pp. 1088–1172). Egg removal may prompt an indeterminate female to continue oviposition by preventing or delaying her incubation behavior, thereby inhibiting necessary hormonal changes which stop egg production. Or, the number of eggs in an indeterminate female's nest may act independently as a tactile or visible stimulus in the neuroendocrinological regulation of her ovarian activity. In contrast, the species-typical clutch size of a determinate female (i.e., her ovarian activity) is, genetically, determined by her internal physiological state and is not regulated by her performance of incubation behavior or by such external stimuli as the number of eggs in her nest.

Budgerigars (*Melopsittacus undulatus*) have been classified as determinate egg-layers (van Tienhoven, op. cit.; p. 1144). However, other, anecdotal, information suggested otherwise. Accordingly, it seemed worthwhile to investigate this apparent contradiction.

Budgerigars do not build nests but generally use a cavity (e.g., a nestbox) in which to lay a typical clutch of four to seven eggs. They lay an egg every other day and begin incubation with their initial oviposition.

Two groups, each consisting of eight heterosexual pairs, were studied. Females of Group A were permitted to retain and incubate the first egg they laid. Subsequent eggs were removed within eight hours following oviposition. Females of Group B were not permitted to retain any eggs: again, eggs were removed within eight hours following oviposition. Consequently, females of Group B were never exposed to the presence of an egg in the nest nor permitted to incubate an egg for more than eight hours at a time.

Results were clear-cut. All females of Group A laid only the species-typical number of eggs per clutch. Each female's ovary, when examined by laparotomy on the third or fourth day after her last oviposition, contained only small follicles (2.0 mm or less in diameter) typical of the inactive non-breeding state. All females of Group B continued to lay eggs until the arbitrary termination of this study, after each female had laid 20 eggs. Laparotomies of Group-B females, on the fourth day after each had laid its twentieth egg, showed that each female still possessed an active ovary containing large follicles of various diameters (8.0 mm or less). Indeed, in the interval between being removed from their breeding cages and the day of laparotomy, six Group-B females had laid an additional, twenty-first egg.

These findings indicate that the cessation of full ovarian activity and egg-production by female Budgerigars may be influenced by the performance of incubation behavior and/or conditions within the nestbox. Therefore, I would suggest that Budgerigars be reclassified as indeterminate egg-layers.

The author is indebted to Mrs. M. Goodrich and Mr. W. Schubach for help during this study. This study was supported by Grant GB-3191 from the National Science Foundation.—Barbara F. Brockway, *Department of Zoology and Entomology, The Ohio State University, Columbus, Ohio. (Present Address: 2175 Tabor Drive, Denver, Colorado.) 2 March 1967.*

A territorial encounter between Screech Owls.—While studying Screech Owl (*Otus asio*) population density on the night of 28 June 1965, at 10:30 PM Hardy Stebbins and I stopped at an oak woods northwest of South Bend, Indiana and observed a territorial encounter between two owls. After our giving only three imitations of an owl call, a gray phase owl responded from 10 m away. This owl flew about 74 m farther away upon our approach with a net. Our second approach flushed the owl about 42 m farther and after a few minutes it was forced about 122 m into the territory of another Screech Owl. The low monotone call of the first owl and our own imitations probably brought in the other owl, whose call descended the scale. As the two owls moved closer together, the quality of their calls changed. During three years of owl-calling I have never heard so many unusually low, angry-sounding, and ominous calls. The first owl was seen 9 m off the ground when the second owl came diving in out of the darkness and struck it on one side. Thereupon they grasped one another and tumbled to the ground, then separated, and flew off in opposite directions. A moment later the owls again moved toward one another giving their unusual calls. We could tell that a fight was about to occur when the calls became increasingly ominous and angry-sounding. The second and third fights were not observed directly, but the owls could be heard tumbling through the leaves to the ground. Finally, the first owl moved back to its original location, and the calling of both owls then diminished rapidly.—Scott C. Rea, *952 Riverside Dr., South Bend, Indiana, 10 January 1967.*

Radiosensitivity of Song Sparrows and Slate-colored Juncos.—The effects of ionizing radiation have been studied on few species of birds. This report adds data about the sensitivity of two species of North American Fringillidae to the lethal effects of exposure to X-ray.

Song Sparrows (*Melospiza melodia*) and Slate-colored Juncos (*Junco hyemalis*) trapped wild near Ithaca, N. Y. were the main subjects of the study. They were obtained by intermittent trapping from mid-March to late April, 1964. The birds were maintained in outdoor, sand-floored, wire cages measuring 6 feet by 9 feet by 6 feet high. Corrugated aluminum sides, ends and top protected one-third of each cage. Cracked corn, cracked wheat, and water were provided at all times with some "wild-bird seed" added most of the time. Confinement of one to six weeks preceded irradiation, usually with groups of 20 or less per cage.

For irradiation the birds were transported in large cloth bags to the Large Animal

Table 1

Mortality Data

Day of death post-irradiation	Song Sparrow		Slate-colored Junco	
	800r	1000r	800r	1000r
3	2 males soiled vent 1 female soiled vent 1 female no symptom	1 no observation 1 male soiled vent		
4	1 male soiled vent pale liver 1 male soiled vent			
5		1 female no symptom		
6		1 male soiled vent 1 no observation		
7		1 no observation		
8				1 female liver pale internal bleeding, clots
9	1 female liver pale gut enlarged, flaccid			
10			1 male large clot in neck, many coelomic nematodes	2 females liver pale 1 with internal clots 1 gut enlarged, flaccid
11		1 no observation	1 female no symptoms	1 male liver pale gut enlarged few coelomic nematodes
12		3 no observations		
13		1 no observation		1 female liver pale
18				1 male liver pale

Clinic of the New York State College of Veterinary Medicine where they were restrained in cloth baby socks which were pinned to a wooden table. Radiation was from a Picker Vanguard X-ray machine (280 Kvp, 20 ma, HVL 1.5mm copper). A dose rate of 90 roentgens/minute was measured in air with a Victoreen r-meter (a thimble ionization chamber). Immediately following exposure to 800r or 1000r the birds were removed from the socks and transported in the bags back to the cages. The total time from cage to return ranged from 40 to 75 minutes.

As a preliminary experiment two juncos, a Tree Sparrow (*Spizella arborea*), and a Fox Sparrow (*Passerella iliaca*) were given a dose of 1000r. The Fox Sparrow died on the third day and a junco on the thirteenth day. On the basis of these results 14 Song Sparrows were given a dose of 1000r and another 14 sparrows were given 800r. Of the 14 given 1000r, 11 were dead within 30 days following irradiation. Seven of the 14 given 800r died within 30 days. Of the five birds kept as controls and handled exactly the same (except that while in the socks they were not irradiated), one died on the eleventh day of the experiment. It showed no obvious cause of death.

Eight juncos were exposed to 1000r and another group of eight to 800r. Six of the 1000r group died within 30 days, while only two of the 800r group died in the same period.

Because of the limited numbers of birds involved, these data must be considered as no more than suggestive. The $\text{LD}_{50/30}$ (dosage producing death to 50 per cent of test birds within 30 days) for the sparrows is about 800r and for the juncos about 900r as indicated by a logarithmic probability plot. Table 1 summarizes the times of death and some observations of possible causes of death. For various reasons circumstances were unfavorable for examination of some specimens for determination of sex and possible causes of death. The "soiled vent" term in the table refers to discolored feathers around the vent, presumably caused by diarrhea. In several autopsies the "soiled vent" was found associated with gut abnormalities. In a limited supplementary study it was found that the "pale liver" condition was associated with a low red blood cell count. From the earlier deaths and the greater incidence of apparent diarrhea, there is the indication that the gastrointestinal tract of the Song Sparrow may be more sensitive to the irradiation than that of the junco.

I would like to acknowledge the following of Cornell University whose help made this study possible: Dr. C. G. Sibley for use of cages; Dr. R. Slusher and his staff for administration of the X-ray; and Dr. A. P. Casarett for suggestions, help and encouragement throughout. The work was conducted while the writer participated in the 1963–64 NSF–AEC supported Academic Year Institute in Radiation Biology at Cornell University.

—Franklin W. Sturges, *Biology Department, Beaver College, Glenside, Pa., 29 November 1965.*

THE PRESIDENT'S PAGE

This year will bring the 80th anniversary of this organization, which was founded on 3 December 1888 as "The Wilson Ornithological Chapter of the Agassiz Association." Its first publication was *The Curlew*, which soon became *The Wilson Quarterly* and, eventually, *The Wilson Bulletin*. During the first 25 years of its existence, members of the Wilson Ornithological Club, as it came to be known, knew the organization solely through its quarterly journal. For not until 1914 was there an Annual Meeting of this society.

In this connection, it is revealing to read now the comment which the Editor of *The Auk*, Witmer Stone, made on the subject (1914. *Auk*, 31:290–291): "The first of the proposed annual meetings of the Wilson Ornithological Club was held in Chicago on February 5 and 6, 1914, and plans were formulated for similar annual gatherings at points in the middle section of the country. For an initial gathering it was well attended and the business done will mean much for the cause of ornithology throughout the region which the club especially covers. Such a movement will, we feel sure, prove of immense benefit to the A.O.U. and will pave the way for a meeting of the latter body in Chicago or vicinity some time in the near future." Dr. Stone's words were prophetic. For, in October 1922, the A.O.U. held its first Middle Western meeting, in Chicago.

Meanwhile, the early-1914 Chicago meeting of the Wilson Club appears to have been so successful that the club held a second meeting there that same year. Yearly meetings have followed, except in the war years (1918 and 1942–1945, inclusive) and in 1933 and 1948. By states and the Province of Ontario, our Annual Meetings have numbered as follows: Illinois, 9; Ohio, 5; Michigan, 4; Tennessee, 4; Missouri, 3; Pennsylvania, 3; Indiana, 2; Iowa, 2; Minnesota, 2; West Virginia, 2; Kentucky, 1; Louisiana, 1; Maine, 1; Nebraska, 1; New Hampshire, 1; New Jersey, 1; New York, 1; Oklahoma, 1; Ontario, 1; South Carolina, 1; South Dakota, 1; and Wisconsin, 1.

Our most recent Illinois meeting was held in Urbana in 1941. It is both opportune and appropriate that, in the 80th year of our society's existence, we should hold our 49th Annual Meeting at Southern Illinois University, in Carbondale, during 2–5 May 1968. And we may hope that "the business done will mean much for the cause of ornithology"—without restrictions as to its geographical application.

Aaron M. Bagg

ORNITHOLOGICAL NEWS

Many years ago the Editor came into possession of his first real ornithological book, W. E. C. Todd's "Birds of Western Pennsylvania." While I was duly appreciative of Mr. Todd's compilation of ornithological data, I was greatly impressed by the wonderful set of paintings that illustrated this work. It was my first encounter with the name of George Miksch Sutton, but it was not to be my last. Not too long after that I learned that some of my classmates actually *knew* this perceptive artist. After all he was, for a time, a resident of our native state. However, it was not until many years later that I met George Sutton, but in the intervening years I had heard much of him. Mostly I heard of him through the Wilson Ornithological Society. He was the President when I joined the Society, he was one of the outstanding Editors of *The Bulletin*. In fact for many years George Sutton, and Wilson Ornithological Society have almost been synonymous. In May of 1968 George Sutton will celebrate his 70th birthday, a fact that most people who know him find extremely hard to believe. To honor him on this occasion and to show the appreciation of the Society for his long and faithful service to it, Volume 80 of *The Wilson Bulletin* in 1968 will be in part devoted to a continuing symposium on arctic ornithology. There is little doubt that George Sutton's great love has been the Arctic, and he has contributed much to our knowledge of arctic birds. This series of papers, then, seems a most appropriate way of wishing George Sutton a Happy Birthday.—G. A. H.

John W. Aldrich of the Bureau of Sport Fisheries and Wildlife has been awarded a "Citation for Distinguished Service" by the Department of Interior. The citation, by Secretary of the Interior Stewart Udall, cites Dr. Aldrich's many contributions to conservation education as well as to the advancement of science.

Roger T. Peterson is spending the months of February and March as the first Distinguished Scholar in Residence at the Fallingwater estate, an educational and cultural center of the Western Pennsylvania Conservancy.

The Asa Wright Nature Center in the Northern Range of Trinidad was dedicated on 5 November 1967. This first neotropical nature center consists of nearly 200 acres, partly in cultivation. The colony of Oilbird (*Steatornis*) on the property is the most accessible one known. The center has facilities for lodging and meals for amateur naturalists, students, and professionals engaged in research. Details can be obtained by writing (air mail): The Manager. The Asa Wright Nature Center, Spring Hill Estate, Arima, Trinidad, W. I.

Mr. Humphrey A. Olsen, 416 Franklin Street, Cambridge, Massachusetts 02139, is preparing a book on Alexander Wilson. He would appreciate any information about letters, drawings, etc. by Wilson that our members might have.

The colored frontispiece was subsidized by a generous contribution by a member of the Society.

LETTER TO THE EDITOR

EFFECTS OF COLORED LIGHT ON OVIPOSITION IN JAPANESE QUAIL

Hosick (1966. *Wilson Bull.*, 78:434–443) has attempted to assess the effects of colored light upon oviposition in the Japanese Quail (*C. coturnix japonica*). The summary states that "intensities at which laying took place were found to be independent of light color." For a number of reasons this assertion is totally unjustified on the basis of the experiments reported.

Using wide-band cellulose filters across a low wattage tungsten source at one end of the cage, the author noted the number of eggs laid at various distances from the source. The "intensities" along the illumination gradient in the cage were measured with an unspecified photometer. Graphs (Fig. 4, p. 438) were then made of the number of eggs in each measured "intensity" range for each of five colors of filters employed. Most of the eggs were laid at the dark end of the cage.

To begin with, "intensity" is an entirely ambiguous term in this experiment. "Intensity" can refer to the source or stimulus (measured in energy or number of quanta per unit time), or it can refer to the stimulative effect on the receiving organism. Since the latter depends upon the spectral sensitivity of the receiver, which is unknown for quail (and is presumably being determined in this experiment), the proper measure of intensity should have been radiometric (i.e., energy or quantum flux). The measurements given in the paper are in foot candles, which is a photometric unit related to the spectral sensitivity of man. Two stimuli of different wavelengths having the same photometric intensity (brightness) will appear equally bright to a human observer, whereas the same two wavelengths having identical quantum intensities will not (except for certain pairs of wavelengths to which the eye is equally sensitive).

If one assumes that the quail's spectral sensitivity is identical with that of man, a photometric measure would be acceptable (as a measure of apparent brightness to the quail). Even granting this unlikely assumption, the reported experiment is ambiguous because of another source of error. Nearly all photometers have a spectral sensitivity different from that of man's eye (most photometers are far more sensitive at shorter wavelengths than is our eye). The foot-candle calibration on these meters may be used only for white light, and then the values are only approximate. Therefore, the "intensities" used in this experiment with colored lights are entirely meaningless: they correspond neither to physical intensities nor to subjective brightness intensities.

It is impossible from the data given to compute even a rough estimate of the effect of color upon oviposition. There are two ways in which this might be done, but both require further information: the spectral transmission curves of the filters plus either the spectral output of the source or the spectral sensitivity of the meter used.

There are additional matters for concern about the experiments on colored lights, and some of these matters also apply to the experiments with white light. For instance, there are no statistical analyses of any data given. The histograms of Figure 4, which plot the number of eggs versus the "intensity" for each of the five colors of illumination used do *not* appear to be identical. Picking the data from the published histograms, I cast the values into a one-by-two table for each color: number of eggs at "intensity" range 0.5 to 2 versus eggs at 2 to 20 units. (The lumping is necessary because of the low expected values in each of the separate categories within this range. The lumping, by the way, biases the comparison *away* from establishing any differences.) Each 1 × 2 table was then compared with all the others in turn, so that 10 comparisons were made between pairs of colors. The 2 × 2 tables thus formed were tested with the standard Chi-square method.

The results show that three of the 10 comparisons were indeed significant (two with probabilities less than 0.005) and a fourth comparison nearly significant (p between 0.10 and 0.05). Thus, despite that statistical method that biases the outcome away from providing a difference, the distribution of eggs in violet light is significantly different (or nearly so) from the distribution of eggs in all other colors. (Other differences might also prove significant with a more sensitive test.) In sum, even if the "intensity" given is taken to mean something, the position of laying is not proven independent of color.

Apparently the author concluded that there were no differences due to color because the modes in all of the histograms occur at the lowest "intensity" provided. This fact seems to indicate only that the wrong range of illumination was chosen for the experiments, since the hens always laid in the darkest place provided. Would complete darkness be yet preferred over these low illumination levels?

Actually, all the histograms are grossly misleading due to the unequal amounts of floor-space available in each intensity range plotted on the graphs. The diagram of the apparatus (Fig. 1, p. 435) shows that in more than half of the area of the cage the illumination was less than 2 "foot-candle" units. The histogram for violet light in Figure 4 shows that about 26 eggs were laid at less than 2 units and about 32 eggs at greater than 2 units. Therefore, my conclusion about intensity for this graph is just the opposite from that of the author. The measure employed should not have been the number of eggs at each "intensity," but, rather, the number of eggs *per unit area* at each "intensity." Thus, the 60.8% of eggs laid at less than 2 units (Fig. 2, p. 436) were laid in roughly 60 per cent of the total space available at any intensity, which fact practically eliminates the claim for any effect of intensity at all!

Finally, it might be mentioned that a number of important parameters of the experiments are not specified. For instance, how long was each experiment run: for a set number of days, or until a certain total number of eggs had been collected? Of the "approximately twenty birds to a cage" (p. 434) how many never laid an egg? Were the modes due to a few prolific individuals? The fact that "several of the female quails were becoming blind" (p. 440) during the tests is more than mildly disturbing.

In sum, the author's two main conclusions appear to be just the opposite of what the data may show, namely, (1) that it *cannot* be proved that quail prefer the lowest illumination provided, and (2) it *can* be shown that differences occur between the experimental groups with different colors (although what these differences mean must be left unresolved).

I am indebted to Drs. Wolfgang Schleidt and Douglass Morse for discussion concerning these matters: responsibility for the above comments is, of course, mine.—JACK P. HAILMAN, *Department of Zoology, University of Maryland, College Park, Maryland.*

ORNITHOLOGICAL LITERATURE

THE WILD TURKEY, ITS HISTORY AND DOMESTICATION. By A. W. Schorger. University of Oklahoma Press, Norman, 1966: 6¼ × 9½ in., xiv + 625 pp., 1 col. pl., 48 bl. and wh. pls., 20 figs., 34 tables. $10.00.

The great American bird known as Turkey has had a tremendous influence on the culture and economy of both primitive and civilized man. Native to the temperate regions of North America, the Turkey was domesticated by the relatively highly civilized Indians of Mexico and subsequently has spread all over the world in numerous domestic varieties.

A. W. Schorger, by his characteristically patient and exhaustive search of the literature, has brought to light an enormous amount of information on the history and biology of this extraordinary bird. The rapid-fire citation of references, although related to each other under general headings, is not conducive to a smooth flow of ideas. However, the author has handled this type of presentation skillfully.

The format of the book is attractive and it is adequately although not liberally illustrated by appropriate photographs and line drawings. One plate in color by Owen J. Gromme depicts three gobblers in a woodland setting.

In Europe, before the discovery of America, any large bird which spread its tail, including the Capercaillie, came to be known as "turkey." Most of these were probably peafowl which may have received that name because it was known to have reached Europe via the trade routes from the Orient through the general region then known as "Turkey." Later when the American bird, which we now know by that name, was taken to Europe by the Spanish explorers and later reached England, it likewise appears to have been confused with the peacock and acquired from it the name turkey.

During his march to Mexico City, Cortez found domestic Turkeys in practically every town, and early explorers found them confined extensively in pueblos of the Indians in what is now the southwestern United States.

On a map of original ranges of Turkey subspecies in the United States and Canada, the extension of the Rio Grande Turkey up the Pecos River to meet the Merriam's Turkey in southeastern New Mexico is questionable as is also the extension of the range of Merriam's Turkey down the Canadian River in eastern New Mexico to meet the Rio Grande Turkey in the short grass plains of the Texas Panhandle. There would seem to be no reason for assuming that Merriam's Turkey was formerly any less confined to mountain habitats than at present.

The map of original distribution of wild Turkeys in Mexico, based on extensive and difficult literature search, is a valuable contribution to our knowledge. It eliminates the disturbing gap in the range of the southern race (*gallopavo*) shown on maps in other recent publications.

Attempts to estimate pre-Columbian Turkey populations by state are an interesting exercise but seem rather futile in view of the difficulty experienced by modern game managers in the same states with the much more reliable information available today.

In the field of classification, the fossil record of extant and extinct species of turkey is described. Taxonomic affinities of modern turkeys based on morphological characters, hybridization tendencies, and protein relationships are discussed. Generic distinctness of *Meleagris* from *Agriocharis* is considered justified but no opinion is offered as to the distinctness of the family Meleagrididae from Phasianidae.

In discussing the much debated application of Gould's *mexicana*, despite a question over the type locality, Schorger came to the logical conclusion that, based on measurements of the type specimen, *mexicana* is referable to the large Turkeys of the Sierra Madre Occidental of Northwestern Mexico, not the small bird of the mountains in the latitude of Mexico City.

Schorger believes that there probably are few wild Turkeys in the United States today without some admixture of domestic blood because of the considerable amount of opportunity for interbreeding. This concept appears to overlook the principle of natural selection. Leopold (1944) produced evidence of genetic characteristics of "wildness" in wild Turkeys not found in domestic birds. These traits, presumably, are selected for survival by the wild Turkey's exacting environment. Birds with characteristics that might result from crossing with domestic stock would tend to be eliminated before reaching reproductive age. Evidence both for and against this thesis is given in the chapter on characteristics but no proof is shown that either domestic Turkeys or those of mixed blood have become established as wild birds in other than semi-domestic environments or notably predator-free areas such as the Hawaiian Islands.

Interesting evidence of inborn fear of predators among pure wild Turkeys was shown by an experiment in which a silhouette model having a short neck and long tail when moved in view of young Turkeys in a normal fashion simulating a hawk aroused the birds to fear; when pulled tail first, "simulating a goose," they showed no fear. There seemed to be general agreement in references cited that wild Turkeys could not be thoroughly domesticated in one generation. Successive generations in captivity produced tamer birds. Presumably, selection of more tractable individuals was involved.

The author points out the great variety of environments occupied by Turkeys in different parts of their range and different times of the year. He then proceeds to show that different races of Turkey seem to have quite limited tolerance for environmental conditions and that their ranges tend to fall rather neatly into regions having different amounts of precipitation.

One chapter is devoted to management and there is a wealth of citation of pertinent published information under such subjects as legal protection, winter feeding, food planting, controlled burning, water supply, rearing in captivity, standards for wild Turkeys, capture of wild birds for restocking, drifting following release, determination of sex and age, and population census. Causes of Turkey mortality such as predation, weather, accidents, diseases, and parasites are documented in detail and will serve as a valuable source of reference for wildlife managers. A conclusion was reached that successful management of Turkeys is tied to good wild stock and a range of adequate size and quality. Since wild Turkeys will not breed successfully in captivity, this means transplanting from wild stock to increase range. Although the author states in his preface that management is treated very lightly because it is aside from his main objective, much of significance in this field is included not only in this chapter but in those on other subjects particularly on restoration and introduction. In fact, the book is a well-balanced monograph on the wild Turkey from all aspects.—John W. Aldrich.

The Bird Faunas of Africa and Its Islands. By R. E. Moreau. Academic Press, New York, 1966: 6 × 10 in., viii + 424 pp., 65 figs. (photos and diagrams). $18.00.

No more timely book on African ornithology has appeared in recent years than Mr. Moreau's "Bird Faunas of Africa." To those of us fortunate enough to have witnessed African birds and lived with them, the full breadth of this book should at once be apparent. It is more than just an account of the composition and origins of the bird faunas of Africa; the subject matter covers nearly every aspect directly or indirectly affecting the bird life for the past 100 million years.

Early in the book a distinction is drawn between birds of evergreen forests and birds of other habitats; and also between lowland and montane species. Within each of these categories, there is a further subdivision into five groups: (1) water-bird families, (2) raptors and owls, (3) game and other ground birds, (4) other non-passerines, and (5) passerines. With these divisions in mind, the reader is better able to comprehend the zoogeographical effects of the different habitats on their respective faunas. Indeed, these divisions reflect the logical approach of the entire book.

It is possible to detect a history of rapid speciation among African birds. The history of the African continent too is shown to be one of rapid and considerable changes, even within the last ten or twenty thousand years. Only 12,000 years ago, for instance, the distribution of montane birds was apparently much more extensive than it is today. Changes are at present being effected by man who seems to be busy devastating the African continent at great cost to its wildlife. In the Foreword (which is, incidentally, the best and most competent review of the book!) Moreau draws our attention to this. "By the time the Africans are ready," he says, "to become amateurs of field biology most of them will have to scrabble about in the ruins of their fauna and flora, as everyone else in a 'developed' country must do . . . ." I think that the devastation of Africa is perhaps not yet widely acknowledged by the rest of the world. Today we can still study the "grand designs" of African biomes; we are privileged to have the scholarship of Moreau to produce for us this book at this time, for tomorrow may be too late.

The breeding seasons of African birds have long been studied by Moreau in East Africa, so that it is not surprising to find in Chapter 2 an account of African climates and vegetation types and an analysis of how these affect avian breeding seasons. The bird faunas of a selected number of African vegetation types are outlined in Chapter 15, for the most part very adequately, but it is a little disappointing that the section on the Kalahari neglects the excellent information provided by Smithers' "Check List of the Birds of the Bechuanaland Protectorate" (1964). Even if this part of Moreau's manuscript was already complete by 1964, it would have been as well to revise it. The South African bird faunas have been somewhat neglected; this may have been deliberate, since they are so well covered elsewhere in the literature. The emphasis placed on North and East Africa is understandable in view of Moreau's long personal experience in these regions.

The grand designs of the African biomes are frequently and enlighteningly compared with corresponding biomes in other parts of the world—such far-flung places as North and South America, the Palaearctic Region, Australia, and India on the broad scale, with narrower comparisons with Arizona, the Thames Valley, and Spain. The comparisons between the bird faunas of the Palaearctic and Ethiopian Regions are particularly relevant in terms of actual species composition in the area north of the Sahara, while a comparison of Somaliland with Arizona indicates the wealth of ground birds in Africa.

The biological poverty of West Africa, when compared with the rest of Africa south of the Sahara, is a fact that emerges repeatedly. Only South America, among the larger land masses, has an avifauna richer in species than has Africa south of the Sahara. The richness of these two continents reflects their large tropical areas which provide more ecological niches than do more temperate regions.

As with the African continent, so with the islands. The chapter on Madagascar is totally fascinating. How many ornithologists are aware of the existence of *Coua cursor*, a terrestrial cuculid of the subdesert regions of Madagascar, recalling the Roadrunner

(*Geococcyx californianus*) of America? Following the accounts of the island bird faunas is a chapter discussing them in some detail. It is interesting that the adaptive radiation within groups of African island birds is not as extensive morphologically as in the Galápagos and Hawaiian Islands.

What this excellent book has done (and it is, I believe, what it set out to do) is to summarize our present state of knowledge and to indicate very clearly where the more important gaps occur. The problems raised are challenging and often quite as intriguing as the facts presented. The few minor typographical errors (is it "Socotra" or "Sokotra" (pp. 302–303): and is it "Gillmore" or "Gillmor" (pp. 105–109) ?) and the mistaken substitution of "miles" for "km." in Figure 23 do nothing to detract from the immense value of this book. The Bird Faunas of Africa and Its Islands is a work conceived and executed on a grand scale.—Gordon L. Maclean.

A Field Guide to the Birds of New Zealand and Outlying Islands. By R. A. Falla, R. B. Sibson, and E. G. Turbott. Houghton Mifflin Company, Boston. 1967: 4½ × 7½ in., 254 pp., 18 pls. (6 col.) and 63 line drawings by Chloe Talbot-Kelly. $6.95.

Nobody knows better than I the need of this Peterson-type field guide for New Zealand. On a recent sojourn for birds in that country I had to refer repeatedly to as many as four different publications in combination for nomenclature, description, vocalizations, distribution, habitat, and breeding habits. Now, belatedly, here is all information between two covers—and in generous amount.

In preparing this book, Messrs. Falla, Sibson, and Turbott have not been forced to skimp on facts and condense phrases to the intelligible minimum as have the authors of similar guides to continental birds. With only 200 or so species, including those on the outlying islands—from the Kermadecs in the north and Chatham on the west to Macquarie in the south—they have had enviable space in which to introduce each bird family and to give details about each species. This is not to say that they have resorted to discourses and essays. Their writing is tightly composed and their factual material judiciously selected.

Descriptions of all species are satisfactorily thorough, with appropriate emphasis on the more obvious features useful in identification. For the endemic species, the write-ups take up a page or more, giving fact-filled summations of range and status, habitat preferences, food and feeding habits, history since human settlement, and nesting data. Such highly unique New Zealand forms as kiwis, the Weka (a flightless rail), Wrybill (a plover), Kakapo (a nocturnal parrot), Kea (mountain parrot), wrens (acanthisittids), and wattle-birds (callaeids) get extensive treatment. Even so, the winter visitants and the many introduced and now well-established birds receive a large share of attention. All in all, the book proves to be much more of a reference work than one would expect of most field guides.

For all conservationists, a happy message keeps emerging from many accounts of endemic species. As summarized in the preface: "The decline in many native birds, so marked in the nineteenth century, seems to have been arrested. Most in fact are holding their own; some have turned the corner and are utilising new habitats, such as hydro-electric dams, reclaimed salt-marshes, man-made forests of exotic pines, swamp-lands now choked with willow and alder." Though the authors do not tell us, a large part of this improvement is due to aggressive measures undertaken by government agencies for the expressed purpose of protecting and restoring native bird life.

All the species are exceedingly well illustrated. My only criticism is the arrangement of the plates which, though numbered, are widely scattered and hard to find *from references in the text.* Had the plates been "ganged" in one place or had the references to plates borne their opposite page numbers, they could be easily located. As it is, with only the plate number for reference, the reader cannot tell whether the plate is among the pages ahead or behind and consequently has to thumb through the pages in both directions to find it.

This most welcome guide is sponsored by the Ornithological Society of New Zealand and is essentially a compilation drawn from detailed observations and extensive field studies—many commendably penetrating—by scores of the Society's 900 members. Its consequent excellence is a great tribute to all of them as well as to the competence of its authors.—OLIN SEWALL PETTINGILL, JR.

ANIMAL BEHAVIOUR. By Robert A. Hinde. McGraw-Hill Book Company, New York, 1966; 6 × 9¼ in., x + 534 pp., 122 figs. $10.50.

The intent of the author in writing this book has found succinct expression in its subtitle, "A Synthesis of Ethology and Comparative Psychology." He has attempted to bring together the methods and findings of psychology, physiology, and ethology in those areas where these disciplines overlap. Whether a synthesis has been achieved is a moot point, due largely to methodological and terminological differences among these fields. The author's efforts have resulted in a thorough, scholarly, critical presentation of the major findings upon this common ground.

"Animal Behaviour" is not a textbook for an elementary course in the behavioral sciences. Coverage of selected topics in depth, and the concomitant assumption of considerable familiarity with the disciplines under discussion, render it unsuitable as a text in all but the most advanced courses. The addition of a glossary of technical terms would have extended its usefulness somewhat.

It is, however, a valuable tool for the serious student of animal behavior. Discussion of controversial topics is, in most instances, keen, critical, and stimulating. Of equal heuristic value is the author's attention to important topics about which we know little and which are deserving of study. The reference list is thorough and up-to-date.

Causation and development of behavior, both taken in the broadest sense, constitute the two principal sections of this work. A brief discussion of the aims and methods of animal behavior study introduces the text, and an outline of some of the evolutionary aspects of behavior constitutes the fourth and final section. There are 28 chapters in all, and the topics discussed in each are numbered, facilitating reference use of the book. In addition, most chapters end in a clear summary of major points.

The text is illustrated by figures of varying quality, most taken from the literature. Some are well presented but others suffer from poor reproduction, both as regards darkness and size of reproduction, the latter bearing little relationship to the complexity of the figure. Complex figures are sometimes too small for easy comprehension, and simple figures are very large indeed, in some cases more than twice the size they enjoyed in the original work. More serious is the lack of sufficient explanation for a few figures, in either caption or text: these will not be of much use to the reader unless he consults the original source.

This book has been well proof-read, and there are very few errors for its size. The author index and subject and species index add greatly to the usefulness of this volume.

The recent trend in cross-disciplinary sharing of techniques and approaches by students of behavior has been hindered by the difficulty of communication between scientists whose jargon and methods differ. However, nowhere has this trend proved more fruitful than at the Sub-department of Animal Behaviour at Cambridge. Animal Behaviour is in some sense a product of this fruition and at the same time an important step in its promulgation on a wider scale.

Dr. Hinde has done a truly impressive job, showing a remarkably broad grasp of the several disciplines in the behavioral sciences. Any serious student of animal behavior will want to read, and own, this volume.—D. W. Dunham.

Singing Behavior and Its Development in the Song Sparrow Melospiza melodia. By James A. Mulligan. University of California Publications in Zoology, Volume 81; University of California Press, Berkeley and Los Angeles. 1966: 76 pp., 23 figs. (graphs and diagrams), 9 tables. $2.00.

Mulligan's study is one of the most comprehensive of the many valuable papers on bird song which have come from Peter Marler's former group at Berkeley. The Song Sparrow is a challenging species because of the remarkable variety of songs given by each individual. Mulligan describes the song in resident populations of three races in the San Francisco Bay area and endeavors to explain song development through experiments with isolated captives.

In studying so complex a song, it would be easy to lose sight of general features, but Mulligan has chosen to emphasize temporal pattern and major types of syllables. In this way, he identifies a number of species characteristics common to all individuals. Still, the most striking feature of song in this species is that most of the 75 or more syllables and nearly all the song patterns (average 16) given by an individual are unique. Indeed, it emerges that birds of the West Coast have even larger repertoires than those studied by Mrs. Nice in Ohio or Borror in Maine. Mulligan makes the interesting suggestion that this results from the longer period of development of territorial song, largely free from singing of other species, that occurs in his study area.

Development of song was studied in wild birds as well as captives and five stages were recognized. Points of interest are that call notes were not important in song development and wild birds sang more advanced songs when stimulated by rivals. There is also a suggestion, which may prove important in studies with captives, that the singing of a bird caged below others was inhibited. That the variety of adult song cannot be explained simply by either imitation or inheritance was pointed out by Mrs. Nice but it remained for Mulligan's experiments to clarify the role of various factors in song development. Ideally, one would like to have seen larger samples than the 11 birds used. However, the results seem clear and consistent with field observations. No birds were raised from the egg in complete isolation from bird song and this reviewer is well aware of the difficulties that prevented such an experiment. An almost equally valuable result was obtained by having three birds raised from the egg by canaries. These birds were later isolated, sang vigorously, and developed essentially normal songs, though their repertoires were somewhat limited in variety. A series of isolates exposed to training songs at different ages showed that Song Sparrows can learn by imitation during a sensitive period lasting from about four to 10 weeks of age. Judging from experience in our laboratory, the daily training periods used seem rather brief but Mulligan's results show a good gradation of learning by imitation. In a final experiment, a bird which was deafened continued to sing but song development was arrested. Mulligan argues convincingly that imitation, though demonstrated, plays a minor role in song development compared with improvisation and modification of what has been learned. The experiment with the deafened bird indicates the need for auditory feedback in development and Mulligan postulates the existence of an inherited auditory template by reference to which the young bird develops a song normal to its species. In the spring, divergence in song is thought to occur in wild populations instead of conformity by imitation as described for other species such as the Chaffinch.

Mulligan points out that individual recognition of song may be particularly important in conserving energy in dense populations of highly territorial species. While experimental evidence is lacking, I have no doubt that this is true for Song Sparrows. However, I cannot see why Mulligan suggests that such extreme variation is necessary for individual recognition since many other territorial species establish individual identity by means of stereotyped songs. The fact is, we can still only guess why some species have much more varied songs than others. Mulligan contributes some stimulating ideas concerning this problem.

Mulligan's paper is clearly written and his figures and tables are used to good advantage. Specialists will note the use of oscilligrams as well as sonograms. This paper should interest the general ornithologist since the Song Sparrow is a familiar species and Mulligan relates his results to the pertinent literature. Besides being a valuable contribution to the study of bird song, it provides a sophisticated yet readable introduction to a rapidly developing field.—J. BRUCE FALLS.

NORTH AMERICAN NEST RECORD CARD PROGRAM

As many readers are aware, the Nest Record Card Program is now completing its third year on a continent-wide basis. We appreciate the assistance of the hundreds of persons and Bird Clubs whose enthusiasm and patience make this program possible. We are anxious to solicit help from as many clubs and cooperators as possible. If you are interested in helping in this research, please get in touch with the Laboratory of Ornithology at Cornell University for instructions and nest-record cards. Before the new nesting season begins, we urge all present contributors to return any completed cards. We also request that participating clubs and birders order additional cards, if necessary, well in advance of the 1968 nesting season.—LABORATORY OF ORNITHOLOGY, CORNELL UNIVERSITY.

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CONTENTS

General Notes

Female SMITH'S LONGSPUR *(Calcarius pictus)* at her nest at the base of a dwarf birch.

THE BREEDING BIOLOGY OF SMITH'S LONGSPUR[1]

JOSEPH R. JEHL, JR.

SINCE 1930, when the railroad connecting the Canadian prairies with the port of Churchill, Manitoba, on Hudson Bay, was completed, the Churchill area has been the scene of many ornithological investigations. Despite this, many of the region's most interesting birds have remained virtually unstudied. One of these is Smith's Longspur (*Calcarius pictus*). Our present knowledge of this species on its breeding grounds (summarized by Kemsies, in Bent et al., 1968) is mainly from the preliminary accounts of Taverner and Sutton (1934) and Grinnell (1944). My studies at Churchill were primarily concerned with shorebirds, but as time permitted I gathered information on this beautiful and characteristic subarctic bird. Most of my observations were made in 1965 and 1966, but there was high nestling loss in 1965 (Jehl and Hussell, 1966*a*). Therefore, this paper emphasizes observations made in 1966, but supplementary data from 1964, 1965, and 1967 are included.

BREEDING RANGE AND HABITAT

The breeding range of Smith's Longspur extends from the Hudson Bay coast of Ontario westward, presumably along the treeline, into northeastern Alaska; a small population also breeds in northern British Columbia. The Alaskan and Ontario populations have been described as racially distinct from the central Canadian population but, for reasons discussed elsewhere (Jehl, 1968), the species must be considered monotypic.

At Churchill, and probably throughout its breeding range, this longspur is a bird of the forest-tundra—the more northerly part of the transition zone between the boreal forest and the treeless tundra (Johansen, 1963). Within this zone it occurs most frequently where the drier sedge meadows dominated by *Scirpus caespitosus* and dwarf birch (*Betula glandulosa*) are interrupted by low hillocks or small ridges (usually old beach lines) bearing scattered, isolated clumps of black spruce (*Picea mariana*), or, less frequently, larch (*Larix laricina*). The hillocks rise only a few feet above the surrounding area and are dominated by heaths, principally *Rhododendron lapponicum*, *Andromeda glaucophylla*, *Arctostaphylos* sp., *Vaccinium uliginosum*, and *Vaccinium vitis-idaea*; other common plants include *Dryas integrifolia*, *Empetrum nigrum*, *Salix reticulata*, and *Cladonia* spp. (Fig. 1).

The commonest nesting associates of Smith's Longspur in this habitat are

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[1] This paper is dedicated to George Miksch Sutton in recognition of his pioneering ornithological research at Churchill, Manitoba, and elsewhere in the Canadian Arctic.

Savannah Sparrows (*Passerculus sandwichensis*), and Least (*Erolia minutilla*) and Stilt sandpipers (*Micropalama himantopus*).

ARRIVAL

A few male Smith's Longspurs appear at Churchill in late May, but their major influx occurs in the first week of June. Females arrive several days later. In 1965 and 1966 (Fig. 2). most males arrived by 6 June; single females were seen in the first days of June but the peak of arrival was from 7 to 9 June. Early June 1967 was relatively cool and males arrived through 11 June, though females did not appear until that date. Arrival in the exceptionally cold and wet spring of 1964 was even more retarded. A male was observed on 29 May. but the species was not encountered again until 15 June, when another male appeared. On 16 June large flocks of males and females arrived and the species was abundant everywhere on the tundra edge.

Apparently migrants may arrive at any time of the day or night. I have seen flocks arriving from 0400 to 2330 hours. These flocks are small (10 to 30 individuals; maximum 80) and usually consist entirely of Smith's Longspurs, but sometimes a few Lapland Longspurs (*Calcarius lapponicus*) or Snow Buntings (*Plectrophenax nivalis*) are included.

In most years the males remain in flocks of three to five birds for several days after arriving. Females may join these flocks, but they show no evidence of being attracted by the males and pair formation does not occur until after males become territorial. Lapland Longspurs and Snow Buntings may also associate with the flocks, especially early in the season when the wetter feeding areas preferred by the Laplands are still covered by melt waters. While in flocks the birds spend much time foraging. Walking rapidly over the drier regions of the tundra, they peer and peck under small shrubs and trees: later in the season they often hop or make short flights to catch flying insects. I have never seen a longspur scratch at the substrate.

VOCALIZATIONS

Male Smith's Longspurs, when flocking, sing only sporadically, and then almost invariably from the ground. Their commonest vocalization is a rapid, sharp, rattle. *tic-tic-tic-tic*, that has been aptly likened to the sound of winding a cheap watch (Taverner and Sutton. 1934:81). This call, also given by flying birds, functions as a location note (see below) in keeping the flock together, as an alarm, and as a threat. It is similar to the louder and more musical rattle of the Lapland Longspur. Another note, a short, sneezy *syu*. is sometimes given by flying birds. This call is equivalent to the Lapland's *teu*, but unlike that call, which is given commonly throughout the season and in response to many situations (see Andrew, 1957), the *syu* call is rarely

FIG. 1. Treeline habitat of Smith's Longspur at Churchill, Manitoba. A male is singing from the black spruce in the foreground.

heard. Its major function appears to be as a flocking note in flight, but it is also given by females leaving the nest.

The song of Smith's Longspur is warbler-like and is most reminiscent of those of Yellow or Chestnut-sided warblers. Typically it consists of six to eight notes, the first several ascending in pitch, the last two descending (sonagram in Borror, 1961:165); the first two notes are delivered at a very low volume and may not be heard except at close range. There is sufficient variation that individual males may be distinguished by their songs. Borror (1961:162) gives a frequency range of 3300 to 6200 cps.

TERRITORIALITY

In this paper I use "territory" loosely to mean the male's activity space at the time of pair formation. Classical territoriality is either ephemeral or lacking in this species, and even with prolonged observation I have been unable to determine what may constitute a "defended area." I consider male Smith's Longspurs territorial when they restrict most of their activities to a specific area and begin to sing persistently from conspicuous, often elevated, sites in response to other males.

In years when the males arrive late the flocks disband almost immediately, but in more normal seasons the transition from flocking to territorial behavior is less sudden. In 1966 males arrived in the first days of June and remained in flocks until 6 June. On that date many males in flocks began to sing frequently from the ground, but the songs were not directed at other males, and they had no noticeable effect on other members of the flock. On 7 June a few males left the flocks briefly and sang from trees, but later rejoined the flocks. By 9 June no flocks persisted and all males were on territory.

Even during the initial stages of the breeding cycle, when in most species territorial behavior is strongest, male Smith's Longspurs show little concern for the physical defense of territory, song perches, nest site, or mate. In claiming a territory they sing once or twice from the top of a small tree, then fly to another; in territories where trees are absent, ridge tops, boulders, or any conspicuous sites are utilized. No regular route through the territory is used, but often they fly to trees that have just been vacated, or to those in which another singing male is present. It is not uncommon to find three males singing from the same tree at the same time without conflict. Unlike other longspurs, Smith's has no flight song, although birds occasionally sing while flying between perches. This behavior is unusual and I did not notice it more frequently in birds whose territories lacked conifers or other conspicuous song perches.

Chasing of other males begins at about the time females arrive on the territories. Yet, even at this time males are not strongly territorial. Not all trespassers are chased. The chases are usually perfunctory and rarely result in fighting; in fact, many end when the males land and begin feeding together. Occasionally Savannah Sparrows and Lapland Longspurs flying through the

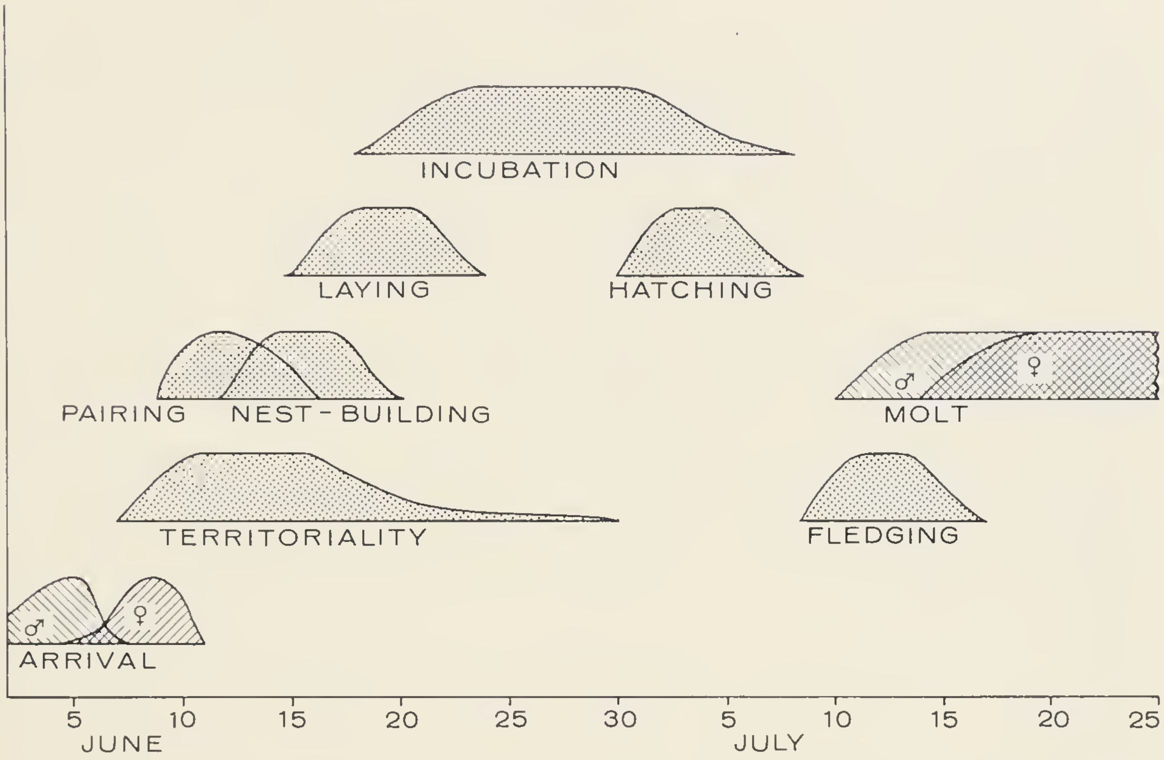

Fig. 2. Summer schedule of Smith's Longspurs at Churchill, Manitoba, in 1966.

territory are pursued, but these chases seem to result from mistaken identity and do not represent occurrences of interspecific territoriality.

By the time females begin building chasing has diminished. At this period males remain near the females in the central part of the territory and rarely wander to the periphery. They continue to sing in response to other males, but the presence of outsiders on the territory provokes no response, as the following observations indicate. On 11 June 1966, a male sang from the top of a small spruce, ten feet away from a potential nest site that his mate had investigated an hour earlier, while another male foraged, and occasionally sang, at the foot of the tree. On 15 June 1966, I watched a pair land 10 feet from a nearly completed nest. The female approached the nest carrying a feather for the lining when a foreign male suddenly flew in and attempted to mount her. A short struggle ensued, after which the female flew away. Her mate, never more than 5 m away, walked around unconcernedly and made no effort to drive off the intruder, which shortly afterwards flew off out of sight.

During the incubation period males again roam through and beyond the entire territory. They may now sing for prolonged periods from one perch, and they still continue to engage their neighbors in brief singing duels, but chasing rarely occurs. Occasionally birds flying over the territory are chased cursorily. Late in the period all semblances of territoriality disappear. Males again join in small flocks and feed together in areas that earlier had contained only one male. Territoriality does not resume in the nestling period. In 1965, after a severe storm during which most nestlings were killed (Jehl and Hussell, 1966*a*), I trapped two pairs of adults feeding young at one nest. Presumably the chicks of one pair died during the storm.

Females at no time defend any part of the territory. I have seen them foraging within a few feet of Savannah Sparrows and Lapland Longspurs without incident. and once two females fed within 30 feet of one's nest. Dummies of male Smith's and Lapland longspurs placed at the edge of the nest and enhanced by taped playbacks of Smith's song failed to attract the attention of the males. Females encountering the mounts for the first time stared briefly, then returned to incubating.

Because overt territorial behavior is of such short duration, and because the males' activity space varies at different times of the breeding season, it is difficult to determine territory size. Two territories mapped during the incubation period measured approximately 4.1 and 6.0 acres. In a 50-acre census area four pairs nested in 1965 and 1967, three pairs in 1966. The closest nests were 125 and 158 m apart. The apparent low density is attributable to the interrupted nature of suitable nesting habitat. Nests of Lapland Longspurs and Savannah Sparrows were found within 30 m of Smith's nests and one sparrow nest was less than 10 m distant; in 1965, Hussell found a Lapland Longspur nest 10 m from a Smith's nest.

Return to territory.—Circumstantial evidence suggests that adults return to their breeding areas of previous years.

1. Many males occur in areas that were used in earlier years, and the boundaries of their territories often appear similar to those used previously. For example, in 1967 territorial males occurred in the immediate vicinity of four of the five nests found in 1966. Areas used by three of these males were virtually identical to those of their 1966 counterparts. The fourth male is discussed below (see 4).

2. In 1965, a banded male was seen on the territory of the only adult male Smith's Longspur that I banded in 1964. Since there has been virtually no banding of Smith's Longspurs away from nesting grounds. probably these observations were of the same individual.

3. The area used by pair 1-66 was reoccupied in 1967, and the male defended approximately the territory of the 1966 male. The female was first seen on the territory on 11 June and had apparently just arrived. When I investigated the old nest site on that date, as I had done on the previous two days, the female sat on a nearby hummock and rattled at me. This behavior is often encountered in females late in incubation and during the nestling period. I did not find the nest of this pair in 1967, but the female's behavior left no doubt that it was within 100 feet of the 1966 site.

4. In 1965, I collected many nests after the young had perished. Nest 4-66 was found in the same depression as nest E-65; the site, a three-inch depression between two tiny hummocks, is an unusual one for this species. Since the female alone picks the nest site, these observations strongly suggest that this bird returned to her previous nesting area. The territory of the male in this area was virtually identical in 1965 and 1966, which also suggests that some pairs are reformed annually.

I shot the male of this pair after the chicks fledged in 1966. In 1967, I again found a pair in the vicinity, but the territory of the new male was shifted westward and included only about half of the area used by the original male. The female nested within 50 yards of the 1966 nest, within that part of the territory that had also been defended by the previous male. On several occasions she rattled when I aproached the vicinity of the original nest.

I have no data on the return of young birds. A few were banded in 1965, but, as noted, nearly all were killed. Seven chicks were banded in 1966; none were found in 1967.

The lack of strongly developed territoriality is one of the most interesting aspects of this species' breeding behavior. One wonders how much of an effect habitat configuration may have on spacing the males, and whether the virtual absence of territorial behavior is in any way related to the physiography. In arctic and subarctic species, breeding time is relatively limited, and long periods spent in territorial defense might be disadvantageous. Re-use of previous territories and their ritualistic defense could reduce intraspecific conflict. On the other hand, Smith's Longspur populations might not attain densities at which competition for nesting space occurs. Thus, selection for active territorial defense may be lacking. Clearly, much additional research is needed to clarify this problem.

NESTING

Pair formation.—As noted, females tend to arrive several days later than males. If they arrive while the males are still flocking, they may join the flocks, but if they arrive later they immediately take up residence on a male's territory. Pairing takes place on the territory and apparently without any conspicuous ground displays such as the wing-up display of McCown's Longspur (DuBois, 1937:235). Often two or three males and one female are observed in rapid, twisting flights over the tundra that extend far beyond the boundaries of any single male, but whether these are pursuit flights associated with courtship or aggressive displays of territorial males toward an already mated pair is not clear.

Nest construction.—Once pairs are formed, the mates are usually encountered together wandering through the territory, maintaining audible

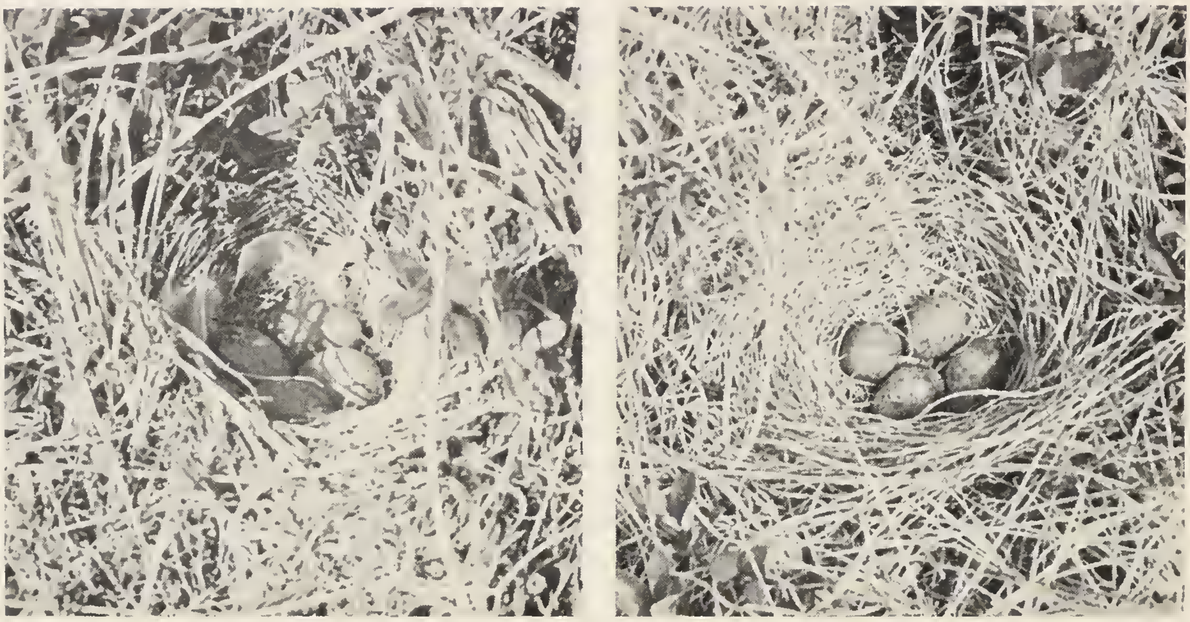

FIG. 3. Left: a typical nest lined with several ptarmigan feathers, among sedges and tiny rhododendrons. Right: an unlined nest concealed among sedges. Note that both nests are unprotected from above.

contact by frequent. single rattles. Several days to a week after pairing the female begins to search for a nest site. She tests the suitability of small depressions by crouching in them and making settling motions. Previous familiarity with an area probably influences the choice of older birds, as noted above. As soon as the site is selected, the female begins to gather nest material. The male takes no part in nest building, although he often accompanies the female to the vicinity of the nest.

Nests are built in three to four days and are made almost entirely of grasslike materials. The outer layer. 8 to 12 mm in thickness, is made of 50 to 85 mm lengths of a coarse, dark brown sedge. The inner layer, 10 to 15 mm thick, is composed of shorter pieces (20 to 60 mm) of a fine, light brown sedge, usually *Scirpus caespitosus*; in some nests a few feathers or tiny scraps of paper are included. The nest cup may be lined with a few feathers; occasionally bits of hair, wool, or reindeer lichen (*Cladonia* spp.) are added (Fig. 3). At 22 nests, the number of feathers in the lining ranged from 0 to 14, with a mean of 3.8. This contrasts strongly with the abundance of feathers found in Lapland Longspur nests. Sandpiper, duck, and Canada Goose (*Branta canadensis*) feathers are sometimes used, but the white breast feathers of winter-plumaged Willow Ptarmigan (*Lagopus lagopus*) are used most commonly, which may merely reflect their greater conspicuousness and abundance rather than color preference by the longspurs. Usually the nest lining is added before or during laying, but one bird added only two feathers after she had begun incubating.

Nest sites.—Unlike nests of Lapland Longspurs at Churchill, which are almost invariably built into the sides of small hummocks and are protected by overhanging vegetation, nests of Smith's Longspurs are commonly unprotected from above, and are built in small depressions atop relatively dry, flat hummocks. Of the thirty nests found, 23 were on ridges: 12 were at the base of a small shrub or tree, 11 were protected only by overhanging sedges. Seven nests were on the sides of hummocks and six of these were concealed by a small shrub or tree, one by sedges; however, not one was as well-protected as most Lapland Longspur nests.

Copulation.—Copulation begins at the start of nest construction and continued at one nest until after the second egg (of four) was laid. It seems to be incited entirely by the female and to occur most frequently after she has added material to the nest. On many occasions I have seen a female fly five to ten feet from the nest, then crouch in a soliciting posture—head back, wings outstretched and vibrating, tail cocked. Twice I have seen behavior that may also be part of a precopulatory display. On these occasions the pair flew off together after the female solicited but failed to entice her mate to mount. On landing both birds leaped a foot into the air and "fought" briefly face-to-face, then dropped to the ground; the female solicited at once, and the male mounted. After copulating the pair may forage together for several minutes. There are no obvious postcopulatory displays.

Laying; eggs.—At two nests for which I have complete data, eggs were laid daily, apparently before 1000 hours, until the clutch was completed. Eggs are pale gray-green with light lavender spots; some are more heavily marked with purplish brown spots or lines, some are almost unmarked. The average dimensions of 16 eggs were 21.6 × 5.7 mm. Extreme measurements are *23.7* × 15.5, *20.2* × 15.4, 22.3 × *15.1*, and 20.5 × *16.2*.

Incubation.—Incubation is by the female only and at three nests began the night before the final egg was laid. At one of these, an apparently incubating female flushed from the nest the night after her second egg (of four) was laid, but at another the female did not protect her three-egg (of five) clutch on a cold (38 F) and damp night when a heavy mist wet the eggs. The female's attentiveness during incubation seems unrelated to weather conditions. I have twice found nests that were soaked and apparently deserted in which the eggs hatched successfully (see below).

From the start of incubation females sit very closely and do not flush until the observer is quite near. In this respect they differ from Lapland Longspurs at Churchill, which tend to slip away while the observer is still distant. When flushed they fly off a few feet, tail widely spread, and white outer tail feathers conspicuously displayed, then land and crouch with wings slightly drooped, back feathers ruffled, tail spread and flattened on the ground. If pursued, they alternate short, shuffling runs with brief, low flights until the intruder is led 30 m or more from the nest. Distraction displays I have observed were always silent. If the intruder remains near the nest, however, they return to the vicinity and rattle until he departs. Distraction displays begin at the start of laying.

Departures from undisturbed nests are much different. Females stand briefly at the edge of the nest, then fly off close to the ground giving a rattle that is almost invariably followed by an abbreviated song. One female watched by Hussell occasionally walked away from the nest and fed in the vicinity. Some females sing fully as well as males, whereas others follow the rattle with only a call note, *syu*. Presumably these vocalizations alert males to the females' departure, but I have never seen a male fly toward a departing female, nor have I seen females fly toward the area in which the male was last heard. When off the nest females rattle every few seconds. The bulk of their feeding is done 25 to 50 m from the nest. Except in the early evening, when they may forage with males anywhere on the territory, females rarely go farther than 100 m from their nest. When returning they fly to about 8 m from the nest and walk in, rattling every few seconds until within 2 m of the nest; this distance is covered silently. After the characteristic departing and returning behavior is recognized nests can be easily located. Hussell observed one female that gave a "quiet and short murmuring note . . . *kwer-kwer-kwer-kwer*" when settling on the eggs.

The constancy of incubation seems to increase as the incubation period progresses. On the sixth day of incubation between 1640 and 1814 hours one female spent 55 minutes on and 41 minutes off the nest; attentive periods averaged 11 minutes (range 8 to 14 minutes), inattentive periods 10 minutes (range 7 to 17). In the midafternoon of the tenth and eleventh days of incubation I watched her for 63 and 56 minutes, respectively; on both days she left the nest only once, to defecate, and returned within one minute. Air temperatures were in the upper 60's on all three days and the female panted continuously while incubating.

Males rarely approach the nest, though they may land nearby and rattle when humans are in the vicinity. The alarm calls of females are usually ignored. Male McCown's Longspurs feed incubating females (DuBois, 1927), but male Smith's apparently do not. I once saw a male land within five feet of an incubating female who immediately began begging, but the male, whose bill was empty, merely paused for a moment and then flew off. Possibly my presence in the blind affected his behavior.

Incubation period.—Jehl and Hussell (1966*b*) reported periods of 11½ to 12 days for eggs incubated during favorable weather in 1965. In addition, a period of 13 days, 12 hours (± 6 hours) in 1966 and a period of at least 13

FIG. 4. Male Smith's Longspur feeding nestlings approximately two days old. The male has already molted the inner primaries.

days, 20 hours in 1967 were determined. All periods were calculated from the time of laying to hatching of the last egg. In both of the latter years inclement weather occurred during incubation and the eggs at both nests were found cold, wet, and apparently deserted, after four and six days of incubation, respectively. It seems probable that chilling delayed normal development.

At eight nests the time required for the hatching of the entire clutch ranged from a maximum of 11 to 36 hours, with a mean of approximately 22 hours. Eggs hatch within a day after the first signs of cracking appear, and often only a few hours are required.

In general, the hatching period for the Churchill population occupies only a few days. In 1965 eggs hatched from 3 to 13 July, but at 17 of 21 nests the hatch occurred between 3 and 6 July. At the five nests that I studied in 1966 the chicks hatched between 1 and 4 July, although subsequent observations showed that a few other nests hatched later. In 1967 hatching dates from 6 to 10 July were recorded; later hatchings were probable.

THE NESTLING PERIOD

For about two days after hatching chicks are fed largely by the female. Caterpillars, grasshoppers, and adult Diptera and Lepidoptera are the most conspicuous foods carried in by the adults, but many other foods are utilized

FIG. 5. Female "airing the bed" at a nest at the base of a dwarf birch.

(see below). Nestlings receive their first feeding within a few hours of hatching; this accounts for the great variation in weights of newly-hatched (D-0) young (Table 2).

The male's role in feeding the nestlings increases gradually and by D-2 or D-3 equals that of the female. In the first days after hatching he forages widely over the territory and feeds the chicks (Fig. 4) at irregular intervals. As his attentiveness increases, his foraging area becomes reduced. Females rarely forage more than 50 m from the nest.

When approaching the nest with food, both parents give a short rattle, upon which the other parent leaves the vicinity of the nest. Fecal sacs are removed by both parents: usually the first sac is eaten, but if the nest contains two or more the additional sacs are carried off. Egg shells and dead chicks also disappear from the nest, and presumably are removed by the adults.

I never encountered males brooding the young, but once on a warm afternoon I watched a male shade the nestlings for approximately one minute. He left before the female returned to the nest. At one nest Hussell reported that the male brooded 2½ to 3-day-old chicks for 5 and 8 minutes after feeding them. After feeding the chicks the female broods them for a few minutes, even on the warmest days. While brooding she may peer into the nest, then probe

Table 1

Observations on the Growth and Development of Smith's Longspur Nestlings

Day 0	Skin pale orange (bright orange for a few hours after hatching: D. J. T. Hussell), mouth lining pale pink; eyes closed. Down buffy (closest to Cartridge Buff of Ridgway, 1912), 10–12 mm long, tipped with dusky gray, thick on capital, humeral, and dorsal region of spinal tract, sparse on femoral tracts; papillae in cervical region noticeable by 4 hours after hatching. Chicks placed on back roll over only with great difficulty.
Day 1	No obvious change in distribution of down; papillae in cervical region dark and prominent. Able to balance and gape. Beg in response to female's rattle.
Day 2	Feather tracts appear all over body (in some birds by D 1½), papillae of primaries visible, but less than 1 mm. Chicks sit up and gape when nest is vibrated. Uric acid adheres to chicks.
Day 3	Feather sheaths conspicuous on crown, neck, scapulars, wings, flanks, less developed on venter. Eyes begin to open on largest chicks; faint, high-pitched begging squeaks. Mouth lining reddish. Fecal sacs deposited.
Day 4	Feathers start to break from sheaths on venter, flanks, a few on back; minor wing feathers well-defined. Eyes open. Begging louder, audible 10 feet from nest. Will gape to visual stimulus as well as sound (Hussell).
Day 5	Like D-4 but feathers longer, many more breaking from sheaths; head feathers nearly free of sheaths.
Day 6	Chicks appear fully feathered dorsally, though tailless; primaries and coverts breaking from sheaths, other wing feathers more advanced. High-pitched begging can be heard 20 feet away. Egg tooth still retained (in some chicks) (Fig. 6).
Day 7	Like D-6 but larger. Primaries free for 3–4 mm, secondaries and coverts almost free of sheaths. Much of venter feathers covered. Largest chicks leave nest. Chicks homeothermal.
Day 8	Larger, belly completely covered by feathers. Nearly all traces of down lost.
Day 9–12	Growing rapidly. D-11, down has disappeared. D-12, wing now a solid flying surface; chicks able to fly a few inches after short runs. Tail 8 mm. Egg tooth visible in some chicks.
Day 13	Able to fly over 18″ wire fence.

vigorously at the lining for a few seconds (Fig. 5). One female repeated this performance six times in the span of a few minutes. I have seen this behavior, which has been called "airing the bed," between D-2 and D-7. Royama (1966:320) believes that its major function is insulative. Of course, rearrangement of a matted nest lining will necessarily aid in heat retention, but I question whether this is the function of the behavior, for I have seen it done by panting females on warm days when the need for increased insulation seems negligible. Whenever I have observed the behavior it has occurred *after* the female has resumed brooding. The probing appears to be directed at one specific area of the nest, not the entire nest lining. During my brief

FIG. 6. A six-day-old Smith's Longspur nestling.

observations the female probed vertically, never at the sides of the nest cup. From these observations I infer that "airing the bed" is primarily a comfort movement. Perhaps the chicks' movements cause small bits of the nest lining to protrude and irritate the brood patch. Hussell (pers. comm.) observed "airing the bed" behavior from an *incubating* female, who removed "a piece of fine grass about 1½″ long . . . and flew away with it." More detailed observations of this behavior, including precise observations on the areas probed, are needed. An experimental approach (artificially tamping the nest lining, inserting stiff bits of grass into the nest lining, etc.) might be used profitably.

Chicks begin to stray short distances from the nest by D-6, but they do not desert it until D-7 or, less frequently, D-8. At this time they are able to run fairly rapidly through the grass, but when approached they crouch motionless under small shrubs. By D-12 the chicks can fly short distances, but several more days are required before they can fly well. Whether the parents play any part in leading the chicks from the nest is unstudied, but I suspect that at least the chicks' initial movements are unguided.

Growth and development of the young.—Observations on the growth and development of nestlings are summarized in Table 1. In Tables 2 and 3, growth

TABLE 2

DAILY WEIGHTS AND PER CENT RELATIVE GROWTH RATES OF SMITH'S AND LAPLAND LONGSPURS

	Smith's Longspur[a]					Lapland Longspur[b]		
Age in days	Number of chicks	Weight: range and mean, g		Mean weight change, g	Per cent relative growth/day	Mean weight, g	Mean weight change, g	Per cent relative growth/day
0	9	1.6–3.0	2.6			2.3		
1	9	3.8–4.9	4.5	1.9	53.4	3.5	1.2	41.9
2	9	6.2–7.8	7.1	2.6	44.8	5.2	1.7	39.6
3	9	8.4–12.5	10.7	3.6	40.4	8.0	2.8	43.0
4	9	8.7–16.0	12.8	2.1	17.6	10.6	2.6	28.1
5	9	9.3–20.2	15.9	3.1	21.6	14.0	3.4	27.8
6	9	11.0–22.4	18.3	2.4	14.0	17.2	3.2	20.5
7	2	21.9, 22.0	22.0	3.7	18.3	18.8	1.6	9.0
8	1[c]		20.3			19.9		
9	1[c]		16.1			21.2		
10	1[c]		18.6			21.3		
11	1[c]		20.5			22.4		
12	1[c]		22.0			21.9		

[a] Data for successfully fledging chicks.
[b] Data from Maher, 1964, Table 2.
[c] Bird retained in wire enclosure at nest.

rates, as indicated by daily weight changes and by the growth of the seventh (i.e., third outermost) primary, are compared with those of Lapland Longspurs (data from Maher, 1964). For individual recognition I dyed chicks lightly on the wing or thigh with Magic Marker until they were large enough to band.

I visited nests daily about midday during the hatching period and noted the condition of the eggs. From this, and from later observations on the size and condition of the young, the approximate hatching time could be established. In this study chicks assigned to D-0 averaged 12 hours old (range 0 to 18), D-1 chicks 36 hours (range 18 to 42). According to D. J. T. Hussell (pers. comm.), Maher's D-0 chicks averaged about 6 hours old, D-1 chicks 24 hours. Thus the more rapid growth of Smith's nestlings indicated in the tables probably stems largely from differences in the average age of chicks in each category. My small sample and my restriction of data to chicks fledged successfully tend to accentuate the differences. I doubt that there are any important differences between these species in growth rate and development.

In 1966, I made brief observations on the thermoregulatory ability of nestlings. Immediately on arriving at a nest, I recorded the chicks' cloacal temperatures to the nearest 0.1 C with a Wesco fast-recording thermometer

TABLE 3

GROWTH OF THE SEVENTH PRIMARY IN SMITH'S AND LAPLAND LONGSPURS

Smith's Longspur[a]				Lapland Longspur[b]
Age in days	Number of chicks	Range and mean in mm		Mean
2	7	0–1.0	0.5 (est.)	0.02
3	7	1.0–2.5	1.9	0.9
4	7	2.8–4.9	3.9	2.3
5	7	5.5–9.2	7.3	5.8
6	7	9.5–13.4	11.5	10.3
7	2	14.8, 20.0	17.4	14.3
8	1[c]		23.5	19.9
9	1[c]		27.0	24.1
10	1[c]		31.5	30.0
11	1[c]		35.0	34.3
12	1[c]		38.0	37.9

[a] Data for successfully fledging chicks.
[b] Data from Maher, 1964, Table 3.
[c] Bird retained in wire enclosure at nest.

inserted to a depth of 12 mm. Chicks were then placed singly in shaded, wind-free areas (usually in my hat and under a small shrub) for ten minutes. after which time their cloacal temperatures and the ambient temperature in the shaded region were recorded. Some representative observations are given in Table 4.

The development of homeothermy was clearly correlated with the growth of the feathers. Pin-feathered chicks three and four days old were unable to maintain their body temperatures under the test conditions for even a few minutes. Improved thermoregulatory ability is evident by D-6, when most feathers of the dorsum have broken free of their sheaths. By D-7, when much of the ventral apterium becomes covered by feathers, chicks are able to maintain their body temperatures for prolonged periods. Maher (1964) found that Lapland Longspur and Snow Bunting chicks were able to maintain their body temperatures at low ambient temperatures by D-7, but that their ability to reduce body temperatures at high environmental temperatures began several days earlier.

DISPERSAL AND DEPARTURE

Disruption of family groups begins shortly after the chicks leave the nest. I have found nestmates 40 m from each other one day after fledging, and several days later the family may be scattered over a quarter-mile of tundra. The parents maintain audible contact for a few days, but within a week after the chicks fledge calling between the adults has virtually ceased, and most

TABLE 4

THERMOREGULATION IN SMITH'S LONGSPUR NESTLINGS

Chick number	Age in days	Cloacal temperature, C	Cloacal temperature 10 minutes after chick removed from nest, C	Ambient temperature, C
4-1-66	3	35.4	24.6[a]	12.0
2-2-66	4	31.5	26.0[a]	13.2
1-3-66	5	35.8	30.0	24.8
1-4-66	5	36.0	31.0	24.8
3-1-66	5	40.4	36.5	not recorded[b]
3-1-66	6	39.1	37.1	21.5
4-2-66	6	39.8	37.6	21.5
3-1-66	7	36.4	37.5[c]	17.0

[a] Body temperature recorded after five minutes.
[b] Ground temperature at nest 40.2 C; chick panting vigorously.
[c] After 1½ hours at 27 C, chick's body temperature was 39.5 C.

chicks encountered are accompanied by only one adult. It appears that each chick, from the time it leaves the nest, is fed by only one of the parents. This enhances rapid dispersal and disruption of the family into two groups. As Maher (1964) pointed out, early fledging and dispersal of ground-nesting passerines is important in reducing losses to predators.

The male's former territorial boundaries have no significance after the chicks leave the nest. Some family groups rapidly disappear from the territory, whereas others remain on it, independently, for prolonged periods. I have found banded D-22 chicks in association with the male parent, within 100 m of the nest site.

Distraction displays by the parents usually cease when the young are able to fly, or at about D-13, but I have seen one from a female with D-20 chicks. However, adults usually respond to humans near their chicks by rattling vigorously from the tops of small trees. while the chicks fly off a short distance.

The chicks are fed for about three weeks after hatching, but in late July the adults leave them and gather in small flocks. Migration begins as early as mid-August in some years (Taverner and Sutton, 1934:80) and by early September all Smith's Longspurs have left the Churchill region. The possibility of differential migration of age and sex classes might be profitably investigated in this species, because of the earlier incidence of the males' postbreeding molt (see below).

PRODUCTIVITY

Clutch size and hatching success data for 1965–1967 are given in Table 5. The median clutch was four and clutches of two to five were found, but the

TABLE 5

CLUTCH SIZE AND HATCHING SUCCESS OF SMITH'S LONGSPURS AT CHURCHILL, MANITOBA, 1965–1967

Year	Clutch size 2	3	4	5	$\overline{X}$	Hatching success by year
1965		2	16	3	4.05	81/85 (95.4%)
1966	1*		4		3.60	16/18 (88.8%)
1967		1	3		3.75	10/11 (90.1%)
Total	1	3	23	3	3.93	107/114(93.7%)
Hatching success by clutch size	1/2 (50%)	8/9 (88.8%)	84/88 (95.4%)	14/15 (93.3%)		

* See text for explanation.

single two-egg clutch is suspect. It was discovered late in the incubation period, one egg disappeared just prior to hatching, and the nestling was killed by a weasel (probably *Mustela erminea*). Possibly this predator removed some eggs on earlier visits. Pough (1946:275), without stated authority, reported clutches of four to six.

Hatching success was consistently high. Only seven of 114 eggs failed to hatch; three disappeared from the nest, two were infertile (egg broken, no embryo present), one was apparently infertile (not examined), and one pipped egg failed to hatch.

Fledging success was poor in 1965. All nestlings in 18 nests under observation on 8 July died from exposure (Jehl and Hussell, 1966*a*) and probably less than five per cent of the eggs produced fledged young. In 1966. 16 of 18 eggs hatched, but only 9 young left the nest. One chick was killed by a weasel. The growth rate of three chicks in nest 1 declined on D-3 and by D-5 two had died. It is difficult to explain this loss, but the male only rarely fed the nestlings, and I suspect that the female alone was unequal to the task. Four chicks in nest 2 grew rapidly through D-3, but on D-4 I found them cold, damp, and begging for food; two days later all were dead, apparently from exposure. At both of these nests at least one parent fed the chicks after they were weighed, so it seems unlikely that nestling loss was attributable to my activities. I have no data for 1967. At the time of my departure there had been no loss of nestlings, and chicks in all nests were growing normally.

In most years productivity should be high. The only potential mammalian predators on eggs or young are weasels, red foxes (*Vulpes fulva*), collared lemmings (*Dicrostonyx groenlandicus*) and voles (*Microtus spp.*): the first two are extremely rare and I have no evidence that the rodents prey on eggs, even in years when their populations are high. Common Ravens (*Corvus

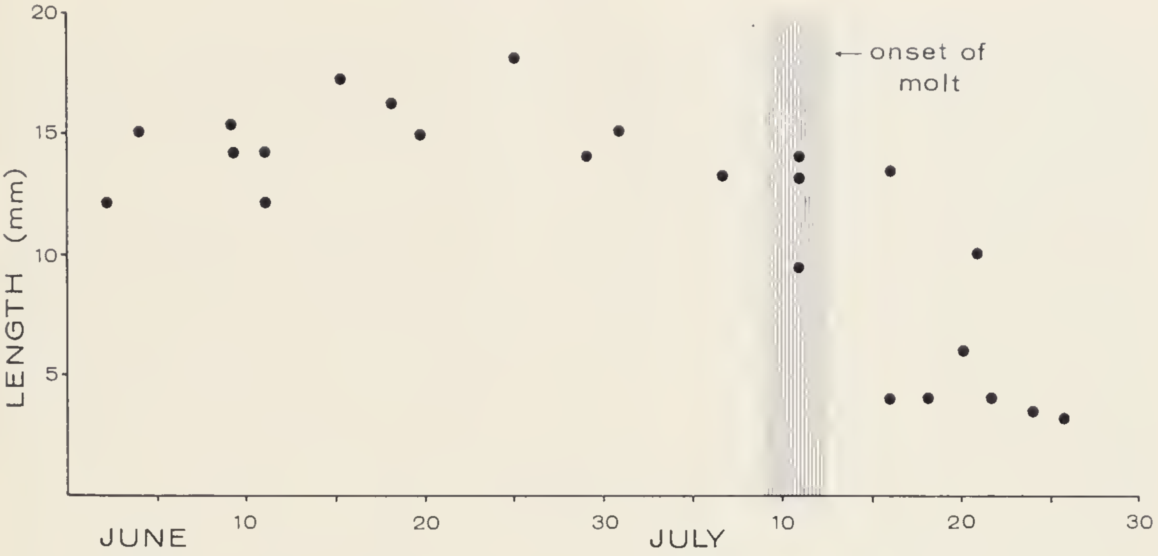

FIG. 7. Seasonal change in testes length of Smith's Longspurs.

corax), Short-eared Owls (*Asio flammeus*), gulls (mainly *Larus argentatus* and *L. thayeri*), and occasionally Parasitic Jaegers (*Stercorarius parasiticus*) may take a few chicks, but their effects seem negligible. In fact, longspurs show no concern about the occurrence of avian predators near their nests. The most important factor limiting productivity in the period of my studies was adverse weather (see Jehl and Hussell, 1966*a*).

I have no evidence of re-nesting, which indirectly suggests little nest predation. Judged by testes size (Fig. 7), the males remain sexually active into early July and thus re-nesting could be attempted if the eggs were destroyed. However, re-nesting did not follow the loss of nestlings in 1965, presumably because testicular regression had begun by this stage of the breeding cycle.

MOLT

Postbreeding molt.—The incidence of the postbreeding molt may be photoperiodically controlled in part, for each year males began molting on approximately 10 July. At this time in 1966 some chicks had already left the nest, whereas in 1967 the nestling period was hardly started. Females start molting four or five days later than males. The innermost primary and its covert are the first feathers lost; a few birds molt primaries 1 and 2 concurrently. The remaining primaries are shed in ascending order, the interval between the loss of adjacent primaries being three or four days. Molt on the upper chest, flanks, and thighs follows, and becomes conspicuous at about the time primary 4 is lost; some birds molt the distal tertial and its covert at this time.

The start of the secondary molt approximately coincides with the loss of primary 7. By this time extensive molt is visible everywhere on the body and the innermost primaries are nearly regrown. The underwing coverts and most of the smaller upper wing coverts seem to be molted after most of the primaries are shed. The replacement of a primary requires about 12 days: one captive bird replaced a secondary in 10 days.

The tail is lost as a unit in late July or early August, or at about the time primary 8 is lost, and its replacement is completed before that of the innermost secondaries. Of three birds collected at Churchill on 25 and 26 August 1936, one had a fully grown tail, those of the others being about 90 per cent grown. These birds had completed body molt, but their outermost primary was only three-quarters grown. Since Smith's Longspurs leave Churchill in late August, many must migrate before finishing the molt.

Young birds begin the postjuvenal molt at about 20 days of age. Presumably this molt involves only the body feathers. I have no data on its duration but, as with the adults, it must often be completed south of the breeding grounds.

Prebreeding molt.—The breeding plumage is attained through an extensive molt that involves all the feathers of the head and body and some, though probably not all, of the smaller wing coverts. The rectrices and the remiges and their major coverts are not replaced. In Lapland (*Calcarius lapponicus*) and Chestnut-collared (*C. ornatus*), and probably McCown's (*C. mccownii*)[2] longspurs, the breeding plumage is attained largely through wear. Both Lapland and Chestnut-collared longspurs molt some head feathers (Dwight, 1900) and a male Lapland Longspur that I kept in captivity also replaced the scapulars and a few feathers on the thigh and upper back. The significance of the more extensive molt in Smith's Longspur remains to be determined.

In captive birds molt first occurred on the insides of the legs and in the interscapular region, and was followed shortly by the loss of a few feathers from the upper part of the chest. Molt of both the dorsal and ventral tracts proceeded gradually tailward, but extensive molt of the ventral tract did not begin until that of the anterior half of the dorsal tract was well advanced. Feathers of the neck, throat, abdomen, flanks, and the tail coverts were replaced next, and finally, the head feathers and some of the wing coverts were molted.

In 1966 and 1967 captives began molting between 20 and 25 March and had virtually completed the molt by late April. It seems probable that this period corresponds to that of wild birds, for Kemsies and Austing (1950:37) reported that four males collected in Ohio on 18 April 1949 were "nearly in full breeding plumage."

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[2] I follow Sibley and Pettingill (1955) in treating *Rhynchophanes* as a synonym of *Calcarius*.

FOOD

Stomach contents of 39 adults and two flying juveniles collected between 2 June and 26 July were examined. For convenience in analysis, the sample was arbitrarily subdivided as follows: 2–9 June (7 stomachs); 13–18 June (5); 25–30 June (3); 1–9 July (4); 11–20 July (14); 21–26 July (8, including 2 juveniles). Because of fragmentation and decomposition, invertebrates encountered were rarely identifiable to family level, which precluded accurate quantitative or volumetric analysis. However, it is clear that Smith's Longspurs feed opportunistically on a wide variety of organisms through much of the summer. In the first ten days of June, plant materials, principally seeds, make up over 90 per cent by volume of the total food intake; invertebrates are taken when available, adults of terrestrial forms (ants, spiders, beetles) and larval Lepidoptera occurring with greatest frequency. In mid-June, as invertebrates become commoner, the birds switch to a largely animal diet; flying insects begin to be encountered at this time. After 20 June or so, more than 85 per cent of the diet is animal matter, of which the bulk is terrestrial forms or immature stages of flying insects.

Few seasonal differences in foods taken could be determined from this small sample. Seeds which compose the bulk of the diet before 10 June constituted an almost negligible portion thereafter. Ants and spiders were also taken frequently in early June, but none were found in July-taken adults; apparently they are ignored as larger invertebrates become more conspicuous. Snails were found in five of 14 birds taken between 11 and 20 July. Their occurrence reflects the drying of small tundra pools, and there is no reason to suggest that they were taken in lieu of grit. From late June through July adults of flying insects appeared to make up less than 25 per cent of the diet. I would expect them to occur with increasing frequency in August, and for seeds again to compose an important part of the diet later in the month. Grit, largely the easily identifiable local limestone, was found in all but three stomachs.

Nestlings.—The stomachs of 29 nestlings killed during the severe storm of 8 July 1965 (see Jehl and Hussell, 1966*a*) were also examined. These were grouped for analysis according to the weight of the chicks: 1.6 to 2.8 g (8 stomachs), 3.2 to 3.6 g (7), 4.1 to 5.2 g (8), and 7.1 to 14.7 g (6); these categories roughly correspond to D-0, D-1, D-1 to D-2, and D-2 and older chicks. I found no differences in foods present among these groups and, as with the adults, no specific foods were found in quantity.

With one exception—the occurrence of spiders in 7 of 29 nestlings, but in none of the adults collected after late June—I detected no differences between food received by the chicks and that taken by the adults between 1–20 July

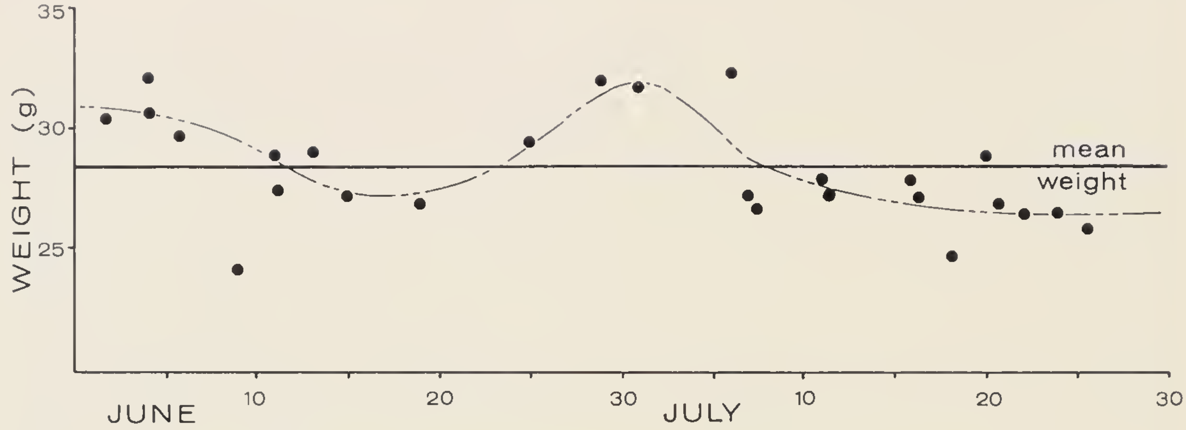

FIG. 8. Seasonal weight changes in male Smith's Longspurs.

(the 1–10 July sample was too small for comparison). Whether or not this difference is significant cannot be determined. I must emphasize that data from the nestlings are potentially strongly biased, since poor weather may have prevented the adults from gathering foods that normally would have been passed on to the chicks.

Entire leaves of plants commonly occurring in the nesting area were found in the stomachs of five nestlings but in none of the adults. They are ingested, as I have observed many times in the field, after accidentally adhering to the chicks' mouth lining. Grit occurred in trace quantities in three of 14 nestlings judged to be D-1 or less, but in large quantities in 11 of the older chicks. Since nests are not placed in gravelly areas, grit cannot be taken accidentally and it must be acquired from the parents.

Foods identified in the stomachs of adults and nestlings are listed below. Unless otherwise noted, all identifications pertain to adult organisms. Arachnida: Areneida. Odonata: Zygoptera. Orthoptera: Acrididae (adults and immatures), Locustidae. Dermaptera: unassigned adult. Hemiptera: Circadellidae. Lepidoptera: Geometridae? (larvae), Noctuidae, unassigned larvae and pupae. Diptera: Tipulidae, Anthomiidae (larva), unassigned larvae, pupae, adults. Coleoptera: Cantharidae, Chrysomelidae (larva), unassigned adults. Hymenoptera: Formicidae, Pompilidae?, unassigned adults. Mollusca: *Stagnicola* sp., *Gyraulus* sp. Plant Material: seeds (including *Potentilla?*), leaves (*Salix reticulata*, *Dryas integrifolia*, *Arctostaphylos* sp.), other (stem fragments, *Cladonia* sp.).

WEIGHTS

Seasonal weight changes in male Smith's Longspurs are plotted in Figure 8. Data for 1966 and 1967 are included, but because breeding began later in 1967 the data for that year are adjusted to the 1966 schedule by plotting them five days early. The changes are not random but vary predictably with respect to the birds' activities (see Fig. 2). Males arriving on the breeding grounds retain small amounts of subcutaneous fat and are relatively heavy. Their weight declines coincident with the start of territorial behavior, increases late in the incubation period after territoriality has ceased, and declines again in early July, when the males begin feeding the nestlings and molting. I have insufficient data to determine whether seasonal weight changes also occur in females.

The mean weight of 26 males was 28.1 g (range 24.1–31.1), that of 11 females 25.9 g (range 23.8–28.9).

RELATIONSHIPS OF SMITH'S LONGSPUR

The genus *Calcarius* comprises four species, of which three are Nearctic: Smith's Longspur is a subarctic, treeline form; Chestnut-collared and McCown's longspurs inhabit the plains of the western United States and southern Canada; the Lapland Longspur is a Holarctic, tundra-breeding species. Since relationships within this genus are unstudied, I had hoped that this investigation might clarify whether Smith's Longspur was more closely related to the tundra or prairie species. Unfortunately, there is insufficient evidence to resolve this point. Since Smith's lacks some attributes of Laplands that are usually associated with arctic birds, derivation from a tundra-adapted ancestor cannot be strongly contended. For example, Smith's Longspurs nest in exposed situations, Laplands in more sheltered spots. Smith's nests, unlike those of Laplands, are never heavily insulated with feathers; the average clutch size of Smith's (3.93 for 30 nests) is smaller than that of Laplands, even of the southern, Churchill population (4.48 for 19 nests). In these respects Smith's is more like the prairie species (nests unprotected and rarely insulated; clutch sizes relatively small: *mccownii*, 3.58 for 52 nests; *ornatus*, 4.24 for 21 nests; DuBois, 1935), but these are inadequate reasons for suggesting relationship to those species. Smith's Longspurs' early postbreeding molt is an apparent adaptation to high latitudes; however, the molt of other longspurs has not been studied in detail, so the significance of this character is unknown.

There is, in fact, little to indicate that Smith's Longspur is closely related to any modern species of *Calcarius*. Its plumage color and pattern are unlike those of other longspurs, and its simple, warbler-like song is quite different from that of *lapponicus* or *ornatus* (see sonagrams in Borror, 1961:165, 169; Robbins et al., 1966:324) and presumably, *mccownii* (description in Peterson, 1947:239; Borror, 1961:173). Furthermore, unlike the other species, *pictus* lacks a flight song.

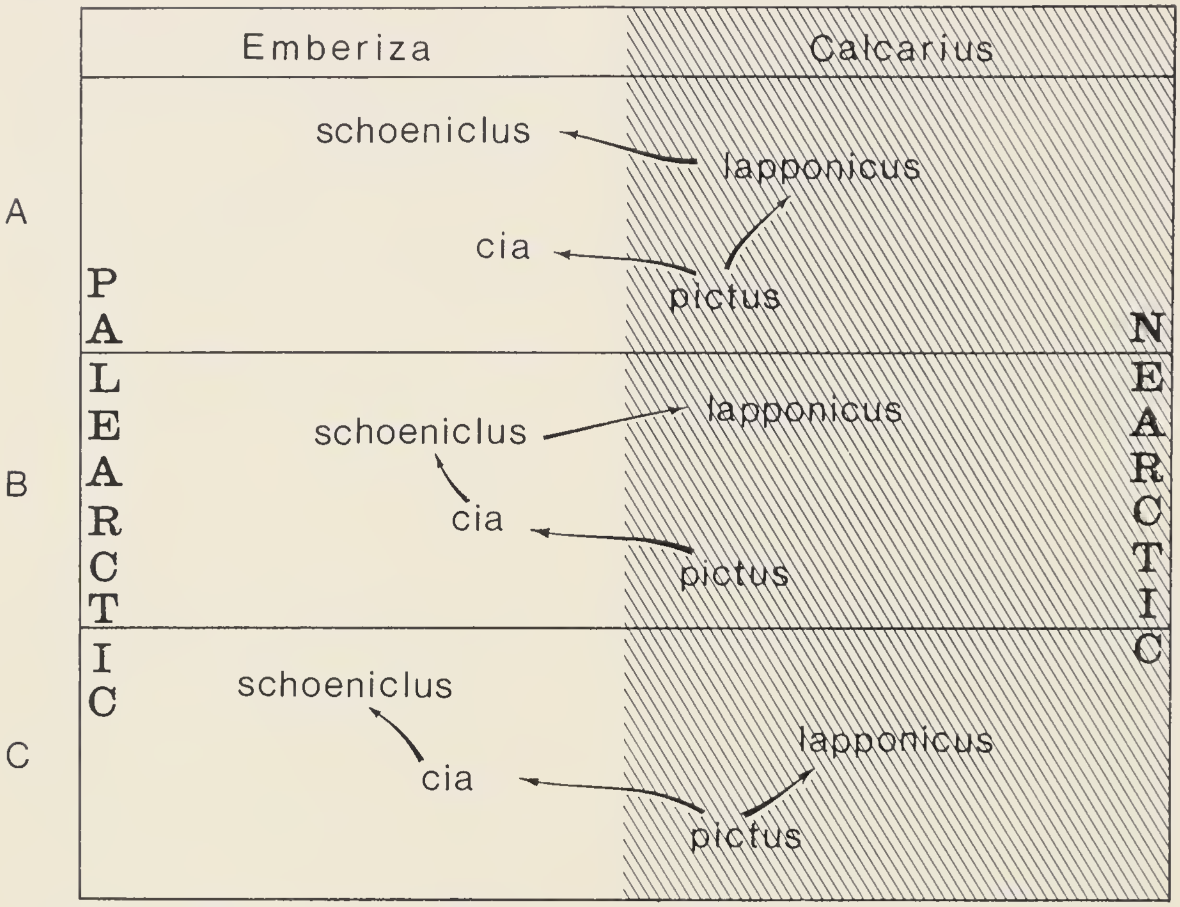

FIG. 9. Some possible relationships between longspurs (*Calcarius*) and Old World buntings (*Emberiza*).

It may be unwise, however, to speculate on longspur interrelationships without also considering the Old World buntings. It is generally acknowledged that *Calcarius* is most closely allied to the Old World genus *Emberiza*. Harrison (1967:26) recently suggested that "the Old World buntings in their evolution from the New World sparrow stock have passed through a phase similar to that shown by the longspurs, or share a common ancestry with them . . . Such a derivation would be a reasonable conclusion since the spread of Nearctic Emberizidae into Eurasia would be most likely to have occurred via a northern land-bridge or short sea crossing and would have occurred most easily if the invading stock was adapted to tundra-like conditions . . . The notion of a common ancestry of longspurs and Old World buntings could be further argued with reference to the close similarity between the Lapland Longspur [*C. lapponicus*] and the present Eurasian longspur [= *C. lapponicus* subsp.?], and the buntings of the Little Bunting (*E. pusilla*)-Reed Bunting (*E. schoeniclus*)-Rustic Bunting (*E. rustica*) subgroup."

This suggestion is reasonable. However, plumage similarities between Lapland Longspurs and Reed Buntings are comparable to those between

Smith's Longspurs and Rock Buntings (*E. cia*). Thus, by similar reasoning, a *pictus*-like ancestor for *Emberiza* can be postulated. Harrison's theory that *Emberiza* was derived from a "tundra-adapted" species seems to gain support from the fact that *Emberiza* includes forms similar to *pictus* and *lapponicus*, but not to either of the plains longspurs.

Ramifications of Harrison's view on the origin of *Emberiza*, diagramed in Figure 9, seem pertinent to understanding relationships within *Calcarius*. For simplicity, I have arbitrarily assumed that Smith's Longspur is most like the stock from which *Emberiza* was derived. In Figure 9A, for example, postulated that a *pictus*-like ancestor gave rise to "*lapponicus*" and that each of these gave rise to different species groups now placed in *Emberiza*. By this scheme, *Emberiza* is polyphyletic. In Figure 9B, "*pictus*" is postulated to have given rise to the "*cia*" group of *Emberiza*, from which the "*schoeniclus*" group was derived, and which, in turn, gave rise to another "longspur," *lapponicus*. This view regards *Calcarius* as polyphyletic. In Figure 9C, it is assumed that "*pictus*"gave rise to "*lapponicus*" as well as to the "*cia*" group, and that the *schoeniclus* group was derived from the latter. This scheme retains monophyly for both genera, but it raises the problem of explaining the parallel evolution of similar plumages in *Emberiza* and *Calcarius*. (Note that these diagrams may be read in reverse, by assuming that "*lapponicus*" is more like the ancestral stock; however, this in no way relieves the taxonomic dilemmas.) Each of these speculations is consistent with Harrison's thesis, but none is currently testable. Hopefully, as further information on the biology of other species of *Calcarius* and *Emberiza* becomes available, the evolutionary relationships within and between these genera will be clarified. Data on vocalizations of species in the "*cia*" group of *Emberiza*, on the timing of the molts and the extent of the prebreeding molt in *Emberiza* and the other species of *Calcarius*, and on the presence or absence of a flight song in *Emberiza* species may prove to be of greatest importance.

SUMMARY

Observations on the summer biology of Smith's Longspur (*Calcarius pictus*), a subarctic species that nests along the treeline from Ontario to Alaska, were made at Churchill, Manitoba, in the summers of 1964, 1965, 1966, and 1967. Males arrive at Churchill in small flocks in late May or early June, the females a few days later. Several days after arriving flocks break up and males begin to claim territories. There is evidence that some birds re-use territories in subsequent years. Territoriality is not strongly developed in this species, and males make little attempt to defend their activity space, song perches, mate, or nest site. By a week after pair formation, which takes place on the territory and without any conspicuous displays, territorial behavior virtually disappears.

Nests are built entirely by the female, usually in small depressions atop relatively flat, dry hummocks; they are lined with few feathers. Eggs are laid daily, the mean is

four. Only females incubate. Incubation periods of 11½ to at least 13 days 20 hours have been recorded.

For about two days after hatching, chicks are fed mainly by the female; by D-2 or D-3 the male's role equals that of the female. Detailed notes on the growth and development of the nestlings are included. The chicks become homeothermal by D-7, when they begin to leave the nest; they are able to fly short distances by D-13.

After leaving the nest, chicks are fed mainly by only one of the parents, which hastens the disruption of the family. When the chicks are about three weeks old, the parents desert them and form small flocks. Smith's Longspurs leave the Churchill area by early September.

Hatching success was consistently high during this study, and only 7 of 114 eggs failed to hatch. Fledging success was 50 per cent in 1966, but less than 5 per cent in 1965. In 1965 most nestlings died of exposure during a severe storm. Adverse weather was the most important factor limiting productivity in the period of this study.

The timing and extent of the postbreeding and prebreeding molts are described. The postbreeding molt begins in early July and may not be completed before the birds migrate. Males start molting a few days earlier than females.

Stomach contents of 70 birds, including 29 nestlings, were examined. In early June the adults feed mainly on seeds, but from mid-June through July animal matter, mainly terrestrial insects and larval stages of flying insects, composed the bulk of the diet. Seasonal weight changes in males are correlated with changes in activity.

The relationships of Smith's Longspur are not yet clear. It would appear that interrelationships in *Calcarius* may not be resolvable without also considering the relationship between *Calcarius* and *Emberiza.*

ACKNOWLEDGMENTS

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NATURAL HISTORY MUSEUM, SAN DIEGO, CALIFORNIA, 21 NOVEMBER 1967.

AGONISTIC INTERACTIONS BETWEEN BLUE-WINGED AND "BREWSTER'S" WARBLERS

Andrew J. Meyerriecks and James Baird

Since the days of Brewster (1881) ornithologists have been intrigued by the relationship between the Blue-winged Warbler (*Vermivora pinus*), and the Golden-winged Warbler (*Vermivora chrysoptera*), and their hybrids. There has been a resurgence of interest in recent years, both by systematists (Parkes, 1951; Short, 1963), ethologists (Ficken and Ficken, 1962) and others (Berger, 1958: Gill and Lanyon, 1964). We believe that additional behavioral observations will aid significantly in the solution of the many problems involved in this fascinating complex. From 22 May to 25 June 1961, we spent a total of 25 hours, largely in the early morning, making behavioral observations on two of the forms involved in this complex, a male Blue-winged Warbler and a male "Brewster's" Warbler.

HABITAT DESCRIPTION

The study area was a portion of the Cambridge Reservoir, located largely in Lexington, Middlesex County, Massachusetts (Fig. 1). It may be divided into two major vegetative units: (1) an extensive upland deciduous (oak-hickory) forest, only the southern edge of which was utilized by the "Brewster's" and the Blue-wing, and (2) an abandoned old field or pasture, which had a well-developed peripheral growth of quaking aspen (*Populus tremuloides*), gray birch (*Betula populifolia*), black cherry (*Prunus serotina*), red maple (*Acer rubrum*), American elm (*Ulmus americana*), black locust (*Robinia pseudo-acacia*), staghorn sumac (*Rhus typhina*), gray dogwood (*Cornus amonum*), meadowsweet (*Spirea latifolia*), catbrier (*Smilax* sp.), and blackberry (*Rubus* sp.?). The trees in these stands, which bordered the oak woods and the edge of the reservoir, averaged 20 to 25 feet in height. The central portion had a grassy aspect but was heavily invaded with woody plants. The predominant plant species here were broomsedge (*Andropogon scoparius*), dewberry (*Rubus villosus*), goldenrods (*Solidago* spp.) and asters (*Aster* spp.). There were several large and many small dead elms, which were frequently used as singing perches.

Areas A and B were essentially in the same stage of development and occupied by the same plant species, but area B had considerably more shrubby growth and less open grassy areas (Fig. 2a and b).

METHODS

We observed the birds with 7× and 12× binoculars. All vocalizations were taped with the use of a Nagra III B tape recorder.

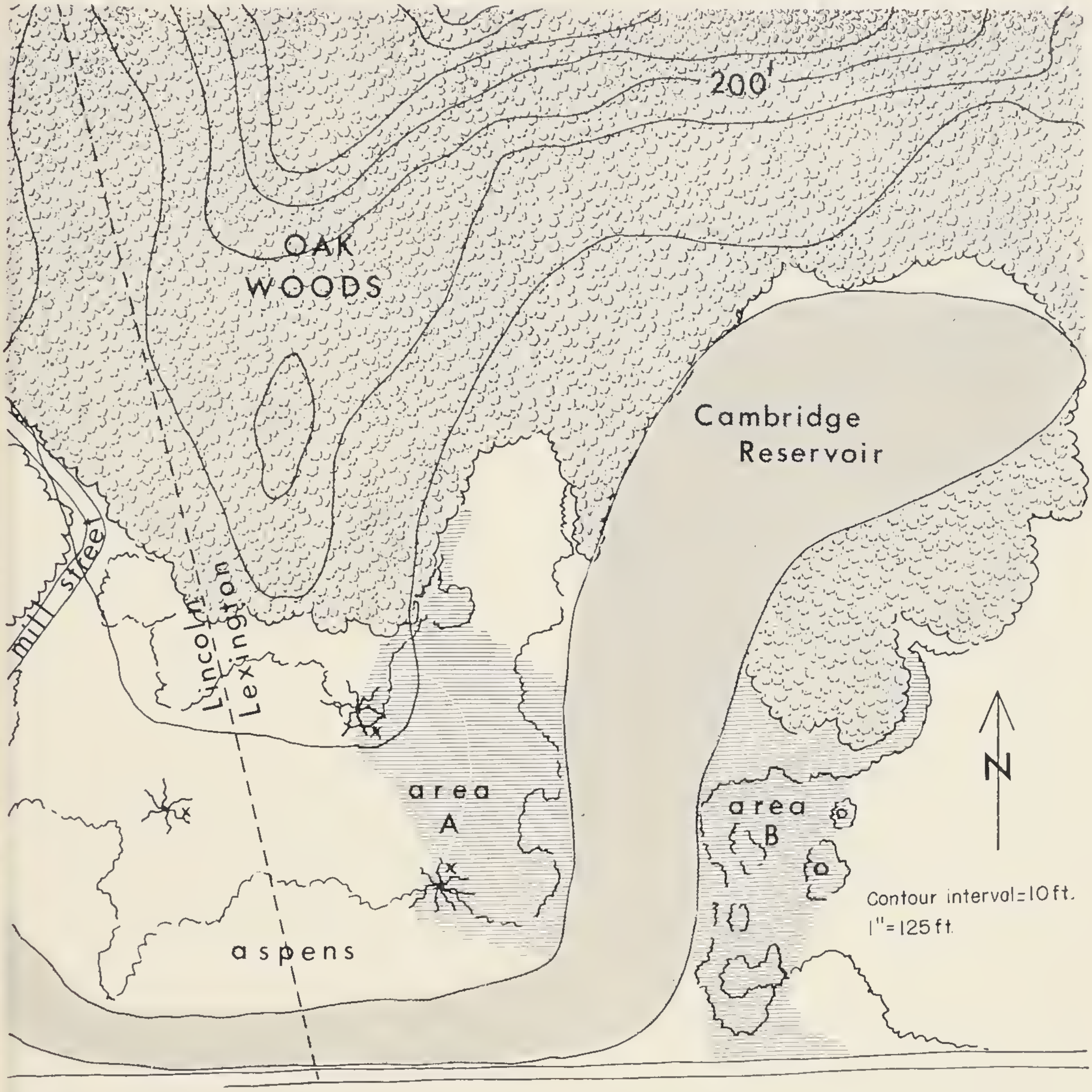


FIG. 1. Map of the study area, part of the Cambridge Reservoir, Lexington, Middlesex County, Massachusetts. Two circles in area B and X's in area A symbolize prominent song perches (see text for details).

AGONISTIC BEHAVIOR

All of the behavior we observed clearly comes under the rubric of agonistic behavior. Since thorough searches during the entire observation period failed to reveal a single female, we are therefore arbitrarily ruling out sexual motivation. For descriptive purposes, the observed agonistic behavior is classified under three subheads; aerial, non-aerial, and vocalizations. For comparative purposes and where applicable we use the terminology of Ficken (1962*a*).

Aerial Displays

Diving Attacks.—Of the twelve Diving Attacks seen, all took place in area B, and eleven were made by the Blue-wing. Diving Attacks typically were launched from a perched position upon either a flying individual or one perched below.

Fights.—Fights were uncommon (we observed six). They consisted of the birds flying up together, briefly meeting in midair, then parting.

Spiralling.—This behavior took place during a chase and began when the birds landed in a small tree or bush. Usually, the uppermost individual hops or makes short flights downward and around the periphery of the tree or bush toward its opponent. Once, however, we saw the lowermost bird spiral upward toward its opponent. Spiralling was observed eleven times and ended when the chase was resumed. In no way does it resemble the Circling of Ficken (1962*a*).

Supplanting.—Supplanting attacks were observed seven times and in every case they took place during a chase. The "Brewster's" supplanted the Blue-wing 5 times and the Blue-wing was the supplanter twice. With one exception, supplanting occurred in Area B.

Chases.—Most of the Chases we saw took place well within Area B, the territory of the "Brewster's" Warbler, and most were initiated by the persistent intrusion of the Blue-wing from Area A. Of the 79 Chases observed, the "Brewster's" was the pursuer in 44, the Blue-wing in 35. Our observations of Chases agree in general with those of Ficken (ibid.) on the American Redstart (*Setophaga ruticilla*) with respect to ritualization: the pursuer never caught up with the pursued. An even more striking example of the ritualized nature of chases is shown by those involving a display flight, a slower flight than normal (see below). We heard no vocalization, again in general agreement with Ficken (ibid.). Direct, rapid Chases were observed 29 times; all were short and at low level (less than 10 feet). The remaining fifty involved one or both birds in a display flight:

> *Flutter Flight.*—The Flutter Flight display was most often shown after a chase by the bird going away from its opponent. The flight was usually direct, of short duration at low elevation and without vocalizations. The displaying bird held its head high, the feathers of the crown raised, the bill pointed slightly upwards and it occasionally looked to the rear. The tail was elevated slightly above the horizontal, moderately spread and sometimes fanned. The wings were bowed, and the wing tips fluttered (strongly reminiscent of the flight of the Spotted Sandpiper (*Actitis macularia*) (see Fig. 2a)). The Flutter Flight display, although not exclusively the Blue-wing's display, was more often shown by that individual.
>
> *Tail-fanning* (aerial).—The Tail-fanning display, shown only by the "Brewster's" was similar to the Flutter Flight except in the following:

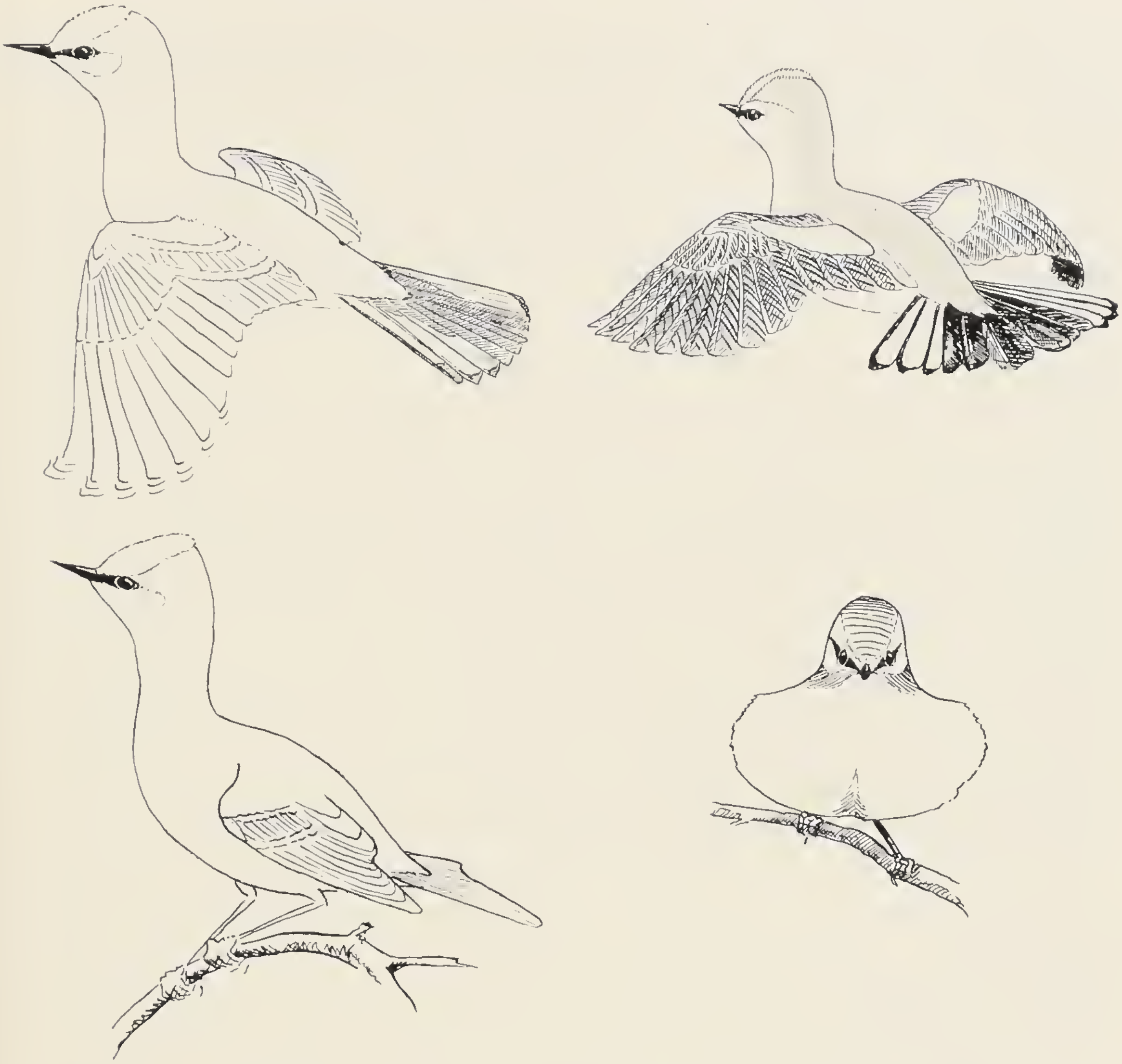


Fig. 2. Aerial and non-aerial displays of the Blue-winged Warbler and the "Brewster's" Warbler. (2a) (upper left) Blue-wing in Flutter Flight Display; (2b) (upper right) "Brewster's" showing Aerial Tail-fanning; (2c) (lower left) Blue-wing in Erect Threat Display; (2d) (lower right) "Brewster's" in Puff Display (see text for details).

(1) the wings were bowed but the wing tips were not fluttered; (2) the wing beats were noticeably slower; (3) the tail was frequently fanned, a movement which made the white tail markings very conspicuous (see Fig. 2b). Occasionally the fanning was extreme.

Non-aerial Displays

Crown-raising.—The "Brewster's" Warbler was twice seen to raise its crown feathers, once in the Puff Display (see beyond) and once as part of a prolonged encounter.

Tail-fanning (perched).—We saw this display given twice by the "Brewster's" and once by the Blue-wing. On each occasion the birds were close to one another. The most extreme fanning (closely approximating the tail spread of the redstart, Ficken (*ibid.*)) was seen as part of the Puff Display (see below).

Erect Threat.—This display was shown only by the Blue-wing. In one instance it raised its head, drooped its wings and quivered them while sidling directly towards the "Brewster's." In the other, it perched erect, with the wings drooped stiffly and the tail partially spread (see Fig. 2c). At first glance, this apears to be the Male Soliciting display described by Ficken and Ficken (ibid.) for the Golden-winged Warbler, but our observations indicate that the context in which the Erect Threat is shown differs from that of Male Soliciting, which Ficken and Ficken state as being an outcome of being "defeated after prolonged boundary conflicts." It is true that this display was shown after prolonged boundary disputes, but the displaying Blue-winged male sidled *toward* the "Brewster's" Warbler. The display seemed to us to be in the nature of a threat to the "Brewster's" rather than submission following an unsuccessful encounter, since the agonistic interactions were resumed at once after display of the Erect Threat by the Blue-wing. In Male Soliciting, according to the Fickens, the displaying bird faces *away* from its opponent, signifying submission after losing the boundary encounter.

Puff Display.—This was the most striking non-aerial display we observed, and it was shown only once, by the "Brewster's," as the terminal display in a prolonged agonistic encounter: The "Brewster's" flew up towards the Blue-wing, stopped when he was three feet away, faced the Blue-wing, ruffled his back feathers, lowered them and then showed the Puff Display—

In this display, the "Brewster's" sleeked his body feathers, then fluffed out his breast feathers until he appeared extremely wide; at the same time he raised his crown until he had what appeared to be a long narrow head with a bright yellow cap. His black eye-stripes, bill and eyes contrasted sharply against the yellow and white of the head (Fig. 2d). The tail was fanned to an extreme degree. The bird held this display for several seconds and then moved closer to the Blue-wing, which flew away. Throughout both birds were silent.

Although birds commonly show Head Forward, Gaping, and Wings Out as part of their agonistic repertoire, the two males observed showed none of these displays.

Vocalizations

Singing was a prominent feature of the overall agonistic situation, but other vocalizations were remarkably infrequent. In fact, we heard vocalizations other than songs only twice: once during a spiralling display the Blue-wing called *tic* several times, and once during an especially long encounter chip notes were heard.

Both birds sang almost continuously during the early morning hours (when most of our observations took place), and on several occasions we heard singing in the late afternoon and early evening. Singing remained vigorous until, at least, 13 June and the Blue-wing was heard singing several times on 25 June. Throughout this period the song patterns remained the same in both birds; with one exception, there was no change to a "second" song (see below).

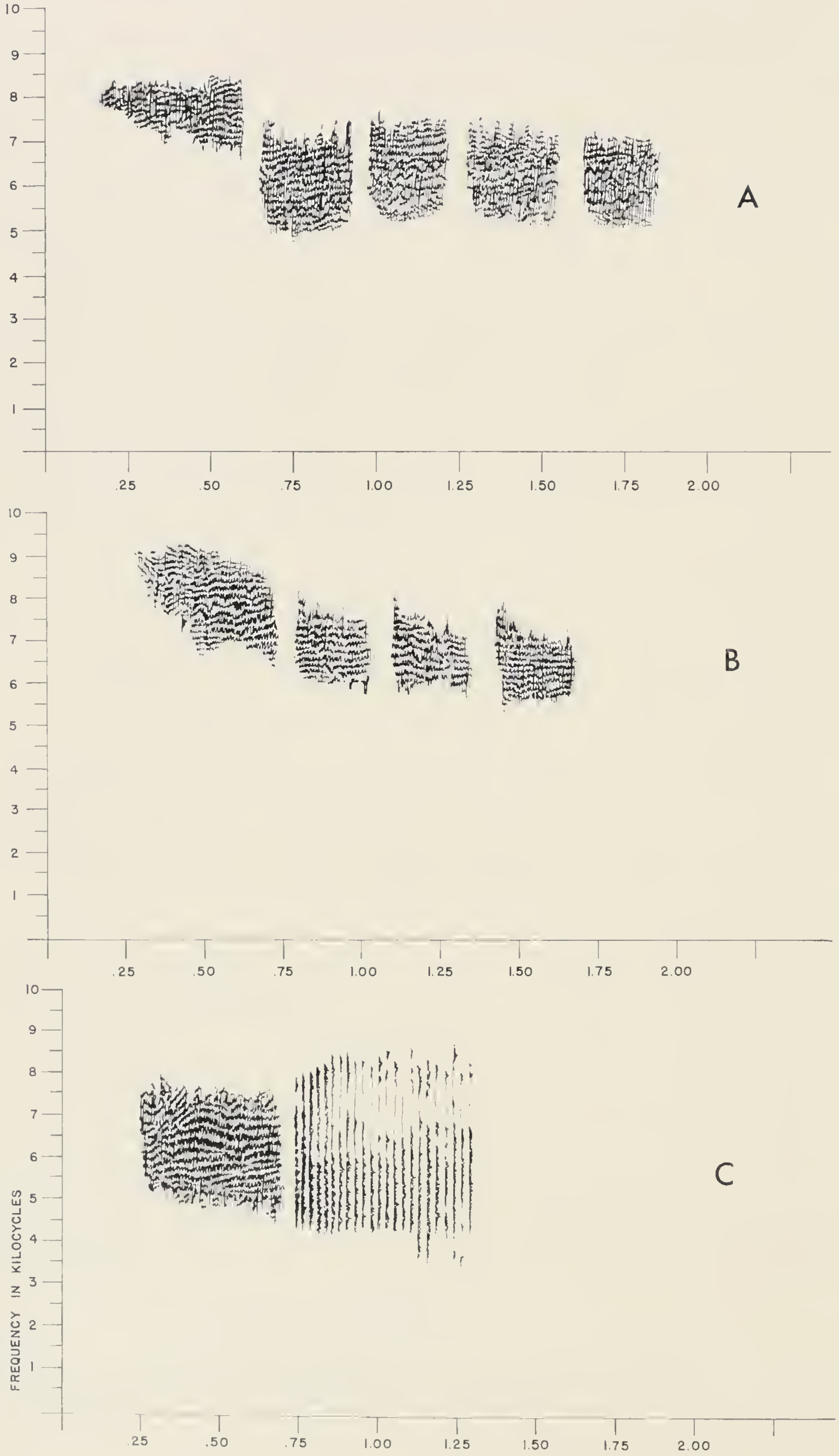
The birds sang most frequently from favored singing perches, which for the "Brewster's" was a small 15-ft. cherry and a similar sized oak in area B (marked with a circle on Fig. 1), while the Blue-wing sang from the upper branches of the many dead elms in area A (marked X on Fig. 1). The Blue-wing did not exhibit as strong a preference for particular singing perches as did the "Brewster's." The birds often engaged in extensive preening while at their singing perches (where they alternately preened and sang), and also sang while feeding but with longer intervals between songs.

As noted above, singing was important in the agonistic interactions between the "Brewster's" and the Blue-wing, and appeared to be an integral part of both the aerial and the non-aerial displays of both birds, as illustrated by the following example from our field notes on 24 May 1961:

> 0801—Both are singing. Brewster's flies across the clearing, chases Blue-wing; both now at right hand edge of clearing. Brewster's comes back, sits in low dogwood, sings. Blue-wing dives upon Brewster's. Blue-wing singing in top of red maple, Brewster's down low. Both still singing. Blue-wing just flew down to left hand side of clearing where Brewster's is singing. A real song duel going on now. . . . . .etc.

We recorded 26 instances of what we referred to as "song duels." These took place in a variety of contexts, but were all similar in that they consisted of a song by one bird given in response to a song by the other. Sometimes, these "song duels" took place with the "Brewster's" in area B and the Blue-wing in area A, but more frequently "song duels" were part of the general agonistic behavior that occurred whenever the two birds met.

The song of the "Brewster's" was a typical *chrysoptera* vocalization, *beee bzz bzz bzz* (Fig. 3, A and B), and was the only song type heard. The Blue-wing had two songs, neither of which was a characteristic *pinus* song type (Fig. 3, C), but were more *chrysoptera*-like; both were similar in form, differing only in the number of *bzzes*, and may be phoneticized as *beee bzz bzz bzz*, or *beee bzz bzz bzz bzz*, all given on the same pitch (Fig. 3, D and E). This part of New England has long been well known as a zone of hybridization between *chrysoptera* and *pinus*, and it is therefore not surprising that the Blue-wing would show some sign that it was not phenotypically "pure,"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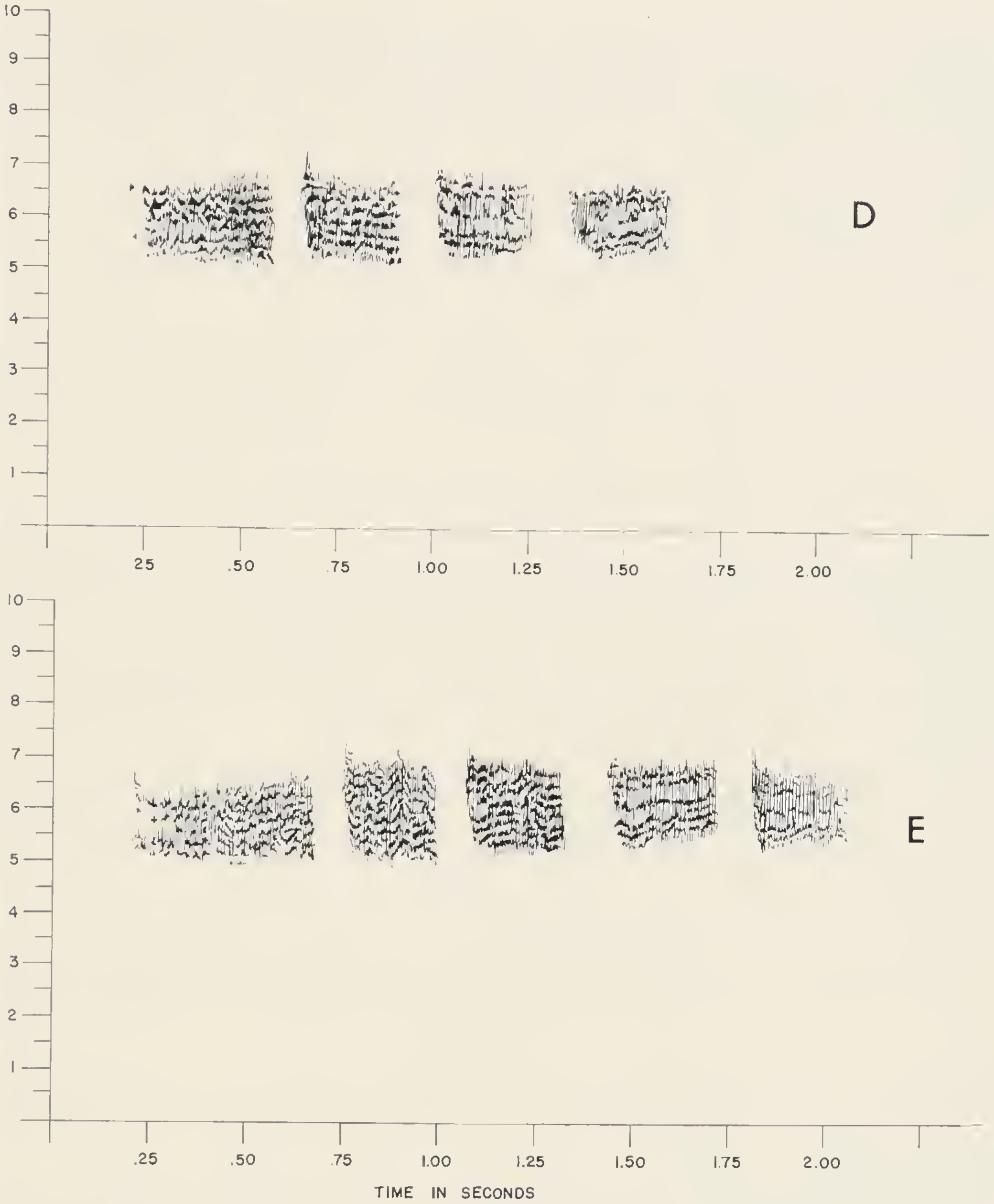

FIG. 3. Tracings of sonograms of the vocalizations of: (A) Golden-winged Warbler—taken from Federation of Ontario Naturalists recording, (B) "Brewster's" Warbler—recorded by the authors in 1961 at the Cambridge Reservoir, Lexington, Massachusetts, (C) Blue-winged Warbler—taken from Federation of Ontario Naturalists recording, (D & E) Blue-winged Warbler recorded by us at the same place and time as B.

although this introgression was not evident in its plumage.[1] The area in which the Blue-wing was found is one where hybridization apparently often occurs,

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[1] Although such was our impression, we must qualify this statement by noting that since we observed the birds through binoculars and did not examine them in the hand, we cannot state with certainty that the Blue-wing did not show some evidence of introgression in its plumage (cf. Short, 1963 p. 150). The same is essentially true of our observations on the "Brewster's," which resembled, in its general morphological characters, a "typical" "Brewster's" Warbler; we did note that it had a conspicuous yellow wash across the breast.

as shown by the observations of Baird who observed on 16 July 1961, in the then-deserted area A, a *Vermivora* family group composed of a male *chrysoptera*, a female *pinus* and four young—one of which was *chrysoptera*-like and another *pinus*-like, and on 18 May 1962 observed a female "Lawrence's" Warbler with a male *chrysoptera* in a maple swamp less than a mile from the 1961 study area.

Only once was the Blue-wing heard singing a song other than those described above. On 30 May, it sang a single "upward" song which was not heard again. A recording was not made of this song, but it would seem to correspond with the description given by Saunders (1951) for the "second song of the Blue-winged Warbler."

DISCUSSION

Although we were not present when the birds first arrived (the "Brewster's" was first seen by another observer on 14 May), it was our impression that on 22 May both birds were attempting to establish territories in area A (see Fig. 1). Very quickly, however, the "Brewster's" was restricted to area B. In fact, it was not again seen in area A after 23 May, and by the end of our observation period its activities were largely confined to an aspen grove at the south end of B. We believe that this ultimate confinement of the "Brewster's" to a small section of the initially larger area was entirely due to the agressive behavior of the male Blue-wing.

The Blue-wing made constant forays into the "Brewster's" territory (area B); these persistent incursions frequently resulted in prolonged agonistic encounters which lasted from 10 to 37 minutes. These long periods of intense interaction involved almost the entire agonistic repertoire of both birds as observed by us: Pursuit Flights (more than 80), Supplanting Attacks, Fights, Song Duels, etc.

This dominance by the Blue-wing is also indicated by the fact that the Blue-wing often sang from one of the primary song posts of the "Brewster's." Secondly, although the "Brewster's" actively engaged the Blue-wing in aggressive encounters, it never pursued the Blue-wing beyond area B.

Additional suggestive evidence of this Blue-wing dominance is found in the positional relationship of the birds and the number of diving attacks seen. We observed repeatedly, at a ratio of 10 to 1, that during and after prolonged agonistic encounters, the Blue-wing would land higher than the "Brewster's." Although we do not have a clear-cut correlation between height and diving attacks, it is suggested that this might confer an "attack" advantage for the Blue-wing, since it was the attacker in 11 out of the 12 Diving Attacks seen.

As was noted earlier, at no time did we observe any females, and we believe that the absence of females contributed to the intensity and duration of this wholly agonistic relationship. Support for this view may be found in the fact that the observations of Gill and Lanyon (1964) on the territorial behavior of male Blue-wings known to be mated, differed markedly from our bird. We saw practically none of the displays which they associated with territorial defense (i.e., Tail Pumping, Wing and Tail Flicks), and they apparently saw none of the more striking displays we observed. Since it is known that the songs of many warblers change after nesting begins (including *pinus* and *chrysoptera*), it could be expected that there are associative behavioral changes as well.

However, M. S. Ficken states (in litt.) that the "encounters may be more intense when females arrive, e.g. more fights than you observed, at least from our observations in somewhat comparable situations." She further suggests that the behavioral differences between Gill and Lanyon's (ibid.) Blue-wing/Blue-wing encounters and our Blue-wing/"Brewster's" encounters may be due to plumage differences: "From what we know of visual releasers, it might be expected that they [Blue-wings, Golden-wings and hybrids] would not react quite the same to a bird with another plumage. I have also found that in mixed pairings of Brewster's male and Blue-wing female, the male and female behaved differently toward each other than in conspecific pairings of Blue-wings."

It seems to us that all of these suggestions have merit, and to one degree or another may be applicable, but it is obvious that a better foundation of ethological understanding of these species will be required before such a complex set of interactions can be properly interpreted.

SUMMARY

One male Blue-winged Warbler and one male "Brewster's" Warbler were observed for 25 hours during a series of prolonged agonistic encounters. Aerial and non-aerial displays and vocalizations are described and illustrated. Morphologically, the Blue-wing and the "Brewster's" seemed "pure." The "Brewster's" sang a typical *chrysoptera* song. Two song types of the Blue-wing were more like *chrysoptera* than *pinus*. At the end of the observation period the "Brewster's" was confined to a very small part of its initially large territory, due, we believe, to the persistent aggressive behavior of the Blue-wing.

ACKNOWLEDGMENTS

We are indebted to Mrs. Jean Baxter for locating and calling to our attention the "Brewster's" Warbler. We also wish to thank Dr. Robert W. Ficken for providing us with sonograms of the songs, and Dr. Millicent S. Ficken for reading the manuscript and making many helpful suggestions.

APPENDIX

Maintenance behavior

In the course of our 25 hours of observation in 1961, we had several opportunities to observe maintenance behavior in both the Blue-winged and the "Brewster's" Warbler. Due to the paucity of such information we would like to comment briefly on this behavior:

Head-scratching.—Indirect head-scratching was observed 9 times. During preening sessions the Blue-wing was seen to head-scratch twice and the "Brewster's" five times. Twice the "Brewster's" was seen to head-scratch without comfort movements preceding or following it.

Preening.—Both the Blue-wing and the "Brewster's" were observed preening several times. On each occasion, preening was accompanied by such other comfort movements as head-scratching, wing-stretching, and tail-spreading. Preening was essentially the same in both birds (as illustrated by the following protocol): "preened breast feathers several times, preened scapular tract on both sides while drooping wing, preened flank and rump feathers. Shuffled body and wing feathers while spreading and shaking tail." Both birds were seen to preen while singing.

Stretching movements.—Only one stretching movement was observed (the wing and leg sideways stretch of Ficken, 1962*b*). The Blue-wing was seen during a preening session to stretch its left wing to the back and side (over its left leg?), while spreading tail. The "Brewster's" was seen to do the wing and leg sideways stretch several times.

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COURTSHIP OF BLUE-WINGED WARBLERS, GOLDEN-WINGED WARBLERS, AND THEIR HYBRIDS

Millicent S. Ficken and Robert W. Ficken

Comparative studies of courtship of hybridizing avian species in nature have rarely been attempted with the exception of the Anatidae (e.g., Johnsgard, 1960). A rare opportunity to study birds whose courtship pattern is different than waterfowl is presented by Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*), which commonly hybridize in their extensive area of sympatry. There is preferential conspecific mating in at least some areas of sympatry and hybrids are selected against, demonstrating the operation of reproductive isolating mechanisms (Ficken and Ficken, 1968*a*). Thus a study of this species complex offers an unusual chance to further the understanding of the role of courtship in the speciation process.

Courtship includes the activities of the male and female from the time of pair formation through copulation (Morris, 1956). We describe the general pattern of courtship activities and displays for conspecific pairs of both species and two pairings involving hybrids. Interspecific sexual attractions are discussed. By comparison with courtship of several other parulids. we arrive at some conclusions concerning the selective pressures which have affected courtship in these *Vermivora*. Finally, the role of courtship in reproductive isolation is discussed as are those aspects of behavior which increase interbreeding.

METHODS

Observations of both species and Brewster's hybrids were made in Varna (Tompkins Co.), New York during 1961–1963 and 1966. Daily observations took place from 0630 to 1100 E.D.T. during the courtship period. Notes were spoken into a pocket tape recorder.

During the four-year period we observed pairings in a total of 15 Blue-wings, five Golden-wings, three Brewster's hybrids mated with Golden-wings. and five Brewster's hybrids mated with Blue-wings. No interspecific pairings were observed. Detailed accounts of pairings in the colony are given elsewhere (Ficken and Ficken, 1968*a*). Courtship activities were studied closely in three Golden-wing pairings, five Blue-wing pairings and two pairings of male Brewster's hybrids and female Blue-wings. Both hybrids gave Blue-wing songs but they differed somewhat in coloration. one having white underparts, the other a yellow wash across the breast. By "Blue-wings" and "Golden-wings" we refer to individuals that phenotypically resembled one or the other parental species, but it must be noted that there was introgression in this population (Short, 1962).

OBSERVATIONS

First we describe the general pattern of events in courtship and then proceed to a more detailed discussion of pair interactions and displays.

General pattern of courtship.—Males maintain a territory, usually a little over an acre, where they sing persistently before the arrival of females. Unmated males of the two species often have overlapping territories, although interspecific agonistic encounters occur during a brief period when at least one (and often both) males first become mated. After a few days these interspecific interactions cease and the birds resume territorial overlap without friction.

Females usually arrive a day or two later than males of the same species. Pair formation occurs immediately after the female's arrival. As soon as a female arrives on his territory the male spends much time following her. During this period the male approaches the female many times, apparently attracted by her call notes (*Tzips*) and she usually stays low in the undergrowth. Although both sexes are often aggressive toward each other, aggression is more marked in the male. The female initiates a bout of sexual activity by assuming the Soliciting posture; the male sometimes displays as he approaches her while she is displaying and copulation may follow.

Early arriving females wait a day or two before beginning nest building but later females may begin nest building the day of arrival. Sexual activity is most intense just prior to and during the first day of nest building. No sexual activity was observed after this time and probably did not occur since males spent much less time near their mates during later stages of nest building and females no longer gave the location call.

Pair formation.—Although we did not see the initial meeting of a pair, we made many observations of pairs early the first morning of pairing. The male spent a great deal of time approaching and chasing the female. We saw no special displays associated with early pair formation, the process being similar to that in the American Redstart (*Setophaga ruticilla*) (Ficken, 1963). Pair formation occurs very rapidly and probably involves responsiveness to color pattern and song by the female and responsiveness by the male to her visual and behavioral characteristics (Ficken and Ficken, 1968*a*).

Attempts at interspecific pairing.—Although no interspecific pairings occurred, we observed several situations where there were interspecific attractions. We observed a female Blue-wing which had arrived very late, approach a male Golden-wing which was mated to a Golden-wing. The Golden-wing ignored her completely but his mate gave the *Tzip* vocalization

TABLE 1

PAIRINGS ATTEMPTS BY UNMATED MALES APPROACHING FEMALES MATED TO CONSPECIFICS

Unmated male	Female	Ultimate state of unmated male
Brewster's hybrid	Blue-wing	Unmated
Brewster's hybrid	Golden-wing	Mated to Golden-wing[1]
Blue-wing	Golden-wing	Unmated
Golden-wing	Blue-wing	Mated to Golden-wing

[1] Not the same individual as the one that was approached.

indicating mild alarm and the strange female soon left. She then approached a mated male Blue-wing on the same territory; his responses were not observed but she soon left the area.

In another type of interspecific attraction, unmated males were attracted to the female of the male occupying an overlapping or adjacent territory (Table 1). These approaches were usually followed by intense encounters between the two males. In no case did the invading male "steal" the female from her mate. Berger (1958) cites an observation of three males—a Brewster's hybrid, a Blue-wing, and a Golden-wing—engaged in encounters centered on a Golden-wing female.

Agonistic and sexual interactions of the pair.—The pre-nest building period was marked by many male approaches toward the female; only rarely did the female come to the male. In many cases the male simply flew to within one foot of the female, assumed no special posture, remained a few seconds, and then flew off while the female uttered *Tzips.* This type of approach was termed non-aggressive (Table 2). In other cases the male flew directly to the female, she fled and he chased her. When she did not flee he lunged and fights often occurred. We term these approaches aggressive. Blue-wing and Golden-wing males were similar in the percentages of aggressive and non-aggressive approaches of the female (Table 2). However, the incidence of aggressive approaches was much lower in Brewster's hybrids paired with female Blue-wings. This difference between pairings involving a hybrid and conspecific ones is statistically significant using a Chi Square test ($P < 0.05$). For the purpose of this comparison sexual interactions were excluded.

Females responded to males' approaches in a variety of ways which we also categorized as non-aggressive or aggressive. Non-aggressive responses included remaining (often giving *Tzips*) and fleeing. Aggressive responses included lunges at the male, often with Bill Snaps and flying attacks directed at the oncoming male. Again both Blue-wing and Golden-wing females paired with conspecifics showed a similar pattern, females being aggressive

TABLE 2
NUMBER OF AGGRESSIVE VS. NON-AGGRESSIVE APPROACHES OF THE MATE IN CONSPECIFIC AND HYBRID PAIRINGS (n = NUMBER OF PAIRS)

	Aggressive	Non-aggressive	Total	Per cent aggressive
Male's reaction to female:				
Golden-wings ($n = 3$)	8	9	17	47
Blue-wings ($n = 3$)	19	18	37	51
Brewster's hybrid and Blue-wing females ($n = 2$)	6	15	21	29
Female's reaction to male:				
Golden-wings ($n = 3$)	5	14	19	26
Blue-wings ($n = 3$)	10	31	41	24
Brewster's hybrid and Blue-wing females ($n = 2$)	2	17	19	11

to males during an average of 25 per cent of the male approaches. However. female Blue-wings paired with Brewster's hybrids showed a lower incidence of aggressive responses to the approach of the mate (Table 2). This difference was statistically significant using a Chi Square test ($P < 0.05$).

Females frequently uttered *Tzips* before nest building but were usually silent later on. *Tzips* were sometimes uttered when the male was away; he often then responded immediately by approaching. *Tzips* were also given in apparent response to the song of the mate, especially after he had been silent for a long time and then suddenly sang. *Tzips* were given also by the female when the male approached. This call note seems to serve several related functions: (1) it informs the male of the female's location which is important since females wander greatly around the territory the first few days. (2) it stimulates male approaches, and (3) it also may be important in cementing the pair bond. The form of the *Tzip* was identical to our ears in all birds. However. a brief series was often given by female Blue-wings. while female Golden-wings uttered it singly.

The two species and the Brewster's hybrids sometimes showed behavior indicating conflict when near the mate. Both sexes frequently Tail Spread after approaching or being approached. Tail Spreading in flight. so prominent in agonistic encounters between males (Ficken and Ficken. in press) was rare in interactions between the pair: most of the Tail Spreading was given in a stationary posture. Pivoting. in which a perched bird rotated the body without moving the feet, was often accompanied by Tail Spreading. Wing and Tail Flicking sometimes took place as well. Crown Raising. on the other hand, was seen only in the male Golden-wing when near the female. However, since the Blue-wing does not have such a well-delineated crown patch, we possibly overlooked this display.

Males of both species performed two different flight displays near the female. In Moth Flight the male usually flew slowly with marked wing beats and the head held high. In both species this display occurred as the male flew away from his mate and usually he did not react aggressively to her afterward. Once Moth Flight preceded a copulation by a Blue-wing. In Gliding the male held the wings out rather stiffly in a long coasting flight. Gliding occurred in slightly different contexts than Moth Flight, being given more often as the male approached the female. After Gliding the male sometimes chased his mate.

Bill Dueling was observed several times in both species, occurring just after the male approached the female. She then either flew out to meet him or sometimes remained perched and they pecked at each other's bills. Occasionally they seemed to grasp bills and then fell down toward the ground still holding on. Bill Dueling was different from fighting in that it did not involve striking with the feet and was also sometimes associated with sexual activity (see p. 166).

Wing Extension was seen only twice and in a male Blue-wing. The perched bird held the wings lifted to the side and somewhat spread. On one occasion the display preceded a Hover near the female and another time Gliding.

The male performed Hovering a few inches away from the perched female. The male's breast feathers were very fluffed, the tail was spread and the bird fluttered with rapid wing beats in front of the female. It occurred once when the male approached in apparent response to female Soliciting and in two other instances was also associated with sexual activity.

The only primarily sexual display given by the female was Soliciting which is similar in form in many passerines. In the most exaggerated cases the neck was extended, the breast lowered, the tail markedly raised and the wings vibrated (high intensity Solicit). Sometimes these components were less pronounced (low intensity Solicit). In none of the seven Solicits that were seen did the birds give vocalizations accompanying the display. In both species the only copulations observed followed Soliciting. Because of its obvious importance and the variable situations in which Soliciting occurs, we give summarized accounts from our field notes on Soliciting and copulation.

Case 1.—Male Brewster's hybrid No. 1 paired with Blue-wing female, second day after pairing. Male makes many non-aggressive approaches of the female, coming to within a few feet and peering at her as she forages in the undergrowth. Female silent except when male near. Suddenly she gives a short flight, uttering *Tzips*, the male flies in from about 30 feet away and chases her. She lands and immediately gives high intensity

Solicit. Male remains within three feet for five minutes, with no special postures and makes no attempt to copulate. Shortly after Soliciting the female picks up a leaf (she has not previously been observed doing any nest building) but soon drops it.

Case 2.—Blue-wing pair No. 5, third day after pairing. Male has approached female to about one foot at least six times in the last few minutes. During one approach she briefly Solicits at low intensity, but he leaves with no attempt to copulate.

Case 3.—Golden-wing pair No. 4, first day after pairing. Female gives *Tzips* constantly. Suddenly she Solicits at low intensity, male which was off about 20 feet, immediately flies in and mounts her with much fluttering of wings while on her back.

Case 4.—Golden-wing pair No. 2, first day after pairing. Blue-wing male No. 3 moves into this Golden-wing's area. Males chase and fight and female Golden-wing approaches them. Female Solicits, male Golden-wing which had been near her, ignores her and flies back toward the male Blue-wing which remained about ten feet away. A few minutes later male Golden-wing Hovers near his female but then flies off.

Case 5.—Blue-wing pair No. 3, first day after pairing. There have been many encounters in the last half hour between this male and Golden-wing male No. 2 whose female is also in the area. During a fight of the two males, female Blue-wing Solicits at high intensity, but the male does not approach and is still engaged in encounters with the other male. Male Golden-wing chases female Blue-wing and she immediately Solicits on landing. There are no approaches by either male. After a minute or so she Solicits again and then flies off and the male Blue-wing follows her. She again lands and Solicits and the male Blue-wing approaches but does not mount. A minute later she again begins a high intensity Solicit and the male Blue-wing which was 20 feet away and still engaged in encounters with the Golden-wing male flies in, but we are unable to see if he mounts her. She continues Soliciting but both males are engaged in encounters. During one Solicit, the Golden-wing female which is nearby flies in and chases her. The Blue-wing female still Solicits and is followed by the Golden-wing female as she moves through the undergrowth in this posture. Males continue to have encounters. Blue-wing female Solicits at high intensity in presence of Golden-wing female 10 feet away, and is ignored by her. Blue-wing male comes in and chases Blue-wing female. She Solicits immediately after the chase and the Blue-wing male approaches her again, this time with Moth Flight, and they copulate. He performs a Hover in front of the female and then flies off. She shakes the feathers of her cloacal region. She resumes Soliciting, he gives a Moth Flight toward her and they Bill Duel and fall down into the undergrowth with bills held together.

From these observations it can be concluded that the male's response to a Soliciting female is variable; he may leave without attempting to mount as in Cases 1, 2, 4 and 5, or copulation may take place as in Cases 3 and 5. Male displays preceded copulation in some cases but not in others. Soliciting followed aggressive approaches by the male in Cases 1 and 5. Cases 4 and 5 occurred during interspecific encounters, and while these encounters only occupied at most a few hours of the approximately 100 during which pairs were watched closely, Soliciting was seen in females of both species and copulation in the Blue-wing. Thus it seems that direct aggressiveness by the male, or participating in and observing aggressive encounters stimulates Soliciting in both species.

There was one case of an interspecific sexual reaction (Case 5) when the female Blue-wing Solicited after being chased by the Golden-wing male. The same female also Solicited after a chase by the Golden-wing female. This indicates that Soliciting is not given exclusively in the presence of the mate but occurs when the female reaches a high degree of sexual readiness brought about by intense agonistic activity.

There were insufficient observations for detailed comparisons of the courtship behavior of the two species and hybrids. Our inventory of courtship displays is undoubtedly incomplete, since Baird (1967) noted a courtship display and courtship feeding in the Golden-wing that we did not observe, but his accounts of Gliding and Hovering in this species are similar to ours. The general pattern of sexual behavior is similar in both species as are male displays and the contexts in which the female Solicits.

DISCUSSION

Evolution of courtship behavior.—Comparative studies are a prime source of information concerning the selective pressures affecting the behavior of closely related species (Tinbergen, 1965). We have derived some ideas concerning the probable selective pressures affecting courtship in these *Vermivora* species from a knowledge of their general breeding behavior and from comparisons with other warblers, particularly the American Redstart (*Setophaga ruticilla*) as well as some *Dendroica* species (Ficken, 1963; Ficken and Ficken, 1962, 1965). The redstart is probably closely related to *Dendroica* (Parkes, 1961; Ficken and Ficken, 1965) and not very distantly related to *Vermivora*. Griscom (in Griscom and Sprunt, 1957) combines *Vermivora* and *Dendroica* in the same genus.

One difference between these *Vermivora* species and several species of *Dendroica* and *Setophaga ruticilla* is that a special vocalization accompanies Soliciting in *Dendroica* and *Setophaga* but not in *Vermivora*. The lack of a Soliciting vocalization in these *Vermivora* may be due to the fact that the female usually Solicits when the male is nearby. In *Setophaga* and *Dendroica* the female often Solicits spontaneously after a bout of nest building but the male is usually some distance away and unable to see her; her Soliciting calls are necessary to communicate sexual motivation and location to her mate. Furthermore, this difference in Soliciting is related to the difference in courtship pattern of the two groups of warblers. Males of these *Vermivora* spend a short time intensively courting the female and are near her much of the time. Hence, they are more likely to be close by when she is sexually motivated. On the other hand, courtship is more protracted in *Setophaga* and *Dendroica*, and males are often not near the female when she is sexually motivated. Soliciting vocalizations are present in many passerines and seem to have been secondarily lost in these *Vermivora*. In the absence of direct selection for this vocalization in courtship, such vocalizations would probably be selected against because their conspicuousness would attract predators.

Female warblers give another type of vocalization, the location call, which is not confined to sexual contexts and is different in form from the Soliciting vocalization. Females of *Setophaga* and *Dendroica* continue to give location calls until the nest is built, while female *Vermivora* cease giving location calls at the onset of nest building. This difference seems correlated with the general courtship pattern of the two groups. The location calls of the female function to keep the male informed of the female's location and to stimulate his approaches. Since courtship ceases in these *Vermivora* species when nest building is under way, there is no necessity for female location calls. As in the case of Soliciting vocalization, silence in females after this time may decrease conspicuousness to predators.

We have pointed out that some differences in vocalizations are related to the general pattern of courtship in the two groups. In *Setophaga* and *Dendroica* courtship activity occurs in short bursts over a period of a week or more; in these *Vermivora* species it often occurs in one day and at the most during a three day period. The selective pressures for rapid vs. slow courtship seem impossible to determine with our present scanty knowledge of their life histories. However, it may be significant that the average arrival time of redstarts is about a week earlier than the two *Vermivora* species in the Ithaca, New York area, and the two *Vermivora* species also depart from the New York City area several weeks earlier in the fall than do *Setophaga ruticilla* and *Dendroica pensylvanica*, although *D. petechia* also leaves early (Bull, 1964). Thus the two *Vermivora* species have a shorter time available for reproduction than the other group and a more rapid courtship may be necessary for this reason. The timing of reproduction is related to many other environmental conditions, such as food supply, and is very complex. However, it seems significant that the two *Vermivora* are very specialized and restricted in their way of feeding (Ficken and Ficken, 1968*b*), even more so than *Setophaga ruticilla*, and much more so than the *Dendroica*. The late arrival and early departure of these two *Vermivora* may be related to their feeding habits.

Behavior of hybrids.—Pairings of a hybrid and a parental species are relatively frequent in the area of sympatry (Ficken and Ficken, 1968*a*). Because of the similarity of courtship of the two species, hybrids would be expected to behave in a manner similar to both parental types and courtship would be expected to be equally successful in intraspecific and hybrid matings. However, since the two species differ markedly in color and pattern and hybrids show varying degrees of intermediacy, lowered responsiveness to visual releasers may reduce courtship success in hybrid pairings. Both sexes in the hybrid pairings which we studied were less aggressive to each other than were conspecific pairings, probably due to reduced responsiveness to the visual releasers of the mate. We also showed that female sexual behavior is often stimulated by male aggressiveness. Therefore, the courtship of hybrid pairings would be expected to be less successful than conspecific ones. Although fertility does not seem to be reduced in pairings involving a hybrid (Ficken and Ficken, 1968*a*), there could be a slowing of courtship with consequent deleterious effects on breeding success.

There are few detailed accounts of the behavior of avian interspecific and backcross pairs. However, in some cases the courtship of hybrids is less successful than "pures." Dilger (1960) studied the courtship of F_1 hybrids and both parental species in parrots (*Agapornis roseicollis* and *A. fischeri*). Although hybrid males possessed normal sexual vigor, hybrid females were more refractory than parental females in reaching sexual readiness as a result of male courtship. In addition, hybrids showed a partial loss of recognition of individuals of their own kind and there were more territorial violations. In F_2 ducks studied by Lorenz, the motor patterns of the displays were disrupted and occurred in unusual combinations (Dilger, 1960). If a proper sequence of courtship displays is important for copulation, these hybrids would be less successful.

In some cases interspecific pairs are as successful as conspecific ones. Hinde (1956) studied two kinds of cardueline interspecific pairs as compared to conspecific ones in captivity and found no difference in the proportion laying eggs. These interspecific matings are very rare in the wild and he concludes that specific differences in plumage and behavior are probably important in preventing interspecific pairing but do not hinder reproductive success under conditions of forced pairings.

Interspecific sexual relations in Blue-wings and Golden-wings.—Observations of unmated males approaching non-conspecific females and of unmated females approaching non-conspecific males show that there is a responsiveness to the other species. We suggest that this usually occurs when there is a threshold lowering due to a shortage of conspecific mates (Ficken and Ficken, 1968*a*).

We have a few observations indicating that there are opportunities for interspecific sexual behavior to occur with a bird other than the mate. This is likely to arise, although probably rarely, for several reasons: (1) Interspecific territorial encounters occur. Since females also participate, this enhances interspecific contacts between the sexes. In cases 1 and 5 (p. 166), the male of the other species was within 20 feet of the Soliciting female, although he did not approach; (2) The Soliciting female is likely to be non-specific about the male that she copulates with since her sexual motivation is so strong. A female Solicited after being chased by a male of the other species, and also seemingly in response to a female of the other species; (3) Soliciting postures are similar in the two species so the male might be non-specific as well; (4) Both species are sexually active at the same time; and (5) Aggressive interspecific encounters increase the female's sexual motivation.

We observed a male Golden-wing watching intently and sometimes following, a female Blue-wing on his territory. At first we thought she was his mate, since his behavior was similar to males in the early courtship period. However, several hours later we found a female Brewster's hybrid with a completed nest on his territory. Subsequent observations showed that the Blue-wing female had strayed from an adjacent territory and the hybrid female was indeed the mate of the Golden-wing. Thus "pure" males, even when mated, are capable of responding to a female of the other species. However, it is possible that during pair formation each sex rapidly learns the visual and vocal characteristics of the mate and normally confines overt sexual responses to birds possessing these, even though the mating is with a hybrid or interspecific. Initial "mistakes" at pair formation could be maintained by this rapid learning mechanism. Thus the critical responsiveness occurs during pair formation and pairs once formed are not likely to break up.

Ethological isolating mechanisms involved in courtship.—Hybrids and the formation of mixed pairings are selected against during pair formation and probably during later stages of courtship as well. Interspecific pairings are probably the result of low thresholds for mating, as in the examples of unmated birds approaching non-conspecifics cited here. Differences in arrival time of the two species in some areas of sympatry also decrease chances of interspecific pairing (Ficken and Ficken, 1968*a*). Interspecific pairings are relatively rare compared to pairings involving hybrids, probably due to hybrid intermediacy in releasers and hybrid receptivity to both parental species. However, hybrid males are less successful in obtaining mates than "pures" of either species. A discussion of species recognition and reproductive isolating mechanisms concerned with pair formation appears elsewhere (Ficken and Ficken, 1968*a*).

During courtship there is a continual interaction of the members of the pair involving both behavior, including vocalizations, and visual releasers. Since in interspecific and hybrid pairings visual releasers are different from those normally responded to, courtship is probably slower and ultimately less effective. Thus species differences in receptivity may serve as an isolating mechanism.

Courtship patterns facilitating hybridization.—Although reproductive isolating mechanisms are operating in this species complex (Ficken and Ficken, 1968*a*) several aspects of the courtship patterns of the two species facilitate hybridization. The courtship displays and sexual reactions of the two species are similar. This similarity should facilitate the success of interspecific pairs once they are formed, although the difference in visual releasers may slow the courtship process. Compared to other parulids, courtship proceeds very rapidly in Blue-wings and Golden-wings. Such rapid courtship and the lack of intricate displays preceding copulation probably facilitate hybridization. Also, chances for hybridization would be increased where one sex, in this case the female, initiates sexual activity, rather than when there is a complex interaction of both sexes preceding copulation (e.g., Morris, 1956).

SUMMARY

Interactions between the sexes from pair formation through copulation are discussed. Courtship displays are similar in the two species. Courtship is rapid, the time from pair formation to copulation being only a day in some cases. Male aggressive displays seem to stimulate female Soliciting. Two pairs consisting of Brewster's hybrid males and female Blue-wings differed from conspecific pairings in the lower level of aggression each sex showed toward the other. It is suggested that courtship of pairs involving a hybrid is less successful than conspecific pairings. Although no interspecific pairings occurred in the study area, there were several unsuccessful attempts at interspecific pairing and weak sexual responses were directed at a non-conspecific in some cases. Isolating mechanisms are apparently operating both in pair formation and in later stages of courtship. Hybridization, on the other hand, is probably facilitated by the similarity of courtship displays in the two species, their simplicity, and the rapidity of courtship. Courtship of these two *Vermivora* species is compared with other warblers and selective pressures affecting courtship are discussed.

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DISTRIBUTIONAL CHANGES AND INTERACTION BETWEEN PRAIRIE CHICKENS AND SHARP-TAILED GROUSE IN THE MIDWEST

Paul A. Johnsgard and Robert E. Wood

The "prairie grouse" of North America present an interesting example of the effects of human activities on breeding distribution patterns of birds, with resulting changes in geographic distribution and spacial isolation. Thus, the Heath Hen (*Tympanuchus cupido cupido*) was one of the most familiar birds to the early colonists, who relied heavily on it for food. Ultimately, loss of habitat caused the Heath Hen's extinction. When the vast tall-grass prairies west of the Appalachians were settled, Greater Prairie Chickens (*T. c. pinnatus*) were probably more plentiful, and greatly increased as woods were cleared and grain crops supplemented native grasses. With the further advance of settlers to the more northerly and westerly portions of the prairies, the Sharp-tailed Grouse (*Pedioecetes phasianellus*) was encountered. Unlike the Prairie Chicken, which "followed the plow," thc Sharp-tailed Grouse quickly retreated before it, and thus the Prairie Chicken soon spread over a wide range that previously had been occupied by Sharp-tailed Grouse. In some areas both species found adequate habitat for survival, and their similar niche requirements resulted in increased contact between the species. The new area of contact was probably most extensive in Nebraska, the Dakotas, and the Lake States, and later spread to the Prairie Provinces of Canada. The resulting interactions between the two species in the form of ecological overlap and degree of hybridization have yet to be fully documented, but a short review of the available information would appear to be warranted. Emphasis will be placed on the situation in Nebraska, which is probably fairly representative of the Midwest as a whole.

ORIGINAL AND ACQUIRED DISTRIBUTIONS

Although it is impossible to plot original presettlement distribution patterns of the prairie grouse with complete certainty, an attempt has been made to do this for the states south of Canada (Figs. 1 and 2). Similar rangc maps have previously been published for these two specics (Aldrich and Duvall, 1955; Aldrich, 1963), but in the case of Prairie Chickens their original ranges were not distinguished from their acquired ranges. Such a distinction was made by Baker (1953) and McClanahan (1940), and although the maps presented here were nearly completed before these wcre consultcd, a con-

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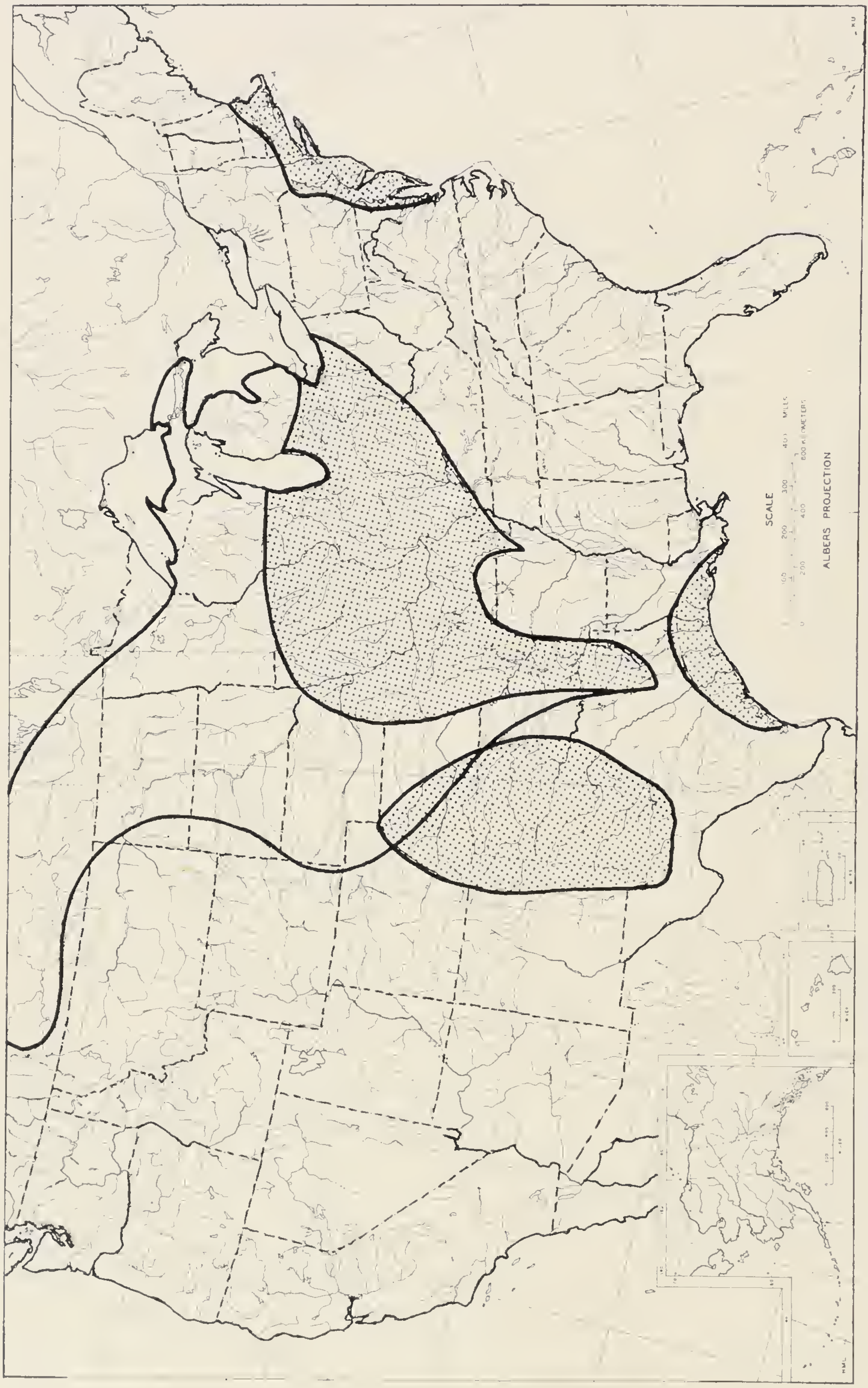

FIG. 1. Original (stippled) and acquired ranges of Prairie Chickens in southern North America.

FIG. 2. Original (shaded) and acquired ranges of Sharp-tailed Grouse in southern North America. The indicated break in range between the Plains and Columbian races of Sharp-tailed Grouse is conjectural.

siderable degree of agreement with them exists. Following the precedent of Aldrich, the Lesser Prairie Chicken (*T. pallidicinctus*) is included as if it were a geographic race of *T. cupido*, although there is still considerable doubt as to its actual systematic status. The Gulf Coast population of Attwater's Prairie Chicken (*T. c. attwateri*) is now universally regarded as a race of *T. cupido*. The southern and eastern boundary of the breeding range of the Greater Prairie Chicken is of less immediate significance than its northern and western boundaries. Baker's (1953) map agrees closely with ours in regard to the original western boundary, but extends a shorter distance north in Iowa, Wisconsin, and Michigan. Since these states, plus Illinois and possibly Minnesota, present the only areas of original possible sympatry between Prairie Chickens and Sharptails, the question is of special significance. Evidently Lewis and Clark observed Prairie Chickens as far north as the James River near Yankton, South Dakota (Burroughs, 1961) and, additionally, Coues (1874) reported that between Fort Randall and Yankton a dividing line between the two species' ranges could be drawn. Prairie Chickens evidently originally bred in northern Iowa almost to the Minnesota border, but Roberts (1932) believed that the species did not enter southeastern Minnesota until sometime prior to the middle of the nineteenth century. However, Leopold (1931) suggested that the region around St. Paul may have been the original northern limits of Prairie Chicken range, and he plotted a line suggesting that the original boundary between the two species extended from that area southeastward along Wisconsin's western tier of counties and across the northern tier of Illinois' counties toward Chicago. There is no doubt that Prairie Chickens occurred at least as far north as central Illinois in the 1830's, and that Sharp-tailed Grouse extended in wooded areas south to Chicago, indicating a definite zone of original sympatry in northern Illinois. Leopold suggested that within this zone of overlap a significant ecological separation occurred, with Sharptails occupying the "oak openings" and the Prairie Chickens found in typical prairie habitats. Schorger (1944) hypothesized a more northerly original Wisconsin range of Prairie Chickens, extending roughly across the middle of the state. In Michigan the Prairie Chicken probably originally occurred only in scattered grassy openings in the two southernmost tiers of counties (Ammann, 1957).

The probable early southern breeding limit of Sharp-tailed Grouse is obscured by their migratory movements but evidently included much of Kansas and Nebraska, nearly all of South Dakota (Coues, 1874), perhaps northern Iowa (McClanahan, 1940), essentially all of Minnesota (Roberts, 1932), and most or all of Wisconsin (Schorger, 1944). However, upper Michigan was probably later colonized by Sharptails in the early 1900's

(Ammann, 1957), as fires and logging activities cleared the forests. This last region apparently represents the only area in the United States where the Sharp-tailed Grouse has acquired any important new breeding range.

In contrast to the Sharp-tailed Grouse, Prairie Chickens initially prospered and rapidly followed agriculture northward, colonizing North Dakota in the 1870's (Johnson, 1964), and reaching Manitoba, Saskatchewan and Alberta by 1900 (Rowan, 1926). They also extended westward across Nebraska and Kansas to northern Colorado, which represents the original range of the Lesser Prairie Chicken. Almost as quickly as they flourished, Prairie Chickens began to suffer from the effects of too intensive agriculture. After peaking near the turn of the century, they quickly declined and disappeared from northwestern Ohio before 1930 (Leopold, 1931) as well as being exterminated from Kentucky, Arkansas and Texas. The last known active booming ground in Iowa was seen in 1954 (Stempel and Rodgers, 1961), and only a tiny handful of birds still remain in Indiana (Hamerstrom and Hamerstrom, 1961).

An attempt has been made to plot the present distributions of Prairie Chickens and Sharp-tailed Grouse (Fig. 3), based on a review of the recent literature. Particular attention has been paid to those areas of probable current sympatry, and less concern has been given to those parts of the west where Prairie Chickens have never occurred. Some recent state distribution maps or range descriptions for one or both species have been published and provide more details than could be shown here. Thus, relatively detailed state maps or statements of status are available for Sharp-tailed Grouse in the western states of Washington (Yocom, 1952), Oregon (Masson and Mace, 1962), Nevada (Gullion and Christensen, 1957), Montana (Anon., 1959), Colorado (Ryder, 1960; Bailey and Niedrach, 1965), and Utah (Hart et al., 1950). Similarly, recent range maps have been published for the Attwater's Prairie Chicken (Lehmann and Mauermann, 1963), and for the Lesser Prairie Chicken in Colorado (Hoffman, 1963), Kansas (Baker, 1953), Oklahoma (Copelin, 1963), and Texas (Jackson and DeArment, 1963).

The distribution of the Greater Prairie Chicken (Fig. 3) has obviously shrunk alarmingly, even during the last decade. Thus, it now appears to be almost completely gone from western Canada (Hamerstrom and Hamerstrom, 1961), and has retreated from the western limits of its acquired range in the Dakotas and Nebraska. A series of detailed maps showing historical changes in Prairie Chicken and Sharp-tailed Grouse ranges has been published for Michigan (Ammann, 1957). Historical changes in Prairie Chicken ranges and abundance have also been documented for Ontario (Lumsden, 1966), Kansas (Baker, 1953), Missouri (Bennett and Nagel, 1937; Schwartz, 1945), Iowa (Stempel and Rodgers, 1961), Illinois (Yeatter, 1943, 1957, 1963),

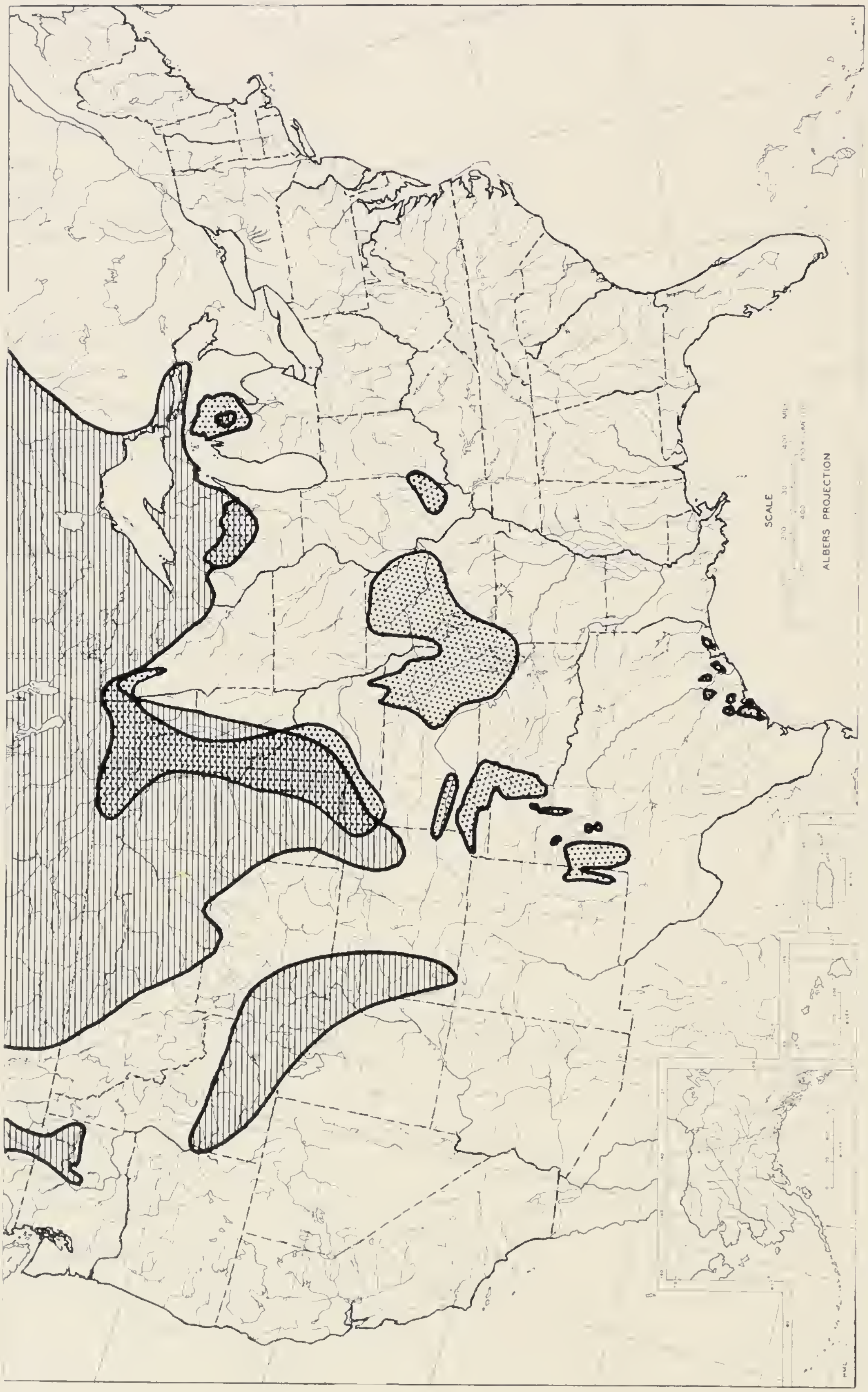

FIG. 3. Present ranges of Sharp-tailed Grouse (shaded) and Prairie Chickens (stippled) in southern North America, based on published and unpublished information through 1966.

Wisconsin (Schorger, 1944; Grange, 1948; Hamerstrom et al., 1957), North Dakota (Johnson, 1964), and to some degree for Nebraska (Viehmeyer, 1938, 1941; Beck, 1957; Kobriger, 1965). The current status of the two species of prairie grouse in Minnesota has been shown by Farmes et al. (1960), who indicate that the Prairie Chicken is largely restricted to the eastern edge of the Red River valley between Polk and Wilkin counties, where there is little contact with Sharp-tailed Grouse. Mr. James L. Ruos (letter of 28 April 1966) indicated that, although no hybrid specimens are in the Minnesota Game and Fish Collections, about one bird out of every 600 Sharp-tailed Grouse shot is of hybrid appearance. Grouse are not hunted within the major part of Minnesota's Prairie Chicken range. Prairie Chickens have been protected in North Dakota since 1945 (Johnson, 1964), and now occupy a discontinuous range in a few eastern counties such as Stutsman, Ransom, and Grand Forks, where Sharptail populations are only fair to poor (G. D. Kobriger, letter of 22 March 1966). Both species occur in numbers large enough to be regularly harvested in South Dakota, but even in that state the Prairie Chicken occupies a relatively restricted and probably diminishing range, and it is now primarily limited to areas of tall grasses in Gregory, Lyman, Tripp, and Jones counties (Henderson, 1964). Here, average rainfall is somewhat higher than in other counties west of the Missouri River, but agricultural land-use has not been as intensive as in those counties east of the river (Janson, 1953). Thus, in Nebraska alone both species are still sufficiently widespread and common to be major game species.

The geographic distribution of Prairie Chickens and Sharp-tailed Grouse in Nebraska appears to be a fairly stable one at present. Although Prairie Chickens at one time may have occurred nearly throughout the state (Bruner et al., 1904), it is probable that they never became as common as Sharp-tailed Grouse in the extensive sandhills region of central and western Nebraska. Rather, they evidently penetrated into the sandhills wherever grain crops were planted and supplemented the native grasses, and in particular they probably followed the river systems northwestward into the interior of the sandhills. A range map published by Mohler in 1944 suggests a close relationship between the range of Prairie Chickens and the geographic distribution of the sandhills. With minor changes, including a retraction of the western limits of the range and an inclusion of a few small Prairie Chicken colonies in the southeastern corner of the state that represent the northern limits of the large Flint Hills population of Kansas, his map would probably adequately serve to describe the species' present Nebraska range. But the Prairie Chicken is not so much a bird of the sandhills as it is of their perimeter and, in particular, of their southern and eastern edges, where native grasses and grain crops interdigitate along a broad front. Thus, counties such as Holt, Rock, Garfield, and Wheeler, which border on the sandhills and have an average of 20 or more inches of rainfall (U. S. Dept. of Agriculture, 1941) are the ones having the greatest concentrations of Prairie Chickens. On the other hand, Sharp-tailed Grouse seem to survive best on Nebraska's undisturbed grassland, and probably not only originally occurred (Bruner et al., 1904) but also still exist primarily in those drier western counties that are largely or entirely still covered with native grasses.

INTERSPECIFIC HYBRIDIZATION AND MIXED DISPLAY GROUNDS

Presumably because of the minor presettlement geographic overlap and the apparent ecological segregation where such overlap occurred, probably little if any hybridization originally occurred between Prairie Chickens and Sharp-tailed Grouse. The first reported hybrid was described in 1877 by W. Brewster, based on a specimen obtained in Iowa. A few years later, a second hybrid was described (Gurney, 1884), but its place of origin was unknown. Supporting the view that prior hybridization must have been rare is the fact that this later specimen was the first that Elliott Coues had ever encountered, in spite of his extensive travels in the upper Great Plains. Bent (1932) reported examining four hybrids obtained in the Boston markets between 1873 and 1893. Several hybrids have been reported for North Dakota (Gross, 1930), including one killed in 1923 (Bent, 1932). An early hybrid from Colorado was described by F. C. Lincoln in 1918, and more recently another was observed on a Prairie Chicken display ground by Evans (1966). Rowan (1926) reported two hybrid specimens from Alberta, and indicated that hybrids were more frequent in Manitoba. Several hybrids from Saskatchewan are also known (Rowan, 1926; Ammann, 1957).

A number of hybrids have been reported from Wisconsin (Gross, 1930; Ammann, 1957), and about 50 were identified during 13 years of field work in Michigan by Department of Conservation personnel (Ammann, 1957). Mr. Fred A. Priewert, of the South Dakota Department of Game, Fish, and Parks, has provided data (letter of 1 April 1966) indicating that ten identified hybrids were noted among 1,534 grouse banded in Gregory and Lyman counties between 1962 and 1966. Hybrids have also been observed on display grounds in South Dakota; at least 13 were counted on 10 Sharptail grounds (with 133 male Sharptails) and four hybrids were observed on four Prairie Chicken grounds with 36 of the latter (F. R. Henderson, letter of 26 April 1966). Perhaps the highest known incidence of current hybridization is to be found on Manitoulin Island in Lake Huron, where the previously isolated Sharptail race *P. p. phasianellus* from Ontario has recently come into contact with the

Prairie Chicken (H. G. Lumsden, letter of 27 February 1966), resulting in extensive hybridization. On this island possibly 80 per cent of the birds on Prairie Chicken display grounds are not typical Prairie Chickens (Ammann, 1957), and altogether between five and 25 per cent of the population may be hybrids (Mayr, 1963, p. 117).

There are no published records of the early occurrence of hybrids in Nebraska. but the University of Nebraska museum has an obvious hybrid obtained in Cherry County in 1926. An estimated three or four obvious hybrids are noted out of 600 to 1,000 grouse that are observed yearly by Nebraska Game, Forestation and Parks Commission personnel at hunter check stations, but others might easily go unnoticed. In 1966 two probable hybrids were observed among a total of 507 male grouse on display grounds closely examined for possible hybrids. Game Commission records of grouse trapped between 1959 and 1965 indicate that 936 Sharp-tailed Grouse, 310 Prairie Chickens and 15 hybrids were obtained. These figures suggest a minimum hybridization rate of between 0.3 per cent and 1.2 per cent in recent years, or considerably below that now occurring on Manitoulin Island. The fact that contact between the species there may not have been sufficiently prolonged to have allowed a reinforcement of isolating mechanisms (H. G. Lumsden, in litt.), and that assortative mating opportunities may be more limited on that island, might largely account for the marked differences in hybridization rates between the two areas.

Even in the absence of actual hybridization, interaction may occur between the two species in the form of attraction of males to the other's display grounds. Thus, the proportions of single-species and mixed display grounds in areas where both forms occur might provide an indication of the relative degree of reproductive isolation between the species. Such mixed grounds have been previously reported from various areas. Lumsden (1965) mentions the occurrence of mixed grounds on Manitoulin Island, and Ammann (1957) noted that a Prairie Chicken ground in Michigan was later taken over by Sharptails. In Wisconsin. Hamerstrom (1939) reported three mixed grounds among a total of 33 display grounds, and Grange (1944) found numerous mixed display grounds. During 1941 and 1942 Grange observed a total of 19 "hooting" or "dancing" grounds used by Sharp-tailed Grouse only, 58 Prairie Chicken "booming" grounds, and five mixed display grounds that were used by both species each of the two years. Of 13 additional mixed grounds that were used in 1941, ten changed to pure Sharp-tailed Grouse grounds in 1942, and three changed to pure Prairie Chicken grounds. Moreover, three grounds changed from single-species grounds to mixed grounds between 1941 and 1942, and one ground occupied by Prairie Chickens in 1941 was used only by Sharp-tailed Grouse in 1942. Four mixed grounds studied in 1942 had an average total of eight males present, but ranged from two to 11 males. Two of the four had only a single male of one or both species, and the other two had a minimum of three males of each species. Altogether, Grange observed 30 grounds (almost 16 per cent of the total) that were used jointly one or both years, compared with 68 Sharp-tailed Grouse grounds and 94 Prairie Chicken grounds that were used one or both years, if double allowance is made for grounds that changed in status and thus might be counted twice. Considering both years, Grange provides estimated total population figures that suggest an average proportion of about 37 per cent Sharptails to 63 per cent Prairie Chickens.

The existence of mixed display grounds in Nebraska was first documented by Mathisen and Mathisen (1959), who reported that during three years (1955 to 1957) 13 such grounds were observed by Game Commission personnel. Interestingly, the majority of these mixed grounds occurred in those counties where both species are relatively abundant, suggesting that interaction and perhaps hybridization are more likely in such areas than in regions where one species is relatively rare. This same phenomenon also appears to be true of hybridization between Mallards (*Anas platyrhynchos*) and Black Ducks (*Anas rubripes*) (Johnsgard, 1967).

Data on the male grouse constitution of a total of 72 mixed display grounds from Nebraska and South Dakota were available to us, including the 13 grounds listed by Mathisen and Mathisen (1959), records of 58 additional grounds (some of which represent the same grounds counted in different years between 1958 and 1966) in the files of the Nebraska Game Commission, plus records of several mixed grounds from South Dakota provided by F. Robert Henderson and Warren Jackson. These 72 grounds had an average total of 9.8 males present (range two to 22), but had an average of only 2.0 males of the rarer species (range one to six), indicating that many mixed grounds (33 out of 72) contained only a single male of the rarer species. There were an average of 5.3 Prairie Chicken males on these mixed grounds, and in 24 cases this species was the rarer form. On the other hand, there were an average of 4.3 Sharp-tailed Grouse males on the grounds, and in 46 cases this species was the rarer form. In the two remaining instances the species were represented in equal numbers. This difference would suggest that Sharp-tailed Grouse may be more prone to enter Prairie Chicken grounds than is the reverse situation. A chi-square test on the greater than expected frequency of Sharp-tailed Grouse over Prairie Chickens occurring as the rarer form indicates that such a differential response is highly probable ($P < 0.01$).

Hybrid males have been observed on a number of mixed and pure display grounds in Nebraska and South Dakota. Thirteen of 26 such observations were made on Sharp-tail grounds, six involved Prairie Chicken grounds, and on seven occasions hybrids were observed on mixed display grounds.

Some data on the geographic distribution of mixed display grounds in Nebraska are now available, as a result of intensive Game Commission surveys in three areas. These include the National Forest near Halsey in Thomas and Blaine counties, an area near Swan Lake in Holt County, and an area in southeastern Loup County. The relative numbers of pure and mixed display grounds, and total numbers of grouse counted on them, are shown in Table 1 which is largely based on unpublished Game Commission data provided by Mr. Lawrence Blus. In addition, figures for ten Game Commission spring survey areas in the eastern sandhills are included for the years 1963 to 1966.

TABLE 1

OCCURRENCE OF MIXED DISPLAY GROUNDS IN NEBRASKA

Area	Average No. of display grounds			Total average No. of males	
	Dancing	Booming	Mixed (%)	Sharp-tails (%)	Prairie Chickens (%)
National Forest (1962–1965)	35	0.75	0.5 (1.8%)	223 (99.12%)	1.9 (0.78%)
Loup County (1959–1962)	11	6	3.5 (17%)	159 (67.6%)	86 (32.3%)
Swan Lake (1959–1962)	3.5	17	1 (4.6%)	27.5 (16.8%)	141 (83.2%)
Various counties (1963–1966)	16	51	7 (9.4%)	158 (24%)	498 (76%)

In this table a direct relationship between the frequency of mixed grounds and the relative abundance of the less common species is clearly apparent. In theory, mixed display ground frequency should be related both to this ratio and to the average total number of males present on a ground. Thus, if no preferential attraction of males to display grounds of their own species exists, it would be mathematically expected that, where both species are equally common, a display ground containing nine males should be composed entirely of one species or the other only once in 256 instances (0.39%). Display grounds containing smaller numbers of males would have a higher expected proportion of unmixed assemblages, as would grounds in areas where one form is distinctly rarer than the other (Fig. 4).

In an attempt to determine whether the available data fit the hypothesis that the occurrence of mixed display grounds follows such an expanded binomial distribution pattern, the relationship between their frequency and the

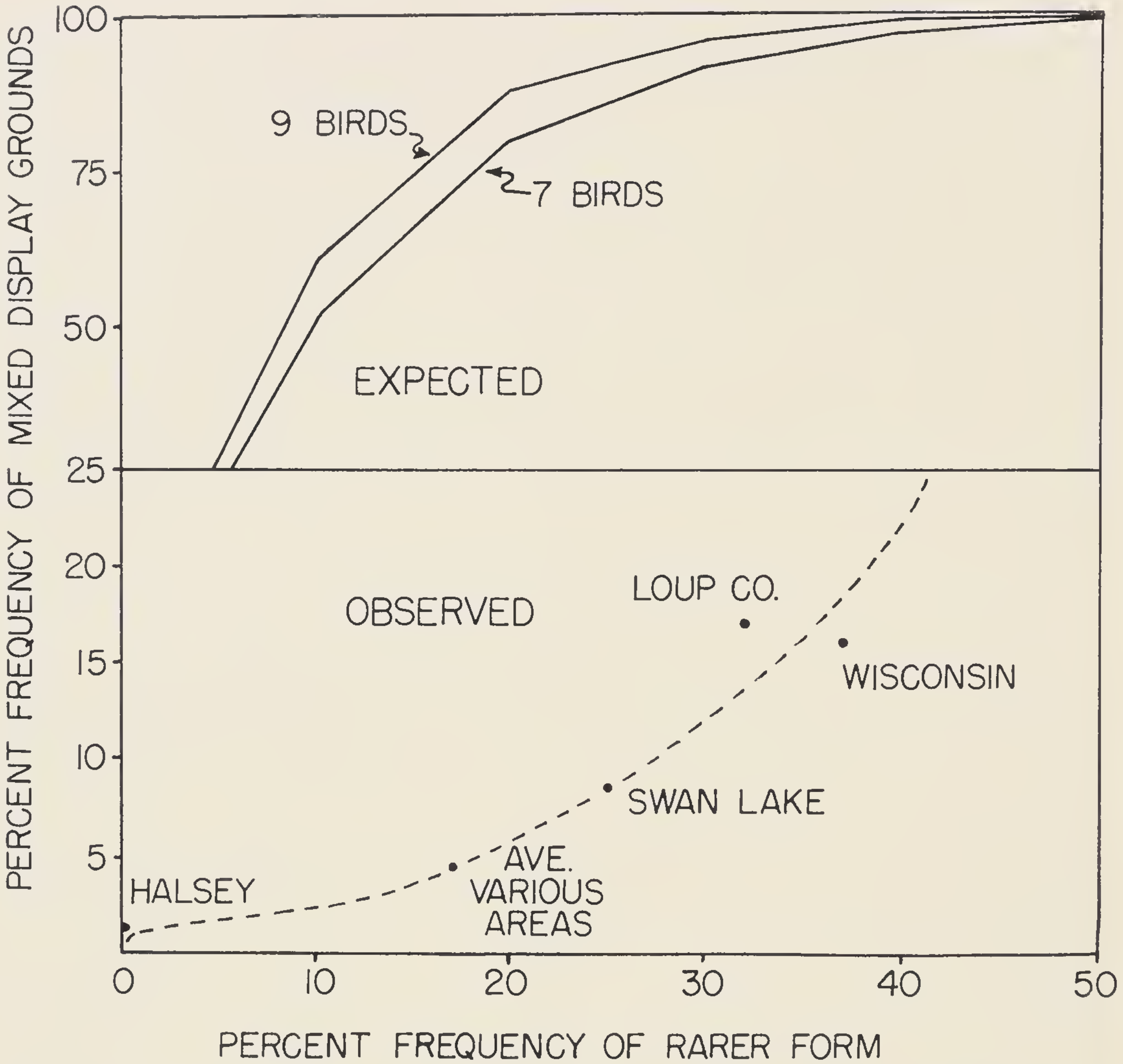

Fig. 4. Comparison of observed incidence of mixed display grounds (below) and calculated incidence expected on the basis of random aggregation and relative abundance of the two species of grouse (above).

frequency of the rarer species has been plotted for the Nebraska areas listed in Table 1 as well as for Wisconsin, based on the figures provided by Grange (1944). Average display ground sizes reported by Grange varied from six to eight birds, and in total averaged about seven. The overall average display ground size for the grounds listed in Table 1 is 9.1 males, and this range of values is about the same as those reported for both species in other states (Ammann, 1957; Yeatter, 1943). A line fitted visually to the points provided by the available data (Fig. 4) supports the contention that mixed display grounds are most prevalent in areas where both species occur commonly, although their apparent frequency is far lower than would be expected if random aggregation of males actually occurs. This difference suggests that males of either species are several times more likely to be attracted to display grounds occupied by others of their kind than to those of the other species.

Of equal or greater interest than the aggregation patterns of displaying males is the probable differential attraction of females of both species to the various types of display grounds, and the relative success of males in fertilizing females of their own species on mixed grounds. Mr. Lawrence Blus informed us that on 14 May 1962 he observed a female Prairie Chicken enter a display ground containing five Sharp-tailed Grouse and a single male Prairie Chicken. The female walked past at least two of the Sharp-tailed Grouse, one of which displayed directly toward her, and stopped in front of the Prairie Chicken, where copulation occurred almost immediately. It is hoped that additional observations on this aspect of the problem will be obtained, and that the reproductive success of hybrids might also be determined.

SUMMARY

A comparison of probable presettlement and present distributions of Sharp-tailed Grouse and Greater Prairie Chickens suggests that their original, probably narrow, zone of sympatric distribution has greatly enlarged as a direct result of land-use changes associated with agriculture. Ecological differences exist in areas of current sympatry that reduce actual interspecific contact, but hybrids have been reported from every state and province where sympatry has occurred. In Nebraska the current minimum rate of hybridization is estimated at between 0.3 and 1.2 per cent of the combined grouse population. A considerable number of display grounds used by both species in the state, and the incidence of such mixed display grounds is directly related to the relative frequency of the rarer species in local areas. The highest known incidence (17 per cent) of mixed grounds in Nebraska occurs where the rarer species comprises almost a third of the total population; this situation compares closely with estimates based on data from Wisconsin. Although a strong tendency exists for males of both species to form single-species rather than mixed aggregations, Sharp-tailed Grouse have been observed to be the intruder species on Prairie Chicken grounds significantly more frequently than the reverse situation. Records of 72 mixed grounds in Nebraska and South Dakota indicate they were of about the same average size as single-species grounds (9.8 vs. 9.1 males), and an average of only 2.0 males of the rarer species were present.

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NOTES ON SOME ARGENTINE ANATIDS[1]

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From mid-August, 1964, until late July, 1965, I was engaged in field work in Argentina studying waterfowl. Although special emphasis was placed on the Black-headed Duck (*Heteronetta atricapilla*), 28 species of anatids were observed in various parts of Argentina. Because so little is known of these species, some general observations are summarized and discussed in the hope that it will point out gaps in our knowledge and encourage additional work on this interesting group. Field work was financed by Grant GB-1067 from the National Science Foundation. Studies of museum specimens in the United States were financed by a Chapman Grant of the American Museum of Natural History, and aided materially in appraising the significance of plumage sequences in Neotropical ducks.

AQUATIC HABITATS

Although the distribution of Argentine birds was considered by Dabbene (1910) and by Olrog (1959), little comment has been made on the distribution of water types and their influence on waterfowl distribution. Some helpful botanical comments are given by Cabrera (1953) for the Buenos Aires region and, Wetmore's (1926) observations on both botany and ornithology are excellent. Although time did not permit detailed botanical work during this study, some obvious differences in life-form of marsh vegetation were recorded in the areas visited (Fig. 1) in relation to the species composition of waterbirds.

The most extensive zone of freshwater and semipermanent marshes is found in an area roughly bordered by the cities of Venado Tuerto (Santa Fe), Buenos Aires, General Lavalle, Mar del Plata and Azul (Buenos Aires). These marshes are dominated by tules (*Scirpus californicus*), but some contain extensive areas of cut-grass (*Zizaniopsis bonariensis*) or of floating broad-leaved plants. Pondweeds (*Potamogeton* spp.) and milfoil (*Myriophyllum* spp.) are common submergents, and floating plants include *Azolla filiculoides*, *Lemna* spp. and *Wolfia* spp. These water areas rarely exceed 4 feet in depth, and shallow areas of 1 to 2½ feet often are dry by late summer. Numerous deeper lakes are found in the Chascomus-Mar del Plata district, but the edges are fringed with bulrushes which may provide feeding, rest and nesting areas. Cattails (*Typha* spp.) are not widely distributed, but some extensive stands were noted in sand-dune marshes near General Madariaga, south of General Lavalle. Areas of sedge (*Carex* spp.) and spikerush (*Eleocharis* spp.) were not conspicuous because of the intensive grazing common to marsh edges, but they occasionally occurred in isolated shallows away from the shoreline.

The greatest density of marshes of this deep-fresh type probably are south of Chascomus, but numerous marsh areas also are found at Junin. This whole zone of northeastern Buenos Aires Province undoubtedly is one of the major waterfowl production areas in

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Fig. 1. Areas visited in Argentina.

Argentina because of the density of marshes and their large size and their configuration which often produces extensive shoreline.

Slow-moving streams are commonly associated with large marshes. In many cases, stream shorelines are vegetated with the same emergents common to the semipermanent marshes.

More saline lakes and marshes are found in western Buenos Aires Province, especially in the area west of Azul and extending southwestward through Guaminí. Most of the lakes I saw near Guaminí lacked fringing emergents; *Scirpus californicus* was rare or absent.

My exposure to river-bottom marshes, such as those along the Paraná, was minimal, but these areas contain fewer tall emergents, more floating broad-leaved plants, and more adjacent woody growth than do marshes of the open pampas.

Farther north, in the Chaco (Resistencia to Presidencia de la Plaza), marshes are rimmed with trees of various heights and cacti of many varieties (Fig. 2). The marshes I encountered were dominated by sedges and grasses. Tules were uncommon. As these marshes seem only seasonally inundated, sedges probably survive best there.

Marshes observed east of Tucumán and the Bañada de Figueroa were either man-made or man-influenced and perhaps were not typical. This generally arid region had few marshes except in association with rivers. Sedge areas were especially extensive in the marshy Bañada de Figueroa adjacent to the canalized Rio Salado River. Where permanent water areas had been formed by impoundment, tules were common.

FIG. 2. Searching for duck nests in a typical Chaco marsh near Presidencia de la Plaza, Chaco.

The vegetation of marshy areas in the puna zone of Abra Pampa (altitude of about 11,000 feet) consisted typically of short emergents, especially spikerush, but a few areas held bulrushes as well. These lakes were extremely shallow and graded into wet meadows of mixed spikebrush and semiaquatic grasses.

Tules also were noted in a few marshy lakes on the continental divide near Bariloche in northern Patagonia. However, most marshes and streambanks there were dominated by spikerush as noted farther north at higher altitudes.

WATERFOWL OBSERVATIONS

Cape San Antonio.—The waterfowl of this area were studied intensively from August 1964 through February 1965 and periodic observations were made from April through July 1965. A detailed summary of the marsh birds of this area has been published elsewhere (Weller, 1967*b*) but anatids for which nests, eggs or broods were observed are as follows, arranged in their approximate order of abundance (common names are from de Schauensee, 1966; scientific names are from Johnsgard, 1965). However, I have modified several common names (often by using some of Johnsgard's terms) in preference to those of de Schauensee, and have followed Woolfenden (1961) on *Metopiana* versus *Netta*: Yellow-billed Pintail (*Anas georgica*), Rosy-billed Pochard (*Metopiana peposaca*), Fulvous Whistling Duck (*Dendrocygna bicolor*), Speckled Teal (*Anas flavirostris*), Silver Teal (*Anas versicolor*), Red Shoveler (*Anas platalea*), Black-headed Duck, Black-necked Swan (*Cygnus melanocoryphus*), Coscoroba Swan (*Coscoroba coscoroba*), Cinnamon Teal (*Anas cyanoptera*), Argentine Ruddy Duck (*Oxyura vittata*), and Chiloé Widgeon (*Anas sibilatrix*). During the fall and winter. Yellow-billed Pintails and Chiloé Widgeon were most numerous; Rosy-billed Pochards, Cinnamon Teal, and Silver Teal were uncommon, and Fulvous Whistling Ducks were not seen. Other species were present during the winter, but in reduced numbers. Only three White-cheeked Pintails (*Anas bahamensis*) were seen; one each on 21 January, 1 March, 1 June. There seem to be no records of nesting by the species in the area.

Gibson (1920) also reported the rare occurrence (during "flood" years) of Brazilian Ducks (*Amazonetta brasiliensis*) and Ringed Teal (*Calonetta leucophrys*). He reported one nest of a Brazilian Duck, but Ringed Teal have not been reported nesting. Grant (1911) reported additional species not seen during the present study, the rare winter visitors, the Ashy-headed Sheldgoose (*Chloephaga poliocephala*) and the Ruddy-headed Sheldgoose (*Chloephaga rubidiceps*).

The nesting season of ducks in the Cape San Antonio area was from September into early December, with a peak during October.

Venado Tuerto.—Several trips were made to the intensively farmed cattle-maize area of Venado Tuerto in southeastern Santa Fe. This is an interesting area ornithologically despite its intensive agriculture and apparent dryness. Possibly, it is the combination of grain availability and several large tule marshes which create suitable wintering areas for concentrations of ducks. These marshes are of the same semipermanent type found in eastern Buenos Aires Province, but several duck species which were rare or absent in the latter area were relatively common in eastern Santa Fe. These were the White-cheeked Pintail and the White-faced Whistling Duck (*Dendrocygna viduata*). Moreover, Peter Miles, a local resident who has hunted in this area intensively, also has seen Brazilian Duck, Ringed Teal and Comb Ducks (*Sarkidiornis melanotos*) in the area, although all are rare. Numerically, birds observed during six field trips from 9 May to 24 July were ranked as follows: Yellow-billed Pintail. Rosy-billed Pochard. Cinnamon Teal, Silver Teal, Chiloé Widgeon and Fulvous Whistling Duck.

During June and July, Speckled Teal were reduced in numbers, and Silver Teal were rare. It appears that Speckled Teal, Silver Teal, Rosy-billed Pochards and Fulvous Whistling Ducks move northward in winter, while other species remain throughout the winter. Here, as in eastern Buenos Aires Province. the influence of water availability is conspicuous, and after a long series of rains in late June, large numbers of Rosy-billed Pochards and even a few Fulvous Whistling Ducks appeared. Peters (in Phillips. 1922) noted a mass movement of Rosy-billed Pochards stimulated by rain after a prolonged winter (May) drought in eastern Buenos Aires Province.

The pintails feed in dry fields and "roost" at night in flooded fields or shallow marshes. In larger marshes, they were found in areas of extensive mudbars. Rosy-billed Pochards and Fulvous Whistling Ducks rarely field-feed in the absence of water and, presumably, move out during dry periods. Their chief wintering area is unknown, although the Paraná River marshlands are probably suitable and are less than 200 miles from the Venado Tuerto marsh areas.

Courtship flights of pintails were conspicuous on 18 May (early winter), and pairs of Yellow-billed Pintails, White-cheeked Pintails, Red Shovelers and Cinnamon Teal were seen on nearly all trips. Relatively few Rosy-billed Pochards were seen in pairs even in mid-July, and no evidence of pairs was seen in Black-headed Ducks or Argentine Ruddy Ducks.

Southwestern Buenos Aires Province.—A brief field trip was made from 2 July to 7 July 1965, to appraise the distribution of water arcas and waterfowl in drier regions of Buenos Aires Province. Of special interest was the distribution of the three species of sheldgeese which winter in southern Buenos Aires: Upland Sheldgoose (*Chloephaga picta*), Ashy-headed Sheldgoose, and Ruddy-headed Sheldgoose. A recent survey by Plotnik (1961) aided in finding concentrations of these "geese."

During this trip, as on several later ones, I was accompanied by Peter Miles of Venado Tuerto. Our route of travel from Venado Tuerto south took us through the dry and often sandy grazing land of southeastern Santa Fe and northwestern Buenos Aires. This area has few water areas. At Guaminí, there is a concentration of large and somewhat saline lakes distributed in WSW by ENE direction. In this region, we saw 11 flocks of Upland Sheldgeese, numbering from 7 to 249 birds. Four of these flocks contained 10 to 77 Ashy-headed Sheldgeese. In most cases, Ashy-headed Sheldgeese were in pairs and were grouped either at the edge of the Upland Sheldgeese or in an area where the density of Upland Sheldgeese was low. Some intra- and interspecific aggression over feeding sites was noted, but too few observations were made to appraise dominance. An Ashy-headed Sheldgoose collected by Miles was in full body and tail molt. The primaries appeared new, but the greater secondary coverts were molting. Other birds of both spccies (seen through a 40× power telescope) were in body molt. Apparently, local residents in Patagonia question whether these birds have a simultaneous wing molt like other anseriforms (Scott, 1954).

The Upland Sheldgeese of both sexes varied considerably in color. The ruddy-colored heads of females could be grouped into three categories: light, medium and dark. The extremes probably are young (light) and adult (dark); possibly the intermediates were 2-year-olds. Males also varied, as noted by Delacour (1954:219). Some were white-breasted, some barred-breasted, and some were intermediate. Head color of males also varied with lightly-barred individuals having a yellowish-white head; presumably these are juveniles as illustrated by Scott in Delacour (1954: Plate XII).

On one of the Guaminí Lakes, Lake Alsina, we noted several other species of waterfowl. A flock of about 200 Yellow-billed Pintails was accompanied by 3 White-cheeked Pintails and several Speckled Teal. In a wind-protected bay, nearly 200 Argentine Ruddy Ducks were diving and sunning. Most of these were in dull brownish-gray plumage, but several males appeared to have rufous plumage over much of the body. Only a few had black heads, however. Pairs and singles or small flocks of Cinnamon Teal, Chiloé Widgeon, Red Shovelers and Black-necked Swans were seen on these lakes, and the ducks also were seen on small streams in the area.

The coastal region between Bahía Blanca and Tres Arroyos has some large, bare-looking sandy lakes, and a few flocks of sheldgeese were seen there. However, the area near Tres Arroyos was the greatest concentration area for *Chloephaga* (Fig. 3). In this area, pilots are hired by farmers' cooperatives to chase off the "avutardas" (an erroneous name for sheldgeese that actually means bustards); such pilots are called "avutarderos." Sheldgeese supposedly compete with livestock and damage wheat and other small grains. Fear of planes makes air-driving an effective means of moving birds to less-prized areas. Although such preventive measures are costly, they seem effective. Killing of nesting females in Patagonia has been recommended, but this seems biologically unrealistic in a sparsely-scattered population—as well as esthetically questionable.

The biggest flocks of sheldgeese were seen in the areas north of Tres Arroyos near Indio Rico. In total, we observed 29 flocks numbering about 2,840 *C. picta*, 205 *C. poliocephala* and 15 *C. rubidiceps*. There appeared to be more of the dark bar-breasted form of *C. picta* and a greater number of the smaller species than near Guaminí. Apparently, it is the small forms which move farthest east and north because these were noted at General Lavalle by Grant (1911).

Just north of Azul, we again found ourselves in the zone of semipermanent, deep-fresh, tule marshes common to northeastern Buenos Aires Province. Such areas were rare south and west of Azul, but increased as we went northwestward to Junin. In the Junin area we began to see numbers of ducks

FIG. 3. A flock of Upland Sheldgeese in a field near Tres Arroyos, Buenos Aires.

common to the deep-fresh marsh type: Black-headed Duck, Rosy-billed Pochard, Coscoroba Swan, Silver Teal, Cinnamon Teal, Yellow-billed Pintail, Speckled Teal and Chiloé Widgeon. Characteristic marsh birds such as egrets, ibis, and herons also became numerous. On 7 July (midwinter) intense courtship and copulation were observed in Chiloé Widgeon.

The Chaco.—Marsh areas north of Buenos Aires and Venado Tuerto are subtropical and are seasonally flooded. The waterfowl found in these areas are those species common to northern tropical regions, although a few species are ubiquitous.

My contacts with marshes of the broad Paraná River were restricted to those areas near the city of Santa Fe. Broad-leaved floating plants of the water hyacinth group were common as were broad-leaved emergents. Such areas were frequented by Wattled Jacanas (*Jacana jacana*) and herons, but few waterfowl were seen.

North of Santa Fe in the region of San Xavier were extensive rice-growing areas. These areas are, at times, plagued with waterfowl and blackbirds. Rosy-billed Pochards and Fulvous Whistling Ducks were said to be especially common prior to fall harvest, and local residents said that some nested in the rice. It was interesting to learn that the invasion of the bulk of these species

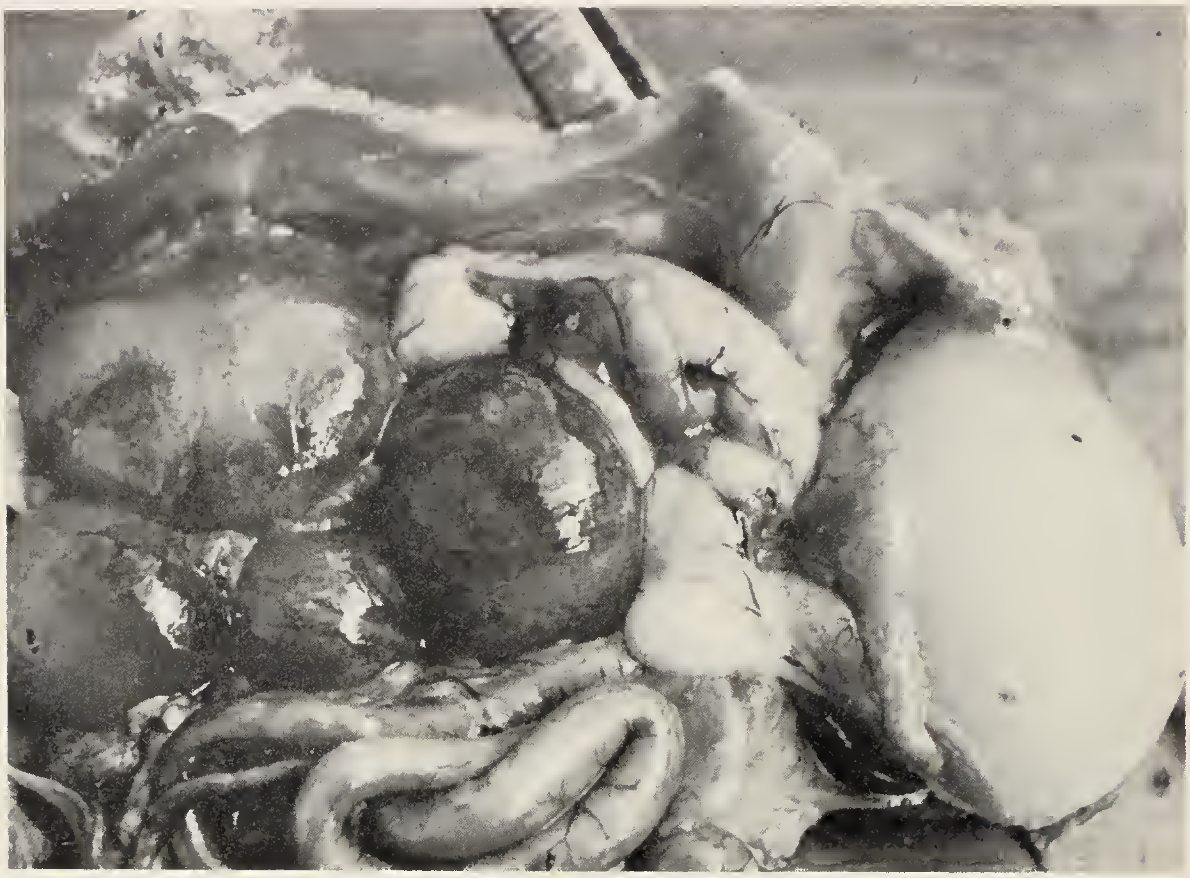

Fig. 4. Reproductive tract of female Brazilian Duck collected near Presidencia de la Plaza on 14 May 1965.

was synchronized with their departure from the deep-fresh marshes of eastern Buenos Aires. During our brief visit in early May (early winter), only a little rice remained unharvested, and few ducks were seen. However, this seems to mark the southern limit of the major range of Brazilian Ducks and Ringed Teal, which were seen in small numbers. A few Yellow-billed Pintails and Red Shovelers also were found near each puddle in the rice fields.

Timbered areas became more common as we drove north toward Resistencia in the region of the Gran Chaco. Like all but the Andean region, this area was level and low. After an extended drought, the area seemed like desert scrub, but we encountered open areas dominated by *Carex*, a type of papyrus (*Cyperus* spp.), and tall aquatic grasses which obviously had been flooded regularly in the past. Only in the area just south and to the west of Resistencia were well-flooded marshes of *Carex* and aquatic grasses noted. These marshes were extensive in places, and slightly higher areas were covered with sizeable, broad-branching trees. At this time, some timber areas were flooded—as they must be briefly each year—but the abundance of cacti and massive ant hills in the forest suggested that dry conditions are common much of the year.

Near Presidencia de la Plaza we encountered several isolated pairs of

Brazilian Ducks and one group of six or seven. Of three collected, a female was found with a large egg in the oviduct and four large ova in the ovary (Fig. 4). The two males both had enlarged testes. Thus, late fall breeding is clearly established for this species in northern Argentina. Nevertheless, all three birds had much body molt, and the laying female had tail molt as well.

The nesting site of the Brazilian Duck has not been adequately investigated or reported. Notes by Azara (1805) and Phillips (1925) are conflicting; our Indian guide agreed with Azara that they nested on sedge hummocks surrounded by water. However, Gibson (1920) reported eggs in the nest of a blackbird. Durnford (1878), on the other hand, flushed them from cliffs where he saw others perched; he was convinced that they nested there. Unfortunately, our search for nests in the Chaco proved futile.

A pair and a single male Ringed Teal also were collected. The pair flew well, although they had the outer two primaries still soft at the bases. Despite their teal-like build and flight, their iridescent plumage, black primaries and elongate tail appear much more like perching (Cairinini) than dabbling ducks (Anatini). The distinctive whistle of their wings was heard (see Dudley, 1958). Both males had highly vascularized gonads of moderate size.

This area also was known for its abundance of Muscovy Ducks (*Cairina moschata*), but we saw only a few in their lumbering flights from one area to another. Several flocks of Silver Teal were seen, and one male Black-headed Duck was observed. A few Red Shovelers and White-faced Whistling Ducks were seen south of Resistencia near Basail.

Another subtropical duck, rarely if ever occurring in the fresh-deep marshes of Buenos Aires Province, is the Masked Duck (*Nomonyx dominica*). A male, a female and then a group of 8 or 9 brown birds, probably immatures, were flushed from flooded sedge in a small patch of taller bulrush (*Scirpus* spp.). Their white wing-spots so matched those of the Ringed Teal that they were not recognized as stifftails at first, especially because of their flight behavior. Dr. C. Olrog of Tucumán (pers. comm.) had told me that this species did not skitter to rise as do other stifftails, and I found his description accurate. They seem to jump straight up, with the body horizontal, and then go into a high-speed, rising flight with fast-moving wings. They showed none of the hesitancy to fly or the flapping-across-water that Phillips (1925) noted in the early literature. However, Wetmore (1965) indicates that they may take flight in either way.

One male Masked Duck was collected. Its trachea was not simple as has been reported but had a clear-cut longitudinal, dorsal slit in the enlarged upper end that was connected to an air sac as noted also by Wetmore (1965). The behavior, elongate body shape (intermediate between Black-headed Ducks and typical stifftails) and unique skeletal features (Woolfenden. 1961) seem to justify placing it in a genus separate from that of the ruddys. Both the smooth egg shell (resembling *Heteronetta*) and the downy young (Bond 1961) add still more evidence of its distinctiveness.

The male collected probably was a first year male and was mainly in nuptial plumage. Its gizzard contained several types of seeds rather than animal matter.

Bañada de Figueroa.—The western dry Chaco and desert scrub of Santiago del Estero contains several extensive marsh areas associated with seasonal overflow by rivers. For purposes of irrigation, the Rio Salado has been impounded northeast of La Banda, and a lake has been created in what formerly was marsh area. From 16 March to 20 March 1965, I accompanied Dr. C. Olrog of Tucumán and Mr. Maurice Rumboll of Buenos Aires in search of fall-breeding Black-headed Ducks and to collect waterfowl. We found the area much drier than normal, but some cultivated fields were flooded by a leak in the dike which retained the river. Here, we found numerous Black-headed Ducks, but the three we collected were not in breeding condition as Olrog had found them in previous years. Flocks of up to 40 were seen in their typical late evening flights. Olrog had previously banded 46 by trapping them in mist nets over water (Olrog, 1963). Two potential host-species, White-winged Coots (*Fulica leucoptera*) and Common Gallinules (*Gallinula chloropus*) were present, but they were not nesting.

The most numerous ducks in these flooded fields were Rosy-billed Pochards and Yellow-billed Pintails, but a few White-cheeked Pintails were seen in most flocks; a male collected was not in breeding condition. Late flying flocks of Fulvous Whistling Ducks were heard, and two were seen with nine Rosy-billed Pochards taken by hunters. Several pairs of Silver Teal were seen, and one was collected. Red Shovelers were present in small numbers. No Brazilian Ducks were seen, but two other subtropical species were observed; two South American Comb Ducks were seen loafing in a shallow water area, and several flocks of 25–30 were seen near the artificial lake formed by the dam. Several pairs and one male Ringed Teal were seen, but none was collected. Local Indians indicated that Ringed Teal nested in trees, especially on old nests of other birds.

The puna zone near Abra Pampa.—The highland puna or altiplano, an extensive area at 11,000–13,000 feet, has its southern limits in northwestern Argentina. The area near Abra Pampa, just south of the Bolivian border in the Province Jujuy, is especially marshy. Dr. Olrog and Mr. Rumboll accompanied me to this area on 23 to 26 March 1965. This area ranges from about 11,000 to 11,500 feet in altitude.

The most conspicuous bird of this highland zone is the large white and

FIG. 5. A nest of the Yellow-billed Pintail in bulrush of a puna zone marsh near Abra Pampa, Jujuy, 24 March 1965.

black Andean Sheldgoose (*Chloephaga melanoptera*). A flock of 150 or more birds were observed grazing with cattle on a flat, broad, dry lake edge about 4 miles north of Abra Pampa. Sheldgoose droppings were widespread in the short-grazed grasses and sedges.

The flock of ducks on this shallow lake was dominated by the ubiquitous Yellow-billed Pintail, but the highland race of the Speckled Teal (*A. f. oxyptera* was nearly as abundant. In lesser numbers were very dark-colored Cinnamon Teal and the highland Puna Teal (*Anas puna*). The latter form, often considered a subspecies of the Silver Teal, has a quite different shaped bill and lacks the yellow at the base. Its isolation in the puna zone suggests that it is a separate species. The most unique ducks present were two Crested Ducks (*Anas specularioides*) which seemed quite curious but still kept out of range. We were able to collect two Puna Teal and one Speckled Teal.

Despite the fact that this area is north of the Tropic of Capricorn, daytime temperatures at this altitude were cool, and nighttime temperatures were below freezing in fall. We were surprised, therefore, to find newly hatched broods of Speckled Teal and Cinnamon Teal, a pintail incubating 8 ready-to-hatch eggs (Fig. 5) and a female Puna Teal with a brood patch. Olrog had noted this fall-breeding before and believed that it was associated with water availability as it seemed to be in the Bañada de Figueroa and in the Chaco.

In the area, we saw American Coots (*Fulica americana*), in the southernmost portion of its range, several Common Gallinules, flamingos and Black-crowned Night Herons (*Nycticorax nycticorax*). Olrog had observed Southern Pochards (*Netta erythrophthalma*) there previously, but none was seen on this trip.

Andean lakes at Bariloche.—The extensive lake zone of Chile-Argentina in northern Patagonia is an excellent waterfowl area. A trip to that area was made on 14–25 February 1965, and several interesting species of waterfowl were observed. The big and deep lakes are generally unattractive to most species of ducks, but a few Yellow-billed Pintails were seen on the shores of even the barest of lakes. Flying Streamer-Ducks (*Tachyeres patachonicus*) could be seen regularly in the busy excursion centers on Lake Napual-Huapi. Remarkably tame, they dived between the moving launches and hauled out on a nearby rocky island to preen. Nine were the most seen together at one time.

Along the Rio Limay northeast of Bariloche, a pair of Spectacled Ducks (*Anas specularis*) was seen on a gravel bar. This general portion of the stream was wooded, although there were extensive open fields away from the river. Two flocks of Upland Sheldgeese were seen, a group of nine swimming in the river and a flock of 60 or more grazing with cattle and domestic turkeys in an open marshy area. In the same marsh were about 30 Chiloé Widgeon, and groups of 5 to 15 widgeon were to be found in almost any quiet backwater area along the stream. Yellow-billed Pintails also were seen in small numbers.

Small marshes are isolated in the dense mountain forests and are not easily located. Marshy edges are common to several of the lakes, and a tall bulrush (*Scirpus* spp.) is common there. Such marshes were frequented by Yellow-billed Pintails, Speckled Teal and Red-fronted Coots (*Fulica rufifrons*).

MIGRATION

Migrations of ducks in South America have not been well studied, but the general observations of workers over the past 80 years demonstrate considerable evidence of some regular seasonal migrations. Seasonal shifts of southern Patagonian forms like sheldgeese are well known (Plotnik, 1961) as are movements of Yellow-billed Pintails, Silver Teal, Speckled Teal and Red Shovelers which nest in Tierra del Fuego (Crayshaw, 1907). But movements also occur in central Argentina.

Early workers such as Grant (1911) and Gibson (1920) noted movements of Rosy-billed Pochards and Fulvous Whistling Ducks which they attributed to water conditions. The unusual occurrence of Rosy-billed Pochards and Argentine Ruddy Ducks on the Falkland Islands was also thought due to dry conditions on the mainland (Bennett, 1922). A seasonal dry period seems to be common in central Argentina and forces the birds into larger water areas (where they probably molt) in late summer. By early fall, these areas often are dry, and birds would find more water and better feeding areas elsewhere. In the Cape San Antonio area, Rosy-billed Pochards, Fulvous Whistling Ducks, Silver Teal and Speckled Teal left the marshes by early to mid-February, while Black-headed Ducks left in early March. Only the Yellow-billed Pintails, Chiloé Widgeon and Red Shovelers, which have extensive nesting areas in Patagonia, remained and even increased in number throughout the winter. Some movements of pintails were seen in mid-April. Wetmore (1926) saw concentrations in October and November that he considered long-distance migrants; I saw some such groups, but had no evidence that these had moved from more southerly areas.

It is of interest that several observers in more northerly areas of Argentina have remarked on population increases of Rosy-billed Pochards and Fulvous Whistling Ducks in late February and early March just following the period of their departure from eastern Buenos Aires Province. Durnford (1877), who lived along the Paraná some 50 miles northwest of the city of Buenos Aires (Baradero) considered both Black-necked Swans and Coscoroba Swans as winter residents and noted increases in Rosy-billed Pochards, Speckled Teal, Cinnamon Teal and Chiloé Widgeon in winter. Barrows (1884), who observed at Concepcíon (Province Entre Rios) along the Uruguay River, noted an increase in Silver Teal in winter, and increases in Rosy-billed Pochards with wet periods. Olrog (1962) observed that the sizable Rosy-billed Pochard populations of the Bañada de Figueroa increased in late February and early March and that birds departed in June and July. His banding data suggest a southeasterly movement to southeastern Brazil.

These notes suggest rather definite migratory patterns. Although some of these movements are local and water-influenced, some birds probably move from the major breeding marshes of eastern Buenos Aires along the natural guidelines of the coast and rivers and up the Paraná and Uruguay Rivers to warmer, wet areas; then northwesterly along the many major streams arising in the Andes to wetland areas in the deserts and along the Andean foothills.

The banding program initiated by Olrog at the Lillo Institute of Tucumán holds great promise for the solution of these problems of migration, but greater national and international effort needs to be directed to support his efforts.

CHRONOLOGY OF NESTING

Phillips (1922) pointed out that waterfowl in tropical South America breed on irregular schedules and are much influenced by local water conditions. Certainly, in Patagonia and as far north as Buenos Aires, there are usually definite spring breeding periods. In more northerly parts of Argentina, seasons appear to be longer than we find in Northern Hemisphere anatids although it is difficult to compare since there are no major waterfowl breeding areas in the same climatic zone in North America.

It is quite possible that the area from about 35° S. latitude and north marks a zone where climate is less limiting and where waterfowl can breed at most times of year. Other factors then may be limiting. Water definitely seems a factor at Bañada de Figueroa (Olrog, pers. comm.), and Partridge (1956 and pers. comm.) considered water availability the reason that Brazilian Mergansers (*Mergus octosetaceus*) nested in June—the coldest time of the year. Water also seems important in the timing of nesting of many common ducks and coots each season since nest initiation began much later and was much reduced in volume in 1965 than in 1964, according to reports from residents in the General Lavalle Area of Buenos Aires and in southern Santa Fe.

There is no evidence of double-broodedness in tropical anatids, but in some areas, both spring and fall nesting (or continuous nesting) is indicated. Wetmore (1926) reported that Ringed Teal in Paraguay were in breeding condition in September; yet, birds collected during this study in May in Northern Argentina had just completed the wing molt. Moreover, specimens from Paraguay in the University of Michigan Museum of Zoology demonstrate late summer and fall breeding: A downy young Ringed Teal was taken on 6 February and a flying immature was taken on 15 January. Downy young White-faced Whistling Ducks also were taken on 6 February, and a downy young Black-headed Duck was collected on 1 March.

Brazilian Ducks were found both in body molt and laying during May in Argentina, and Wetmore (1926) reported males in Paraguay with new wing feathers in mid-February.

Apparently, there is a gradient from normal spring breeding in southern Argentina to a more irregular, possibly longer season in northern Argentina and in Paraguay. It appears that water availability is the major factor influencing fall and winter breeding, even at the latitude of Buenos Aires. Maurice Rumboll (pers. comm.) noted breeding by several species of ducks in southern Santa Fe Province during 1966, following an intensive drought during the normal spring breeding period. Other things such as insects, diseases, and food supplies need to be evaluated. Clearly, much information is needed on the chronology of breeding for these subtropical and tropical habitats.

COURTSHIP, PAIR BONDS, AND BROOD CARE

Based mostly on observations of northern anatids, members of the Anatinae are considered to form pair bonds seasonally only, although many Anserinae pair for longer periods—probably for life (Delacour and Mayr, 1945). However, the presence of "pairs" of many duck species is common at all times of the year in central Argentina. General observations suggest that some of the population remains paired (or at least shows interest in members of the opposite sex) throughout the year. A related fact is that, in many species, males regularly accompany the female and brood, but such behavior in northern ducks is considered rare and has resulted in a series of publications pointing out such unique events.

My general observations in eastern Buenos Aires Province and in marshes near Venado Tuerto, Santa Fe, indicate that pairs were conspicuous after the nesting season, and in fall and winter among Yellow-billed Pintails, Silver Teal, Chiloé Widgeon, Speckled Teal and occasionally in Red Shovelers and Cinnamon Teal. Pairs were not common in post-nesting periods in Argentine Ruddy Ducks, Black-headed Ducks or Rosy-billed Pochards (although few Rosy-billed Pochards were seen in winter).

It also was noted that those species which retain a pair bond are those in which males commonly attend broods. My own records for the Cape San Antonio area show such attentiveness in Yellow-billed Pintails, Chiloé Widgeon, Silver Teal, and Fulvous Whistling Ducks.

Another interesting phenomenon not well documented in northern anatids is the occurrence of active courtship immediately following the main breeding season. Although such events are not common and the lack of continuity in my observations does not permit plotting of the chronology or relative frequency of displaying, courtship was seen regularly. After a September to November breeding season at General Lavalle in 1964, courtship was seen in Chiloé Widgeon, Silver Teal, Speckled Teal, and Red Shoveler in November, and in Cinnamon Teal in March. Pairs of Yellow-billed Pintail, Chiloé Widgeon, and Speckled Teal were seen regularly during the hunting season in April, and aerial courtship flights of Yellow-billed Pintails were seen in mid-May at Venado Tuerto. The latter period would be comparable to courtship periods of related species in the United States in November (Weller, 1965).

Nevertheless, much typical flock behavior also was noted in some of the same species. Flocks of Yellow-billed Pintails were seen fairly early in the breeding period, and those of Speckled Teal were seen just afterwards. The

TABLE 1

ANATIDS EXAMINED IN HUNTERS' BAGS, 4 MARCH–23 JULY 1965, MAINLY IN EASTERN BUENOS AIRES AND SOUTHEASTERN SANTA FE PROVINCES

Species	Adult male	Adult female	Immature male	Immature female	Unknown	Total
Yellow-billed Pintail	71	33	6	10	2	122
Speckled Teal	15	8	–	4	–	27
Red Shoveler	11	8	–	4	–	23
Rosy-billed Pochard	3	4	–	–	9[1]	16
Black-headed Duck	8	7	1	–	–	16
Chiloé Widgeon	6	4	–	3	–	13
Silver Teal	7	2	–	2	1	12
Cinnamon Teal	7	3	1	–	1	12
White-cheeked Pintail	6	5	–	1	–	12
Coscoroba Swan	1	1	2	2	–	6
Fulvous Whistling Duck	–	–	–	–	2	2
Argentine Ruddy Duck	1	1	–	–	–	2
	136	76	10	26	15	263

[1] Santiago del Estero Province.

sex and age composition of such groups is unknown and no observations were made to determine the presence of pairs within these flocks. Phillips (1922) reported that male pintails do leave nesting females and gather in flocks, but the source of this observation was not stated. Tremendous flocks of pintails and other dabblers are seen field-feeding in fall and midwinter, and some bag data suggest that adults and males may dominate some of these flocks. However, pairs are conspicuous in marsh areas even then.

It is possible that the permanency of pair bonds is related to latitude and migration and that southern migratory ducks are less inclined toward (i.e., have less opportunity for) permanent pairing. Such birds would contribute to large flocks, as would young-of-the-year. In fact, strongly migratory segments of duck populations at any latitude may be less prone toward permanent pairing. Unfortunately, neither banding nor observational data presently are available.

HUNTER-KILL

Hunters' bags were checked whenever possible, and in most cases, sex and age data were recorded. Most data were collected from the areas near General Lavalle, Buenos Aires, and Venado Tuerto, Santa Fe, but five areas are represented. A total of 263 birds of 12 species was examined (Table 1). There is general agreement on the relative abundance of species as observed in the

TABLE 2

A SUMMARY OF THE AVERAGE WEIGHTS (IN GRAMS) OF YELLOW-BILLED PINTAILS TAKEN 28 FEBRUARY 1964 TO 23 JULY 1965 AT GENERAL LAVALLE, BUENOS AIRES AND VENADO TUERTO, SANTA FE

Dates	Place	Adult male	Adult female	Immature male	Immature female
28 Feb.–18 Apr. 1965	B. A.	746.2 (13)	663.5 (10)	—	600 (2)
May	S. F.	789.3 (20)	697.0 (6)	770 (1)	650 (2)
June	S. F.	740.3 (23)	707.8 (11)	782.3 (4)	636.8 (5)
July	B. A. S. F.	826.9 (18)	769.3 (7)	670 (1)	—
Totals	B. A. and S. F.	775.6 (74)	705.5 (34)	761.5 (6)	631.6 (9)

field and recorded in hunters' bags. However, there probably is a disproportionately high number of Yellow-billed Pintails because more field shooters than marsh shooters were sampled. This also results in reduced numbers of Rosy-billed Pochards. The near absence of Fulvous Whistling Ducks is due to their departure from shooting areas during late summer and also to their late flight times—when it is too dark for shooting. The two reported were from Santiago del Estero, probably a wintering area. Small samples of Rosy-billed Pochards, Silver Teal, and Speckled Teal are also influenced by their fall migration.

Separated by areas, the major species differences are the abundance of White-cheeked Pintails at Venado Tuerto and their absence at General Lavalle. More Black-headed Ducks were taken at General Lavalle, and Coscoroba Swans were not taken at Venado Tuerto.

The absence of immatures may be a product of both differential migration and gradual maturation of the sex organs used in age determination.

WEIGHTS

A quick survey of the literature demonstrates how little is known of the relative size of South American Anatidae. For this reason, weights of ducks were taken whenever possible; some were from collected birds, but most were from hunters' bags. As a result, samples are small, and few are available from any time period (Tables 2 and 3).

From the available data it seems that Argentine waterfowl follow the pattern typical of Northern Hemisphere anatids: Adult males exceed adult females in weights. Depending on the time of year and the species, adult females may be equaled or exceeded by immature males. In the case of the Yellow-billed Pintails, the small samples of immature males were taken late in

TABLE 3

A SUMMARY OF AVERAGE WEIGHTS (IN GRAMS) OF VARIOUS SPECIES ARRANGED BY SAMPLE AND AGE AND SEX. FIGURES IN PARENTHESES ARE SAMPLE SIZES. BIRDS WERE TAKEN IN THE PAMPAS REGION OF ARGENTINA DURING 28 FEB.–23 JULY (FALL AND WINTER) 1965 EXCEPT FOR LAST THREE SPECIES WHICH WERE TAKEN IN THE CHACO IN MAY, 1965

Species	Adult male	Adult female	Immature male	Immature female
Speckled Teal	429.1 (17)	394.6 (5)	—	388.2 (5)
Red Shoveler	608.3 (10)	522.6 (7)	—	543.0 (3)
Rosy-billed Pochard	1,181.2 (6)	1,004.0 (5)	1,000 (1)	1,000 (1)
Black-headed Duck	513 (11)	565 (13)	360 (2)	453 (3)
Chiloé Widgeon	939.0 (5)	828.3 (3)	—	665.0 (2)
Silver Teal	442.6 (10)	373.3 (3)	—	386.5 (2)
Cinnamon Teal	476.0 (7)	437.0 (3)	494 (1)	—
White-cheeked Pintail	710.4 (7)	670.5 (4)	—	553 (1)
Coscoroba Swan	3,785 (1)	3,200 (1)	1,660.0 (2)*	2,425 (2)
Argentine Ruddy Duck	610 (1)	560 (1)		
White-faced Whistling Duck	831 (1)			
Ringed Teal	350 (2)	310 (1)		
Brazilian Duck	600 (2)	580 (1)		
Masked Duck	400 (1)			

* Probably underweight; several individuals were found sick and dead in the marshes near General Lavalle.

the year when they were nearing adulthood. Immature females are the lightest in weight. A clear-cut exception is the parasitic Black-headed Duck in which females normally outweigh males at all ages.

NOTES ON PLUMAGE

Most Southern Hemisphere ducks have plumage cycles which differ from northern forms by the absence of the "eclipse" plumage (abbreviated "basic" of Humphrey and Parkes, 1959). Some species lack sexual dimorphism, others have sexual dimorphism all year, and some possess the first non-nuptial (basic) plumage strongly developed.

Phillips (1922, 1923) stated that southern anatids have two molts per year, but no details have been available. Five species were observed regularly during the present study, and numerous fresh specimens as well as skins were examined. Based on these general observations, four of the five typically have a complete late summer molt (postnuptial or prebasic) and a partial spring molt (prenuptial or prealternate). Discussions of the following species are arranged according to plumage patterns rather than taxonomy.

Yellow-billed Pintail.—The Yellow-billed Pintail is representative of many Southern Anatini which lack conspicuous sexual dimorphism, both sexes having nearly the same plumage coloration year-round, but which have two molts per year. On the basis of skins in the Museo Argentino de Ciencias Naturales, the natal plumage is replaced by the juvenal plumage which then seems to be held until midwinter (June). However, the juvenal tail is shed earlier, and only a few birds with juvenal tail feathers were seen in hunters' bags in April and early May. A juvenile specimen in the Museo Argentino still has all juvenal rectrices and was collected in mid-January. Immatures examined in hunters' bags in mid-June through July had adult tail feathers with worn tertials. No evidence of a first non-nuptial (basic) plumage was noted, but birds probably were not seen at the age when this plumage is conspicuous.

In June, immatures and adults were found in full body molt, and presumably, this was placing the birds in their nuptial (alternate) plumage. Tail molt was common, and several skins in Argentine and U. S. museums taken during July to September showed body and often tail molt. The timing of this molt seems to vary with locality, but at least a major body molt is apparent in winter and early spring. Presumably, the plumage acquired at this time is worn until the complete annual molt in summer (November and December). Specimens taken in summer are rare.

Based on limited observations of specimens in hunters' bags in late winter, and from specimens seen in museums, the same pattern seems to prevail in Speckled Teal, Chiloé Widgeon, Red Shoveler, Silver Teal, and probably White-cheeked Pintail. There is a complete annual molt in late summer, placing the bird in non-nuptial (basic) plumage which is held until the spring when the nuptial (alternate) plumage is acquired. Because there is no seasonal color dimorphism and the history of these plumages is unknown, homologies are uncertain.

Rosy-billed Pochard.—The general pattern in this species seems comparable to that of the Yellow-billed Pintail except that a "permanent" sexual dimorphism occurs. It differs from northern *Aythya* and *Anas* in the absence of the dull "eclipse" plumage in adults. No distinct first non-nuptial (basic) plumage was noted in skins examined, although it may occur in the head region. The juvenal plumage was replaced by the first nuptial (alternate) plumage in March to June, depending on the geographic area. As in Nearctic Aythyini, the juvenal tail feathers were not replaced until young were 4.5–5 months old in April or May when the body plumage was nearly complete. In six juvenile males in Argentine museums and six in U. S. museums, the alternate plumage was acquired first on the cheeks, then on the midback and flanks, and finally on the chest. The head and neck become almost entirely black before the scapulars, back and flanks are half renewed. The midline of the belly whitens after the breast is partly black.

The first-year male nuptial (alternate) plumage is characterized by the dull blackish-brown head with white-tipped feathers and, often, a white patch in the "V" of feathers between the lower mandibles. Yearling males also retain the brown juvenal wing coverts, while those of adults are black.

Spring molt was noted in adult males in September, October, and November specimens and in females in August and October in the skins in the Museo Argentino. Body and tail molt was noted in three adults taken in July at Venado Tuerto. Immature males, like adults, seem to have breast molt in the spring, and it is uncertain whether this was a gradual completion of the molt started in winter or if it involves another generation of feathers.

Black-headed Duck.—The plumage pattern in this species resembles that of the Rosy-billed Pochard. However, there is a complete postjuvenal, first non-nuptial (basic) plumage which starts to develop before the natal down has been replaced by the juvenal plumage under the wings (Weller, 1967*a*). The tail and back are renewed first. This plumage is held until August and September when the first nuptial (alternate) plumage of males is acquired. The pattern in females is less certain. The nuptial (alternate) plumage of males is replaced by the annual molt in December and January, and the latter plumage is worn all winter until August and September when at least a partial molt occurs, involving the head, breast, back, and tail. This pattern resembles other southern Anatids and differs from the Ruddy Ducks in that the winter non-nuptial (basic) plumage is essentially as bright as is the alternate plumage.

Argentine Ruddy Duck.—The plumage pattern in this species is of interest because it resembles that of the North American Ruddy Duck (*Oxyura jamaicensis*). It has been suspected of having a long-lasting non-nuptial (basic) plumage in winter like the North American form (Delacour, 1959), and this definitely seems to be the case. Males with bright rufous body were noted with female-like heads as early as 26 January 1965, at General Lavalle and similar birds were seen at Venado Tuerto, Santa Fe, in early winter (19 May 1965). In the field, the question arises as to whether these are young males entering their first nuptial (alternate) plumage or adults entering the dull non-nuptial (basic) plumage. This was clarified by a specimen collected at General Lavalle during mid-April 1965. This male had an adult penis and lacked a bursa but had the brown head with a white eye-stripe. The throat is whiter than in females, and the body has a general rufous aspect. However, close examination shows that most of the reddish feathers are worn and that new brown feathers are developing on the back. Another specimen in the Museo Argentino had been collected in May and is still more brown on the body. Some males collected in winter seem to have mottled blackish heads, and it may be that this basic plumage is transitory.

A late winter or early spring body and tail molt (August–October) occurs in both sexes, according to museum specimens at La Plata and observations summarized by Grant (1911).

The juvenal plumage is characterized by distinct juvenal tail feathers as is true of most stifftails (Coues, 1878). There also appears to be a distinct and long-lived first non-nuptial (basic) plumage as six young males in the American Museum have new brown feathers replacing the brown juvenal feathers. Presumably, young males acquire their first alternate plumage in September-October.

Cinnamon Teal.—This species differs from the previous forms in that it resembles the North American subspecies and males of most Nearctic dabbling ducks in possessing a short-lived "eclipse" plumage. Snyder and Lumsden (1951) found a well-developed first non-nuptial (basic) plumage (although they did not use this term). Young males have acquired new tail feathers and most of their alternate plumage by early winter (May). A specimen from Chile in the Museo Argentino had full juvenal plumage (including juvenal rectrices) when it was taken in March. Whether any late winter or early spring molts occur is not positively known, but such may be expected in females. Of three Chilean female specimens in the Museo Argentino, two showed no molt in May or July, but considerable breast molt was apparent in the specimen collected in September. Six adult males from Buenos Aires and Santa Fe were examined from mid-June to mid-July 1965, and no significant body or tail molt was noted.

Adult males of this species do have an "eclipse" plumage as was pointed out by Brooks

(1938) and by Snyder and Lumsden (1951). I suspect some irregularities in this plumage since some birds acquire it very early. Moreover, it seems transitory since a paired male collected on 8 January 1965, was dominantly in dull basic plumage but had some old reddish adult plumage as well as incoming bright alternate plumage. By late February, most adults again are in bright plumage.

SOUTHERN VERSUS NORTHERN PLUMAGE PATTERNS

Most Southern Hemisphere ducks which are sexually dimorphic have plumage cycles which differ from those of northern forms by the absence of the dull "eclipse" plumage of the late summer. This results in "permanent" sexual dimorphism, a sequence which may have resulted from a loss of the "eclipse" plumage (with a molt added in spring), or a change in its color. However, many southern anatids, especially of the genus *Anas*, lack prominent sexual dimorphism. The reasons for these differences between plumages of northern and southern ducks have not been explained and it cannot be assumed that all evolved in the same way.

The above patterns strongly suggest that the non-nuptial (basic) plumage or "eclipse" plumages of adults in northern ducks are relics of primitive plumage patterns as Humphrey and Parkes (1959) have proposed. Fairly typical Northern Hemisphere patterns are apparent in southern Cinnamon Teal and Argentine Ruddys, suggesting that these are recent arrivals to South America. The Argentine Ruddy has a long "winter" plumage resembling that of Nearctic forms, the Cinnamon Teal has a brief "eclipse" plumage, while the Black-headed Duck lacks any dull plumage.

Assuming that seasonal sexual dimorphism evolved first, permanent dimorphism could have resulted from a continuous shortening of the duration of the dull non-nuptial plumage (i.e., "winter" or "eclipse") as seen in the series: Argentine Ruddy Duck, Cinnamon Teal, and Black-headed Duck (or Rosybill). In the latter species, two plumages of the same color occur, and the homologies are uncertain. The forces producing such a loss are unknown but Sibley (1957) suggested that the early acquisition of the nuptial (alternate) plumage (and shortening of the non-nuptial) in northern ducks was associated with early pair formation, a situation which has been supported by observations in some North American species (Weller, 1965). This might imply an almost continuous courtship in species which lack the dull, non-nuptial plumage. However, my own observations suggest that several of the South American species with clear-cut, permanent sexual dimorphism do not pair for life and have a distinct spring courtship period (Black-headed Duck and Rosy-billed Pochard).

The absence of an eclipse plumage in subtropical and tropical areas may not mean that pairs *do* engage in courtship all year but that they *can*. In either dimorphic or non-dimorphic plumages, year-round constancy in plumage is essential to pair formation in birds residing in areas where the time of breeding is dependent on rainfall and other conditions, and where a regular periodicity such as occurs in the northern hemisphere is lacking. Birds constantly in nuptial plumage (bright or dull) are always ready to breed when environmental conditions permit. Presumably, this holds true for many non-waterbirds as well which do not breed at a regular time each year.

The absence of prominent sexual dimorphism, such as seen in the species of the genus *Anas*, could have resulted from early forms which lacked dimorphism or from forms having dimorphic patterns which recently have been lost. Most investigators imply that the latter is most probable in view of the dull plumages of northern ducks isolated on southern islands (Sibley, 1957). Although this loss of dimorphism often is explained on the basis of the lack of contact between closely related species, other possibilities exist. Generally, the Argentine species which lack sexual dimorphism tend to pair "permanently"—or at least some members of the population are in pairs all year. Courtship may be less intense and probably occurs over a longer period than in northern forms. It seems possible that the non-dimorphic (and often dull) plumage may develop in ducks which pair "permanently," do not engage in intense seasonal, social courtship, and which in some cases are not strongly migratory.

SUMMARY

Observations on the habitat ecology, nesting behavior, distribution, and weights of some Argentine anatids are presented. Data were gathered during August 1964 to July 1965 with observations from eastern and southern Buenos Aires Province, the Chaco zone of northern Argentina, the highland puna zone of northwestern Argentina, and the Andean Lakes region of northern Patagonia.

Compared to northern ducks, observations of southern forms indicate a lower degree of sexual dimorphism (especially in the genus *Anas*), a tendency toward permanent pairing (resulting in males accompanying broods), an extended period of courtship—possibly of lower intensity than in northern forms, reduced migration, and the absence of the "eclipse" plumage in males. Notes on plumages of five ducks are outlined to show variations in sexual dimorphism and molt patterns. Observations on several species suggest that the absence of sexual dimorphism is related to long pair bonds, while that of permanent dimorphism in South American anatids may be tied to temporary pair bonds. Loss of the eclipse plumage in Neotropical birds possibly is due to the irregularity of breeding seasons. Birds constantly in the breeding plumage have a definite advantage in being ready to pair whenever environmental conditions permit.

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COMPLEX INTERACTIONS BETWEEN CLAPPER RAILS AND LAUGHING GULLS

Amelia Segrè, Jack P. Hailman, and C. G. Beer

When two species nest in the same habitat it is of interest to study their interactions, since ecological competition, predator-prey relationships and simple propinquity may lead to interspecific aggression. Clapper Rails (*Rallus longirostris*) nest within a large colony of Laughing Gulls (*Larus atricilla*) in coastal Spartina marshes of the Brigantine National Wildlife Refuge north of Atlantic City, New Jersey. In some instances rails' nests occur within a few feet of the nests of gulls. During two summers of field work we have compiled notes on behavioral interactions between these two species; these notes reveal that the relationship between the species is quite complex.

FIGHTS AND DISPLAYS BETWEEN RAILS AND GULLS

During the breeding season of 1965 one of us (A.S.) noted aggressive encounters between the two species on three occasions involving different individuals. Observing from a hide she saw a gull and a rail fighting with bills locked together, beating their wings at one another, while the gull uttered calls that we believe to be associated with alarm. The initiations of these three fights were not seen; the fights ended in each case in departure of the rail. Two of the fights were in the neighborhood of gull nests but some distance from the nearest known rail nests; one took place next to the rail's nest.

On 20 June 1966 C.G.B. observed an encounter in which a rail on its nest was attacked by a Laughing Gull from the nearest gull nest. The gull approached the rail's nest on foot while gathering nest material, flew up within two feet of the nest and then repeatedly swooped and soared at the sitting rail from about eight feet above it. The gull swooped with lowered feet and, passing low over the rail, pecked down at it. Several times the gull appeared to strike the rail and following one of these strikes the rail responded by leaping up at the gull. After a few more swoops the gull flew to its own nest site about 20 feet away where it attempted to relieve its sitting mate.

In nesting areas where a rail nest was located within a cluster of gull nests, incubating gulls frequently, but not always, displayed an "intruder" response to a rail returning to its nest. This display consisted of ruffling the saddle feathers, bobbing the head rhythmically, holding the bill horizontally and open, and uttering an *uhr* call. This behavior pattern was also seen in incubating gulls when they were approached from the ground by a strange gull.

Strife between members of different avian species can usually be accounted for as due to competition over a common source of food, competition for nesting sites or to some form of predator-prey relationship. The clashes that we have described between rails and gulls did not conform to the usual patterns of interspecific fighting over food, and since the birds were already nesting the issues would appear not to have been over nesting sites. Hence defense against predation semed the most likely explanation of the fights between gulls and rails. We made a search of relevant literature but failed to find documented evidence of predation in either direction between the two species.

PREDATOR-PREY RELATIONS

Predation by Rails of Gull Nests.—On 31 May 1966 in the Brigantine gullery J.P.H. flushed a Clapper Rail from among Laughing Gull nests in an area known to contain no rail nests. This rail had a white secondary feather: a rail so marked was nesting about one-quarter of a mile to the northeast. Inspection showed that the gull nest in the center of the group from which the rail flushed had its single egg freshly broken open, with a large hole in the top.

On 17 June 1966 from a blind in a different part of the gullery, A.S. watched a Clapper Rail approach an unattended Laughing Gull nest which contained one gull egg and two experimental wooden egg-models. The rail passed by an adjacent nest with an incubating gull, and this gull made no response to the rail. The rail pecked into the unattended nest several times, and then after a few minutes crept away, passing by another unattended gull nest close to the blind without looking into it. Later inspection of the nest visited by the rail showed the gull's egg to have been broken in two, and its contents eaten; it is not known whether the rail struck the wooden egg-models.

Predation by Gulls at Rail Nests.—On 21 June 1966 C.G.B. made further observations of the rail's nest at which he had seen on the previous day the clash between gull and rail already described. The nest contained two freshly hatched rail chicks, the shells of three hatched eggs and three unhatched eggs. During the two hour watching session no adult rail was seen attending the nest.

As on the previous occasion the male gull of the pair owning the neighboring gull nest approached the rail nest on foot in the course of collecting nest material between attempts to effect nest relief. When three feet from the rail nest, the gull Long-called, dropped its nest material, and made the *kekek* "alarm call." It then walked onto the nest and began pecking down into it. One of the rail chicks made a high pitched squeal. The gull continued pecking vigorously. One of the chicks either leapt or was flung by the gull 18 inches or so out of the nest. The gull continued to peck it. Again the chick

FIG. 1. A nest containing the eggs of both Laughing Gulls and Clapper Rails found in the Brigantine gullery, July, 1966. The fragments of broken shells are from a hatched rail egg. There was a dead rail chick within two feet of the nest. (photo by C.G.B.)

jumped or was flung into the air. The gull continued pecking for a few seconds and then walked off a few feet where it stood for a minute or so Long-calling and preening.

After several more unsuccessful attempts at nest relief, interspersed with collecting trips, the gull returned to the rail's nest and resumed pecking. It picked a chick up in its bill during which the chick squealed and flapped its wings. The gull dropped the chick, pecked hard at it, picked it up and dropped it several times and then began making swallowing movements. A few seconds later the gull was swooped at by another gull and immediately flew to its own nest where it attempted to relieve. A minute or so later the gull returned to the rail's nest and again it was swooped at and chased off by another gull.

Ten minutes later a flock of six gulls, including the bird we have been concerned with so far, was hovering over the rail's nest. One of the gulls descended on to the nest and flew off with a rail chick dangling from its bill and the other gulls flying after it. Later inspection of the nest showed the remains of a partly eaten rail chick lying 18 inches from the nest, no sign of the other chick, and the three unhatched eggs still intact in the nest. It may be significant that there were newly hatched gull chicks in the nest of the predatory gull.

JOINT USE OF NESTS BY GULLS AND RAILS

Once in 1965 and once in 1966 we discovered nests containing eggs of both Laughing Gulls and Clapper Rails in widely separated parts of the colony. Unfortunately, is was not possible to determine which species was in attendance at these nests at the time we discovered them; nor was it possible to judge positively from the nest structure whether the nests had originated as rail nests or gull nests. In one of these nests, rail chicks were also present, but no gull chicks. Furthermore, in 1966 one of us (J.P.H.) found a rail nest of typical structure containing two gull eggs, but no rail eggs or chicks.

Our observations indicate that the average incubation period for the Laughing Gull is 21–23 days. Kozicky and Schmidt (1949) report that the average incubation period for the Clapper Rail is between 18–22 days. The presence of rail chicks in one of the nests suggests that the rail eggs were laid earlier; this might be interpreted as evidence for the nest initiating as a rail nest rather than as a gull nest. Pettingill (1938) reports an incident of a rail consistently retrieving its eggs from more than two feet from the nest rim. This performance was accomplished by carrying the eggs in its bill. It is thus possible that a rail might have retrieved gull eggs from nearby gull nests and placed them in its own nest. The further possibility that under certain conditions a gull egg might appear as a "supernormal" incubation stimulus to a rail, rather than as a food object, would be consistent with this explanation.

On the other hand it has been reported that California gulls (*L. californicus*) sometimes stock their nest with, and incubate, the eggs of other species and that these gulls may transport such eggs by swallowing and regurgitating them whole (Vermeer, 1967). No such behavior has been observed in Laughing Gulls but perhaps it should be kept in mind as yet another possible explanation of the gull-rail nests.

Whatever the truth of the matter, we might have here yet another basis for hostility between gulls and rails: competition for nests and eggs for incubation.

DISCUSSION

We thus have evidence that rails prey upon the eggs of gulls; that, at least on occasion, gulls prey on the chicks of rails: and that the two species are in some sort of competition at nest sites. We have not observed gulls eating rail eggs, or rails eating gull chicks. C.G.B. has observed Laughing Gulls eating one another's eggs and has seen foreign gulls descend on and peck at the eggs of gulls that were tardy in returning to their nests after alarms. Such predatory gulls are viciously attacked by the nest owners, but if the egg-robber has succeeded in gashing an egg the owner will probably devour what remains. Laughing Gulls thus have a taste for eggs so that one might expect that they would prey on those of Clapper Rails if given the opportunity. However, in the attack on the rail nest that we have reported the unhatched eggs of the rail were ignored.

If gulls do take rail eggs the occurrences are probably rare, for the rails give little opportunity for predation of their eggs by gulls—far less opportunity than the gulls give the rails. Whereas a gull flies at alarm, removing its own conspicuous body from the nest and leaving the eggs to the protection of their camouflage, the cryptically colored rail sometimes stays covering its eggs until it is almost stepped on. Furthermore, the dispersion and inconspicuousness of the rail's nest are such that the ratio of return for effort for a gull seeking rails' eggs would be unfavorable, compared with what it is for other available sources of food. By L. Tinbergen's (1960) hypothesis, a "search image" for rails' eggs would probably not be retained by a gull for long. We think it likely, therefore, that gulls offer little if any egg predation pressure to rails.

On the other hand, the quantity and availability of gulls' eggs to a rail would seem to make it worth a rail's while to search out gulls' nests as a source of food. The cryptic coloration of the rail, and its habit of creeping stealthily, silently and with head down through the vegetation would seem to be suited to such predation. It is impossible at present to estimate the extent of Clapper Rail predation on Laughing Gulls' eggs. The rail apparently does not carry the gull eggs away whole from the nest to devour them elsewhere, as does the Fish Crow (*Corvus ossifragus*). Rather, the rail eats the eggs on the nest, leaving the shells behind. But such is also the practice of the Laughing Gulls themselves, so that one cannot, on the basis of what remains in the gulls' nests, work out how much of the destruction suffered by gulls' eggs is due to rails. Among the Rallidae predation of gulls' eggs is not peculiar to the Clapper Rail; according to Densley (1966) Coots (*Fulica atra*) take the eggs of Black-headed Gulls (*Larus ridibundus*).

Since both the rails and the gulls eat gulls' eggs there is a sense in which at least some of the clashes between gulls and rails could be construed as fighting over food. That is, the fighting is over objects that the members of both species eat, but which also happen to be the offspring of one of them.

The fact that the gull's behavior would, for most purposes, be described as defense of its brood rather than defense of a food source distinguishes these fights from typical instances of interspecific fighting over food. But the point is perhaps worth making that we have here an illustration of how the way in which one classifies a piece of behavior depends upon the point of view one takes.

Several interpretations of the attacks by the gull on the rail's nest are possible. Since both of the occasions when it was observed, the gull was engaged in a prolonged series of attempts to relieve its sitting mate, the gull's behavior might have been, at least in part, a consequence of frustration of these efforts. Relief ceremonies sometimes contain elements of overt hostility between the members of a gull pair, particularly at and beyond the time that their eggs hatch. The gull's attacks on the rail's nest, at least in their initial phases, could perhaps have been instances of redirected attack (Bastock et al., 1953). The behavior of the gull towards the rail chick was not unlike the behavior that adult gulls frequently show to gull chicks. Sometimes attacks by a gull on gull chicks follow immediately upon agonistic encounters between the gull and other adults and so occur in a sequence that makes the notion of redirection appropriate.

On several occasions C.G.B. observed adult Laughing Gulls pecking chicks of their own species to death. On one occasion a gull was seen to alight on the unattended nest of another gull and fly off with the rear portion of a newly-hatched chick dangling from its mouth. The calls and postures adopted by the gull attacking the rail chick were typical of gulls attacking gull chicks, and the swooping attacks that it drew upon itself were also typical of what happens when a gull chick is being pecked. Explanation of why adult gulls attack gull chicks still poses a problem. It is doubtful whether one explanation will cover all types of occurrence: at times the adults seem to be treating the chicks as food objects, at other times as tresspassers over territorial boundaries, at others as the objects of redirected attack, but there are many occasions when there is no obvious basis for a gull's hostility to a chick. In any case the similarity between the gull's behavior towards the rail chick and the attacks by gulls on gull chicks suggests that explanations of the two phenomena may be similar.

In sum, the aggressive interactions between gulls and rails are unlikely to have as their basis a simple, unitary explanation. There are elements of mutual predation, nest-site competition, food competition and redirected aggression underlying the interspecific fighting. Only further study can clarify this complex nexus of behavior, and the questions that it raises.

SUMMARY

1. On four occasions, actual fights between Clapper Rails (*Rallus longirostris*) and Laughing Gulls (*Larus atricilla*) on the nesting grounds were observed in detail.

2. Twice, rails were observed preying on gull eggs, and once a single gull and later a group of gulls were seen preying on rail chicks at the nest.

3. One nest of unknown origin contained both rail and gull eggs; another contained rail eggs and chicks plus gull eggs. A typical rail nest was discovered with gull eggs, but no rail eggs or chicks.

4. These results, coupled with observations of gull-gull interactions, make it seem likely that interspecific aggression between gulls and rails has no simple, unitary explanation. The interactions contain elements of mutual predation, the nest-site competition, food competition and redirected aggression, thus demonstrating how complex may be the interactions between two species sharing the same habitat.

ACKNOWLEDGMENTS

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THE USE OF TOOLS BY BROWN-HEADED NUTHATCHES

Douglass H. Morse

The use of tools by individuals in natural populations has been recorded for only a few species of birds. Following Thorpe (1963), tool use here is considered as the manipulation of objects that serve as an extension of the bodily mechanism. Species of birds using tools include various species of Geospizinae (Lack, 1947; Eibl-Eibesfeldt and Sielmann, 1962; Hundley, 1963; Curio and Kramer, 1964), the Satin Bower-bird (*Ptilorhynchus violaceus*) (Marshall, 1954), Black-breasted Buzzard (*Hamirostra melanosterna*) (Chisholm, 1954), and Indian Tailor-bird (*Orthotomus sutorius*) (Wood, 1935). The following observations of tool use in Brown-headed Nuthatches (*Sitta pusilla*) are of considerable interest because bark scales have not been reported as tools and tool-use behavior has not been reported from the Sittidae in nature. Observations were made in the extensive longleaf pine (*Pinus australis*) forests of western Tangipahoa Parish, Louisiana, in the fall and winter of 1963–64 and the fall of 1964.

OBSERVATIONS

Tool use occurred as follows: Brown-headed Nuthatches selected a readily available scale of bark (Fig. 1) from a pine trunk or large limb and used it as an extension of their beak to remove another bark scale from a trunk or large limb. They accomplished this feat by inserting the tool under the scale to be removed and then manipulating it in various directions, in the manner of a wedge and lever. Usually they were successful in removing the attached scale in the process. When the scale was removed the birds usually dropped the tools and both bits of bark fell to the ground. The bird then foraged upon the newly exposed surface, which before this moment formed an excellent hiding place for insects and other potential prey items. Occasionally, they would remove three or four scales before dropping the tool. A maximum of three tools were picked up during any sequence of this behavior that I observed. The process was obviously a random search rather than an attempt to obtain any single item of food. Upon occasions Brown-headed Nuthatches were observed carrying single scales of bark in their beaks and even flying short distances with them. These scales probably were to be used eventually as tools.

Tool use was noted principally outside the seasons of heavy seed crops. This behavior was uncommon, but was observed on several days in the 1963–64 and 1964–65 seasons when the birds were watched carefully for considerable periods of time (Table 1). Tool use was not noted during observations

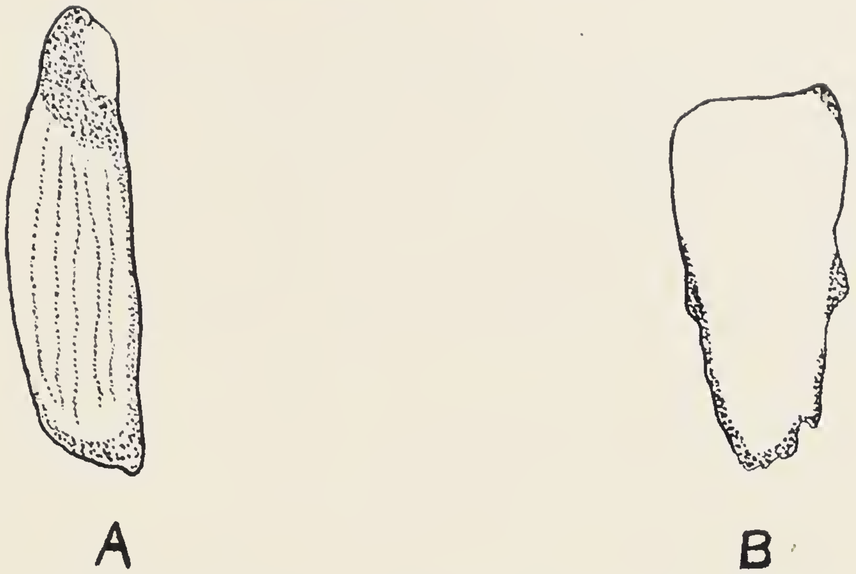

Fig. 1. A. Seed of longleaf pine × 1. B. Small bark scale of longleaf pine used as tool × 1.

of Brown-headed Nuthatches in loblolly pine (*Pinus taeda*) and spruce pine (*P. glabra*) forests 45 km away. The bark scales of these two species of pines do not readily separate from the trunk as do those of longleaf pines.

The use of tools may be confused easily with seed cracking, which in this species is accomplished by wedging a seed into a depression of the bark and hammering upon it with the bill. However, upon two occasions I retrieved the scales used as tools and those removed by using the tools. Both the tool and the scale removed usually were considerably larger than longleaf pine seeds, which are winged and suggestive of red maple (*Acer rubrum*) seeds in shape (Fig. 1).

DISCUSSION

Brown-headed Nuthatches feed extensively on pine seeds when available (Norris, 1958; Morse, 1967). These observations were made in the longleaf pine forests in which seed crops are extremely sporadic. Bumper crops occur approximately every five to seven years, total failures about as often, and smaller crops other years (Wahlenberg, 1946). Thus, the use of tools outside of a heavy seed season very probably improves the birds' efficiency in foraging during these periods.

Longleaf pine has extremely flaky bark, which can be removed with considerable facility by small birds. Many adequate tools (flakes of bark) are available, making these trunks ideal areas for potential tool use. Tool use apparently facilitates the removal of flaky bark scales, including ones that otherwise could only be removed with difficulty, if at all. Additional hiding places of invertebrates thus can be reached readily by their use. In

TABLE 1

TOOL USE BY BROWN-HEADED NUTHATCHES

Condition of seed crop	Observations of tool use	Hours of observations*	Frequency (times/hour)
Few seeds	10	150	0.066
Abundant seeds	1	75	0.013

* Based upon an average of one bird being watched continually during a study period.

other local species of pines, the bark is not flaky enough to facilitate its ready removal, either for a tool or by a tool.

Tool use in Brown-headed Nuthatches apparently is a local characteristic. Norris (1958) did not mention this behavior in his extensive study and literature review of this species; in fact, neither Norris nor Löhrl (1958) mentioned tool use in any of the Sittidae. Thus far, this behavior has been noted only in the Tangipahoa Parish study area, although longleaf pine forests extend over large parts of the southeastern United States. A tendency of Brown-headed Nuthatches to forage heavily in the foliage and small branches during the part of the season that they are largely insectivorous and to feed on pine seeds at other times (Morse, 1967) may limit the utility of developing this trait in other areas.

Tool use of the type described would be expected in Brown-headed Nuthatches more commonly than in other seed eaters of the forest. They are the only common species feeding heavily upon pine seeds that crack these seeds by wedging them into the bark. The other principal users of pine seeds in the longleaf pine forests, Carolina Chickadees (*Parus carolinensis*) and Tufted Titmice (*P. bicolor*), cracked seeds by holding them between their feet and hammering upon them. White-breasted Nuthatches (*Sitta carolinensis*) cracked seeds in a manner similar to that of Brown-headed Nuthatches, but were uncommon and did not feed heavily upon the seeds. Pine Warblers (*Dendroica pinus*) cracked pine seeds in a manner similar to the nuthatches, but did so much less frequently than did Brown-headed Nuthatches, were extremely inefficient at the activity, and probably were completely dependent upon a horizontal position for this activity (Morse, 1967).

In experimental studies, Herter (1940) reported that Eurasian Nuthatches (*Sitta europaea*) were completely unsuccessful in manipulating string to pull up food, although Mountfort (in Thorpe, 1963) reported that this species successfully performed this exercise. The ability to manipulate string in such a manner is more likely if a tendency to manipulate objects with the feet is present (see Thorpe, 1963) than if it is absent. Many titmice

(Paridae) normally manipulate food in this way, but such a tendency has not been reported authentically in the Sittidae (Norris, 1958). Members of this family manipulate food by wedging it into a crack of a solid object such as a tree trunk and then hammering upon it with their bill, the manipulation of food being performed by the bill alone. When cracking seeds or other objects in the bark of longleaf pines, Brown-headed Nuthatches probably sometimes slough off scales of the flaky bark. Following such an occurrence, food might become suddenly exposed. The process of wedging food into a crevice is very suggestive of the way in which a flake of bark is used for a wedge, and the large seeds of the longleaf pine even resemble a flake of bark somewhat. These similarities offer a possible explanation of the origin of tool use in this species. Also, the tendency to manipulate objects with the bill would likely make such a behavioral modification especially feasible.

SUMMARY

A local population of Brown-headed Nuthatches (*Sitta pusilla*) was discovered, whose individuals sometimes used flaky bark scales of longleaf pines (*Pinus australis*) for tools to pry other bits of bark off trunks and large limbs of those trees. This behavior may be of particular aid to them in foraging when the seed crop fails. Tool use in this species closely resembles the process of cracking seeds in the heavily ridged bark.

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NEW LIFE MEMBER

Mr. Ed N. Harrison, of Los Angeles, California has recently become a Life Member of the Wilson Ornithological Society. Mr. Harrison, who is Manager of the Westwood Center office building in Los Angeles, has had a distinguished career as an amateur ornithologist. He is a longtime member and a Past President of The Cooper Society; is currently President of The Western Foundation of Vertebrate Zoology; and is a member of the boards of both the Los Angeles County Museum and the San Diego Museum of Natural History. His principal ornithological interests have been in studying the birds of Central America, and in assembling a library of animal and birdlife. Some years ago he produced a nature film, "Song of the Land" which was nominated for an academy award. Mr. Harrison is married and has three children.

A COMPARISON OF MIGRATION BETWEEN BLACKBIRDS AND STARLINGS

Don P. Fankhauser

Because of the close association between the introduced Starling (*Sturnus vulgaris*) and three native blackbird species, Brown-headed Cowbird (*Molothrus ater*); Common Grackle (*Quiscalus quiscula*); and Red-winged Blackbird (*Agelaius phoeniceus*), a study was made to compare their migrations. These four species often roost and feed together, and they have fairly similar breeding and wintering ranges in the United States and Canada east of the Rocky Mountains.

PROCEDURES

Records for the four species, of birds banded during the period 15 April through 30 November in states and provinces north of and including Maryland, District of Columbia, West Virginia, Kentucky, Missouri, Kansas, and Montana, were obtained from the Bird Banding Laboratory on all interceptions of banded birds from 1920 through July 1962. (The term "interception" is used in this paper to designate banded birds retaken in any way, alive or dead.)

Table 1 was constructed from the interception data to show, by species, for each of nine time-period categories that collectively covered the entire year: (1) the number of interceptions, and (2) the percentage of interceptions, both in the state or province where banded and in the southern states (south of and including Virginia, Tennessee, Arkansas, and Oklahoma). Migration, including the direction and the degree of movement, was determined by analysis of the tabulations.

RESULTS

Data from interceptions of northern cowbirds, grackles, and redwings indicated that the onset of migration and the percentages that migrate to the South are very similar for all three species. High percentages of northern birds were taken in the North during the spring, summer, and fall—until the period 1 November through 14 December, when the percentages taken in the South showed an increase while those in the North decreased.

During the winter period of 15 December through 31 January the proportions of northern-banded cowbirds, grackles, and redwings taken in the southern states were high and comparable (80 per cent, 79 per cent, and 91 per cent). Nine per cent, 11 per cent, and five per cent, respectively, were taken in the state or province where banded indicating that small

TABLE 1

INTERCEPTIONS (1920–JULY 1962) OF BIRDS BANDED IN NORTHERN STATES AND PROVINCES DURING THE PERIOD 15 APRIL–30 NOVEMBER.

	Brown-headed Cowbird			Common Grackle			Red-winged Blackbird			Starling		
Interception period	Sample size	% taken in state or province where banded	% taken in southern states	Sample size	% taken in state or province where banded	% taken in southern states	Sample size	% taken in state or province where banded	% taken in southern states	Sample size	% taken in state or province where banded	% taken in southern states
1 July–14 Aug.	149	89	4	1,660	96	0	277	95	0	270	94	0
15 Aug.–31 Oct.	150	75	10	1,722	91	0	159	69	2	308	93	0
1 Nov.–14 Dec.	104	21	50	646	33	45	115	13	70	442	85	3
15 Dec.–31 Jan.	116	9	80	633	11	79	180	5	91	539	81	7
1–14 Feb.	38	16	66	219	9	80	47	19	79	172	83	4
15–29 Feb.	34	15	71	177	8	83	33	42	54	180	86	2
March	308	82	10	861	58	27	392	90	8	475	88	1
April	1,359	98	0	2,354	92	2	681	99	1	426	91	0
1 May–30 June	1,230	97	0	5,217	96	0	1,216	99	0	998	94	0

numbers either did not migrate or migrated only for short distances. A few records were of birds that moved to a state south of where banded, but not as far as the southern states.

The data suggest slight differences by blackbird species in the onset of northward migration from the southern wintering grounds. Considerable northward migration by redwings occurred in February, but no grackle movement was detected until March. During March, 90 per cent of the redwings were taken back on the northern breeding grounds contrasted with only 58 per cent of the grackles and 82 per cent of the cowbirds.

The percentage of northern Starlings that migrates to southern states appears much smaller than for the blackbirds. In the winter period of 15 December through 31 January only 38 of 539 intercepted starlings (7 per cent) were taken in the southern states, compared with over 80 per cent of the blackbirds, and only 102 of 539 (19 per cent) of the Starlings were taken outside the state or province where banded.

DISCUSSION AND CONCLUSION

Because of continuing efforts made by most banders to recapture birds at the stations where they were banded, these data probably are biased in favor of the birds being intercepted in the state where banded. Therefore. the actual percentages that migrate may be larger than the interception records indicate. The magnitude of this bias may vary among the four species. but it should at least be in the same direction for each. This bias could not be expected to account for the large differences in percentages of migrating individuals of Starlings and the three blackbird species. Thus. it seems safe to conclude that the percentage of northern Starlings that migrate to the southern states is very small compared with the percentage of any of the three blackbird species.

PATUXENT WILDLIFE RESEARCH STATION, LAUREL, MARYLAND, 7 OCTOBER 1966.

GENERAL NOTES

Breeding of the Trumpeter Swan at the Madison, Wisconsin, lakes.—No proof of the breeding of the Trumpeter Swan (*Olor buccinator*) in Wisconsin could be shown in a previous paper (Schorger, 1964. *Wilson Bull.*, 76:331–338). Continued search of the literature has revealed that it formerly bred at the Madison lakes. This supports the reported breeding of the species in Jefferson and Dane counties (Kumlien and Hollister, 1903. *Bull. Wisc. Nat. Hist. Soc.*, 3:31–32). In 1846, H. A. Tenney became a permanent resident of Madison, "a hamlet—the country a wild waste." He wrote further: "The stately swan came fearlessly to feed or make his nest" (*In*: W. J. Park & Co., 1877. "Madison, Dane County and surrounding towns. Madison." p. 541). David Atwood (Madison *State Journal*, 28 August 1867) was at Colliday's Point on Lake Kegonsa in August, 1867, where a swan was floating on the lake. W. H. Colliday informed him that he had captured the bird in spring. Its plumage was then a "light blue," but now snow white. It was completely domesticated, a trait characteristic of the species. H. Albert Hochbaum has informed me that about a year after hatching, at a distance, a yearling cannot be distinguished from an adult. This shows that Colliday's bird was hatched in the area, and that at the time mentioned it was at least a year old.

While trapping for small mammals in the large marsh on the west side of Lake Waubesa, on 26 October 1966, I met William S. Lalor. He was 92 years of age, but appeared to have a very good memory. His grandfather, William Lalor, homesteaded on Section 7, Dunn Township, Dane County, in 1839 or 1840. In pursuit of local information, I asked him if swans once occurred in the vicinity. My journal reads: "He

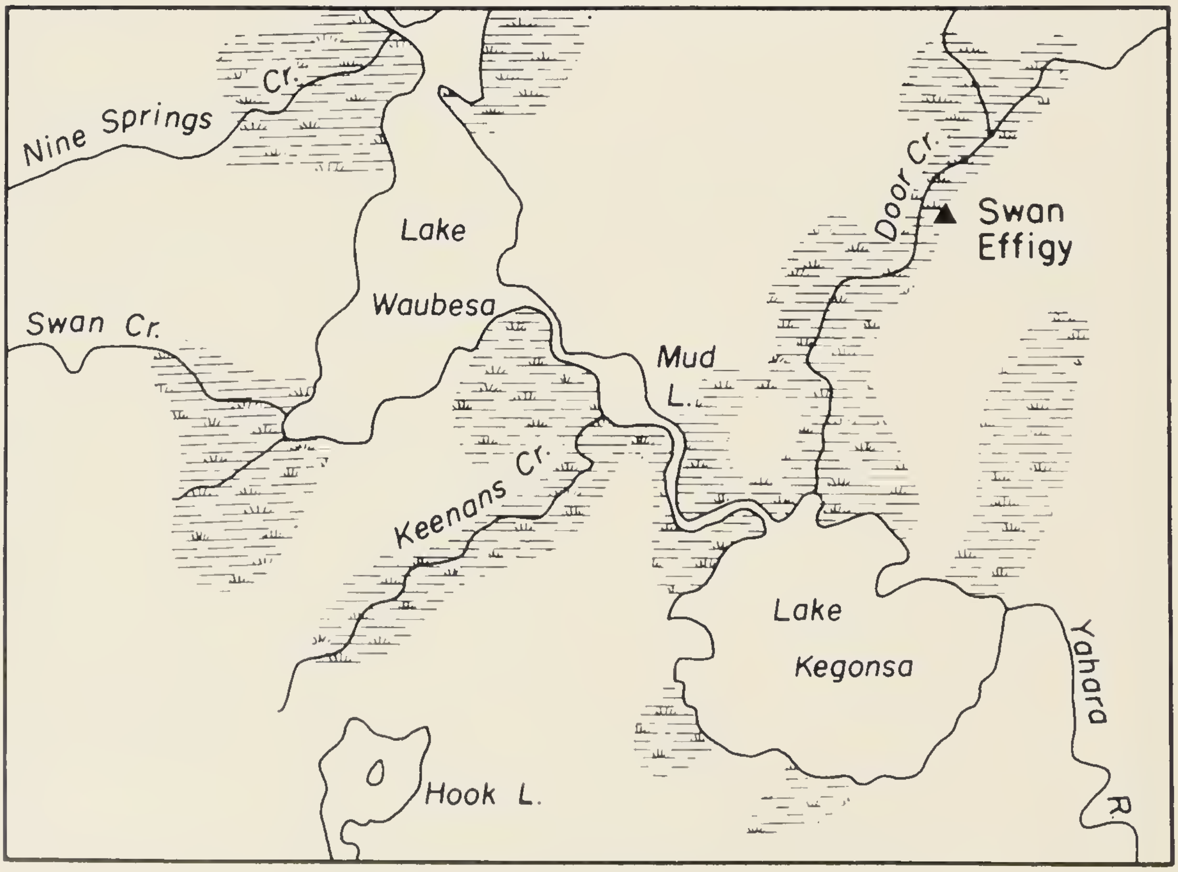

Fig 1. Map of Lakes Waubesa and Kegonsa.

said that when a boy he shot into a group of 8 swans sitting on the bank of Swan Creek with an old musket. He killed one which when hit gave a pitiful cry. This was in late summer. . . . He remarked that swans could be approached easily. Differed in this respect from Sandhill Cranes." In view of the season, these must have been Trumpeter Swans. In May, 1887, Thwaites (1888. "Historic highways." Chicago. p. 43) followed the east shore of Lake Kegonsa on a canoe trip down the Rock River. He wrote: "A stately wild swan kept us company for over a mile, just out of musket-shot, and finally took advantage of a patch of rushes to stop and hide." The species must remain in doubt.

Place names are indicative that swans once bred in the region, as they were too common in migration to leave their name from being merely birds of passage. Swan Creek (Fig. 1) flows through a large marsh to enter the southwest corner of Lake Waubesa. Waubesa is a corruption of *wabisi*, the Chippewa word for swan. In Section 6, Pleasant Springs Township, along Door Creek, is an unmistakable swan effigy mound (McLachlan, 1925. *Wisconsin Arch.*, n.s. 4:191). This type of mound is rare in the state, only one other example being known. Measurements of the mound were: length of body, 55 feet; width of body in middle, 21 feet; and length of neck 30 feet. In the memory of the early settlers, the marshes along the banks of this creek were much more extensive, containing widespreads with water throughout the year.

The reason for naming Swan Lake, thirty-five miles north of Madison, has not been ascertained. Five white swans were reported at Bay City, Pierce County, on 28 May 1873. A week later there was an addition of about twenty birds (Bay City *Herald*, 28 May, 4 June 1873). No information on nesting was found.—A. W. Schorger, *Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin, 6 May 1967.*

Mottled Ducks in Kansas.—An addition to the Kansas avifauna was the discovery, in 1963, that the Mottled Duck (*Anas fulvigula*) is a breeding resident. Heretofore, it had been considered "accidental" in the state by Tordoff (1956. Check-list of the birds of Kansas. *Univ. Kans. Publ. Mus. Nat. Hist.*, 8:314) and a "vagrant" by Johnston (1960. Directory to the bird-life of Kansas. *Univ. Kans. Publ. Mus. Nat. Hist., Misc. Publ.*, 23:12). The species was known for Kansas by one specimen; Goss (1891. "History of the birds of Kansas," p. 57) collected a female near Neosho Falls, Woodson County, Kansas, 11 March 1876.

It was thus unexpected when Marvin Schwilling, Jim New, John Nilsen, and Dr. David Parmelee discovered a Mottled Duck nest containing nine eggs on the Cheyenne Bottoms Waterfowl Refuge in central Kansas on 27 June 1963 (Johnston, 1965. A directory to the birds of Kansas. *Univ. Kans. Publ. Mus. Nat. Hist., Misc. Publ.*, 41:12). This nest was later destroyed by a predator. So far as is known, this is the only far inland breeding population of this species which supposedly has been restricted to the Gulf Coast states.

Mottled Ducks have been observed with some regularity at Cheyenne Bottoms since 1964: one pair observed frequently throughout the summer of 1964; an adult male in molt (flightless) was captured in a drive-trap with other ducks 29 July 1964, photographed, banded, and released. Schwilling (pers. comm.) reports regular observations of as many as five birds at one time, during summer of 1965 and six observations of two to four birds from 13 May to 23 September 1966.

Four Mottled Duck specimens have been collected at Cheyenne Bottoms. A juvenile female was captured by Jim New and the author on 20 August 1963 indicating that the species had nested successfully on the refuge that year. Three have been shot by hunters and saved as scientific specimens: adult female, 26 October 1963; adult female, 11 October 1964; immature male, 23 October 1965. These four specimens are in the collection of Kansas State Teachers College at Emporia.

Singleton (1953. Texas coastal waterfowl survey. *F. A. report series, No. 11, Sect. II—Mottled Duck studies.* Texas Game and Fish Comm., Div. Wildl. Rest., Austin, p. 85–128) found that Mottled Ducks are sedentary, rarely moving over one hundred miles. Wolfe (1956. "Checklist of the birds of Texas," p. 15) reports that in Texas this species "occasionally straggles" to northeastern and northcentral parts of the state. Lowery (1955. "Louisiana birds." p. 166) has written that "the species seldom, if ever, ranges northward in the state above the coastal tier of parishes." There are no records of the Mottled Duck in Oklahoma (Sutton, 1967. "Oklahoma birds," p. 63).

In view of this reported sedentary habit, one wonders how Mottled Ducks happen to be in Kansas and whether this disjunct breeding population is also nonmigratory. As yet, no winter observations of Mottled Ducks have been made at Cheyenne Bottoms. The species has not been reported from other inland areas similar to the Cheyenne Bottoms marsh. This situation suggests that close scrutiny of dark-colored ducks in the midwest is certainly advisable since a Mottled Duck might easily be mistaken in the field for a Black Duck (*Anas rubripes*).

I wish to express my appreciation to Dr. David Parmelee of Kansas State Teachers College, and Mr. Marvin Schwilling, Waterfowl Project Leader for Kansas, for use of field notes. Support was provided through Kansas State Teachers College and the University of Oklahoma under joint research studies financed by the National Institutes of Health (AI 05232-01).—Merril G. McHenry, *Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069, 7 February 1967.*

Chuck-will's-widow and Wood Ibis in central Illinois.—On 10 June 1966, a farmer ornithologist called me to report finding the nest of a strange Whip-poor-will which seemed to have a larger head and more brown about the throat than any Whip-poor-will that he had even seen. He asked me to meet him at a location just north of Liberty, Illinois to identify his strange find. My visit proved the bird to be a female Chuck-will's-widow (*Caprimulgus carolinensis*). The eggs were typical of others of this species that I had examined in trips through North Carolina and Georgia. This bird has never before been reported as nesting either in central or northern Illinois. It was successful in incubating the two eggs and the young were safely fledged.

The A.O.U. Check-list (1957) records the Chuck-will's-widow as breeding from southern Illinois southward into southern Louisiana. Robert Ridgway reported it as a regular summer resident as far north as Olney, Illinois. This record extends the nesting occurrence 150 miles northward in Illinois.

On 11 September 1966, I stopped my automobile at the west end of the Illinois River bridge at Beardstown, Illinois to view two large birds standing on a mud bar in a slough called "Curry Lake." The birds proved to be Wood Storks or Wood Ibis (*Mycteria americana*). Three days later from across the state of Illinois at Quincy, Mrs. William Gerdes recorded two Wood Storks—probably the same birds—moving on their return migration southward. These two records are particularly important as not since 1905 have they been recorded in central or northern Illinois.—T. E. Musselman, *124 S. 24th Street, Quincy, Illinois, 9 December 1966.*

Foraging dives by surface-feeding ducks.—Recently, R. I. Smith (1966. *Wilson Bull.*, 78:483–484) questioned, among other things, the occurrence of foraging dives by Pintails (*Anas acuta*). Foraging dives by mature wild Pintails have been repeatedly seen at the Wildfowl Trust since at least 1954 (Chapman et al., 1959. *Brit. Birds*, 52:60), and this species is only one of several "dabblers" that regularly dives for food there. Other surface-feeding species that we have observed diving for food include Mallards (*Anas platyrhynchos*) (wild resident and wintering birds), Shovelers (*Spatula clypeata*) (wild wintering birds), African Black Ducks (*Anas sparsa*), and Bahama Pintails (*Anas bahamensis*). One of us (J.K.) has also observed foraging dives by New Zealand Brown Ducks (*Anas auklandica chlorotis*), Wood Ducks (*Aix sponsa*), and Mandarin Ducks (*Aix galericulata*); in all cases females of these species have been observed diving more frequently than males. Additionally, one of us (P.A.J.) has noted foraging dives by Gadwalls (*Anas strepera*), Cape Teal (*Anas capensis*), and Gray Teal (*Anas gibberifrons*). Of these three, the Cape Teal has been observed diving much more commonly than the others.

A number of published accounts of diving by surface-feeding ducks probably refer to "dashing-and-diving" during bathing (McKinney, 1965. *Behaviour*, 25:173–174) or to escape-diving, but others are clearly concerned with foraging. Thus, foraging dives by wild Mallards have been reported on several occasions (e.g., Mylne, 1954. *Brit. Birds*, 47:395; Kutz, 1940. *J. Wildl. Mgmt.*, 4:19–20). Wild Black Ducks (*Anas rubripes*) likewise have been reported to dive for food to depths of up to ten or twelve feet (Kutz, 1940. op. cit.; Wright, 1954. "High Tide and an East Wind. The story of the Black Duck.") Cottam (1945. *Condor*, 47:39) also reports foraging dives by these two species, as well as by male Shovelers. Foraging dives by both sexes of Shovelers have been reported (Dean, 1950. *Brit. Birds*, 43:19–20), and similar behavior has been noted in the New Zealand Shoveler (*Spatula rhynchotis*) (Black, 1959. *Notornis*, 8:118–119).

To our knowledge, there are no published accounts of Blue-winged Teal (*Anas discors*) diving for food, but Frank McKinney (pers. comm.) has reported seeing this among both adult and immature birds, particularly during August and September. We have found no record of foraging dives by Cinnamon Teal (*Anas cyanoptera*), and only one (Janssen, 1964. *Loon*, 36:141) for Green-winged Teal (*Anas carolinensis*), but it should be apparent that nearly all normally "surface-feeding" ducks might perform foraging dives occasionally. Incidentally, corroboration of preflight Neck-jerking (or "Head-thrusting") by Pintails is provided by McKinney (1965. *Behaviour*, 25:215), and Lorenz (1952. *Avicult. Mag.*, 58:12) has independently reported mutual precopulatory "Pumping" in Pintails.—JANET KEAR AND PAUL A. JOHNSGARD, *Wildfowl Trust, Slimbridge, Glos., England, and Department of Zoology and Physiology, University of Nebraska, Lincoln, Nebraska 68508. 19 May 1967.*

Records of the Snowy Owl for Utah.—One specimen of the Snowy Owl (*Nyctea scandiaca*) is on record for Utah (Hayward, 1935. *Wilson Bull.*, 47:284), taken on Provo Bench, Utah County, in December, 1908. It is in the collection at Brigham Young University. However, there are several other instances of occurrence of the species in the state and a second specimen has been lately acquired. The additional records are as follows. All observations were made by competent ornithologists.

A Snowy Owl was taken at Huntsville, Weber County, during the winter of 1909 which was mounted and for many years adorned the mountain cabin of J. W. Brewer in Ogden Canyon. Its present whereabouts, if still extant, is unknown. Archie Hull reported that two Snowy Owls were killed by hunters 15 miles northeast of Mantua, Box Elder County, on 1 October, 1925. They were not saved. A Snowy Owl was observed by Ellis R. Wilson in a field south of Centerville, Davis County, on 5 April, 1953. Reed Ferris saw one just north of Ephraim, San Pete County, on 4 January, 1954. Rodney Harvey observed a Snowy Owl on the southeastern outskirts of Salt Lake City in early January, 1961. It was perched near a willow patch where several quail and a pheasant had a haven of refuge.

Two or possibly three additional records turned up during January, 1967, one corroborated by a museum specimen. A Snowy Owl was picked up alive but sick on 26 January, 1967, by Jaren Tolman, 4 miles west of Syracuse, Davis County, on the Syracuse-Antelope Island dike that extends out into the Great Salt Lake. It died that night and was presented to the University of Utah through Jack A. Rensel of the State Fish and Game Department. It proved to be a male, with testes measuring 8 mm in length. Its weight was 1427.8 grams. Upon learning of the rarity of the species in Utah, Mr. Rensel subsequently reported two other observations. Conservation Officer LeVon Thomas saw one on 7 January, 1967, on the Glen McKinnon Ranch, 2 miles south of Randolph, Rich County. At 2:30 P.M. it was resting on a snow-covered haystack and allowed the observer to approach within a few feet before flying off. A decomposed Snowy Owl was found on 22 January, 1967, near the southeastern end of Bear Lake, Rich County. It had become entangled in some old net fencing. This could have been the same owl seen earlier near Randolph which is about 15 miles distant airline.

Thus Snowy Owls, although relatively uncommon in the state, periodically come into Utah during the winter, their range extending as far south as the central part of the state. These data suggest a status of rare winter visitant in Utah.—WILLIAM H. BEHLE, *Department of Zoology, University of Utah, Salt Lake City, Utah, 3 April 1967.*

Breeding range extension of Saw-whet Owl in West Virginia.—On 21 May 1966, I collected two immature Saw-whet Owls (*Aegolius acadicus*) about six miles south of Huntington, and one mile west of Shoals, in Wayne County, West Virginia. They were roosting side by side on a small branch about ten feet above the ground in a small clump of scrub pine (*Pinus virginiana*). They were so close together that one .22 caliber rifle shell loaded with dust shot killed both of them.

Specimen 135-1/256 was a female, overall length 188 mm, ovary undeveloped, and with some fat. Specimen 135-2/257 was a male, same size, but with more fat. Both stomachs contained mouse bones, the stomach of the male contained the entire pelvic region and tail of white-footed mouse (*Peromyscus*). The skins are in the Marshall University collection.

The geographical location of immature individuals of this species in May seems worthy of note. The common impression among bird students is that the breeding of these owls southward is restricted to the high mountains. Brooks (1944. "A Check-list of West Virginia Birds." Bull. 316, Agr. Exp. Station, West Virginia Univ.) states that they breed occasionally in the spruce belt. My note (1950. *Auk*, 67:386–387) lists the known records of young birds in the state, all from high altitudes. These two specimens were taken at an altitude of between 650 and 700 feet. George Sutton, in a letter, states "There is no doubt in my mind that the species nested near where the young birds were found." If this be true, the breeding distribution of Saw-whet Owls is much more extensive than is generally believed.—RALPH M. EDEBURN, *Marshall University, Huntington, West Virginia, 8 March 1967.*

Budgerigar winters in the open in Michigan.—In early October, 1966, a blue-green phase Budgerigar (*Melopsittacus undulatus*) was first seen almost daily, or several times daily, at a feeding station in northwest Detroit. This bird fed on the regular feeding station fare which consisted of seeds of sunflower, millet, wheat, oats and cracked corn. It was observed to feed without conflict along with several Cardinals (*Richmondena cardinalis*), Blue Jays (*Cyanocitta cristata*), House Sparrows (*Passer domesticus*), and Common Grackles (*Quiscalus quiscula*).

The owner of the feeding station, Dr. Fred W. Schwab, was at his home most of each day where he made frequent observations out of a window at a distance of about 25 feet from the feeding station. He told me that, with the exception of one period of about three weeks in early March during some of our coldest winter weather, the bird was a daily visitant to his station. He said that on several occasions at dusk he had seen the bird fly into what appeared to be a good-sized nest about 12 feet above the ground in a thick red cedar in his backyard.

On 25 March 1967 from 6:00-6:30 P.M. I watched for the bird's appearance. It appeared and perched in a large maple tree about 30 or 40 feet from the feeding station where it remained for about five minutes without coming down to feed. Then it flew away with great speed and was not seen again as darkness came on within a few minutes.

Corresponding to the behavior of most pets on escaping from captivity, the bird at first appearance at the station could be approached to within a few feet and appeared to respond to whistles and other human sounds. Its flight at first did not appear to be very strong, indicating that it had escaped only a short time before. In the interval between its appearance and the time of my observation its flight had strengthened markedly until it was probably nearly as swift as that of its wild relatives in Australia.

The survival of this descendant of a species originally from much warmer climatic conditions may appear to be remarkable except for at least two factors which undoubtedly were favorable. These were the availability of an abundant supply of its normal food material and almost undoubtedly a large nest of a squirrel or House Sparrow in which it was protected from too great heat loss, especially at night. The parakeet's instinct for food seeking and its habit of nesting and roosting in cavities in the wild almost undoubtedly permitted it to find such a place of protection from the elements.

I have not been able to find in the literature any reference to outdoor survival of a parakeet during winter in the higher latitudes.—WALTER P. NICKELL, *Cranbrook Institute of Science, Bloomfield Hills, Michigan, 29 March 1967.*

An unusual nesting situation of the Tree Swallow.—During the annual meeting of the American Society of Mammalogists at the Bread Loaf campus of Middlebury College, near Middlebury, Vermont, 11–16 June 1962, many biologists had an opportunity to observe a most unusual nest of the Tree Swallow (*Iridoprocne bicolor*). Unfortunately, none of them has seen fit to put this nest on record, probably expecting that someone else will eventually do so. The nest was seen and photographed by dozens of the attending scientists.

A Cliff Swallow (*Petrochelidon pyrrhonota*) nest, probably of the previous year, was built in the corner of a porch. Beside it was a Barn Swallow (*Hirundo rustica*) nest probably also a year old but at any rate unoccupied. The Tree Swallows were nesting in the abandoned Cliff Swallow nest and used the Barn Swallow nest as a convenient perch.

So far as I know, no one investigated the status of the nest, but it was obviously in use, with both birds in constant attendance.—ALLEN H. BENTON, *Department of Biology, State University College, Fredonia, New York 14063, 11 March 1967.*

Further observations on foster-feeding by Purple Martins.—In an earlier paper (1959. *Wilson Bull.*, 71:96) I reported a single instance of foster-feeding by Purple Martins (*Progne subis*). Since then similar types of behavior have been observed repeatedly during studies associated with the homing ability of this species. The following observations were made at a colony of about 80 pairs located near Indian River (Cheboygan County), Michigan. Between 9 and 17 July 1962, 31 Purple Martins (15 females, 4 subadult males, and 12 juveniles) were removed from the colony for use in homing trials and almost continuous watch was maintained at the colony by me or an assistant. During the absence of one member of a pair, and occasionally even after its return, I noticed unmarked martins serving as "helpers" at 10 different nests. In some instances a "helper" was observed to make several trips to a particular nest. Details regarding these examples of foster-feeding are presented in Table 1.

TABLE 1

DETAILS REGARDING FOSTER-FEEDING ACTIVITIES AT 10 PURPLE MARTIN NESTS

Nest No.	Sex of experimental birds removed	Sex of unmarked helper(s) observed	Comments
10	female	female	"helper" peered into other compartments on same level of house prior to feeding young of #10. One observation.
11	female	female	fed young as did adult male (mate ?). One observation.
12	female	female and adult male	#12 mated to subadult male. Unmarked female fed young occasionally for at least 4 days. Adult male fed once.
14	female	female	one observation
15	female	female	helper fed young occasionally on 2 days.
16	female	female	helper fed young on 2 days.
17	female	female	helper aided with feeding for 2 days.
18	female	female	one observation
21	female	female	helper fed several times during 2 days prior to return of female #21 and also several times thereafter.
40	immature male	im. male and adult male	Two males aided female (mate) in feeding young. Each fed at least once.

The significance of this behavior cannot be determined at this time. Speculation regarding the selective value of this arrangement in a colonial species is possible but as yet premature. Since all foster-feeding observations for Purple Martins have been associated with colonies used in homing trials, there is need for a careful comparative study of marked individuals in an "undisturbed" population and one where particular individuals can be removed for varying lengths of time. It is possible that foster-feeding normally occurs if a member of a pair is killed during the feeding stage of the nesting cycle. This behavior was only observed when the colony was near full capacity, i.e., most of the available nest compartments were full.

A factor which may have stimulated particular instances of foster-feeding during the later stages of the nesting cycle is that fully feathered young occasionally changed nest compartments along the same tier. In these instances, the adults may find their own compartment void of young and, as a result, move to another nest and feed those young. On one occasion, I observed a color-marked martin (No. 22) feeding young in a compartment on the opposite side of the house. I did not know whether or not her young had left the compartment.—William E. Southern, *Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, 14 June 1967.*

Yellow-green Vireo collected in Texas.—The A.O.U. Check-list of North American Birds (1957) includes *Vireo flavoviridis*, a Middle American bird, only on the basis of two accidental occurrences: at Riverside, California, 29 September 1887, and Godbout, Quebec, 13 May 1883. Yet from the lower Rio Grande Valley of Texas there are enough sight identifications for the Yellow-green Vireo to be considered locally a rare or irregular summer resident; even nesting has been reported (Davis, 1945. *Auk*, 62:146, 1966. "Birds of the Rio Grande Delta"; Peterson, 1960. "A field guide to the birds of Texas"; Wolfe, 1956. "Checklist of the birds of Texas"). So far as we are aware, no indisputable specimen record from Texas has been published hitherto, and Col. L. R. Wolfe has kindly advised us (in litt.) that he knows of none. L. Wolf (1961. *Auk*, 78:258) reported a specimen, without locality data, taken 9 May 1938, believed probably from Matagorda County, Texas, on the basis of the sedentary habits of the collector. On 10 May 1966 Richardson collected a Yellow-green Vireo at Ingleside, San Patricio County, Texas. The bird, taken from a mist-net, was a female (ovary 6 × 2 mm); weight 16.51 g. In all features—wing length (78 mm flat), primary formula (ninth shorter than sixth), strongly yellow under tail-coverts and flanks, and facial markings rather indistinct (as compared with those of *V. olivaceus*)—the specimen seems typical of *V. flavoviridis.* The population of eastern Mexico (with which the specimen agrees) is considered the same form found in Central America, nominate *flavoviridis*, a highly migratory bird "wintering" in South America. B. L. Monroe, Jr. (1959. *Auk*, 76:95) has reported a specimen secured and another observed on 4 and 11 May 1958 at Pensacola, Florida. It is of interest that all specimen records north of Mexico, with one exception, relate to birds taken in May. Some authors regard the Middle American *V. flavoviridis* complex as conspecific with *V. olivaceus*, the Red-eyed Vireo (Zimmer, 1945. *Amer. Mus. Novit.*, no. 1127:1–3). Indubitably they are very closely allied, as are also the West Indian *V. altiloquus* and the South American *V. chivi* complexes, each of which includes several subspecies. It is a matter of opinion whether these complexes are best merged into one wide-ranging polytypic species or considered allopatric representative species of a superspecies (see Hamilton, 1962. *Condor*, 64:40–68; Eisenmann, 1962. *Condor*, 64:506–507). We are indebted to C. T. Collins for calling attention to certain literature.—Eugene Eisenmann, *American Museum of Natural History, New York, New York 10024*; James I. Richardson, *Department of Zoology*, and George T. Child, *Institute of Ecology, University of Georgia, Athens, Georgia 30601. 21 April 1967.*

A Slate-colored Junco display.—In a thicket in some vacant land in the northwestern part of Baltimore on 21 February 1938 a complex Slate-colored Junco (*Junco hyemalis*) utterance—a jumble of rapid, flutey *tyou* notes, buzzes, and song trills—led me to two of these birds that were hopping about each other on fallen brush and sometimes in the low branches of shrubs. The brush often obscured my view, but for a time the birds seemed to bob to each other, and every once in a while one of them, which had its breast plumage puffed out, took an erect posture with head raised. The complex utterances continued. After several minutes of this the displaying bird, which I thought was the singer, although I could never see either's bill open, went to the ground, picked up a blade of dead grass, and hopped about the floor of the thicket—and, less often, low branches—as if seeking a place to put it. This now went on for several minutes, then I moved and the birds fled. During the grass-carrying I paid inadequate attention to the other bird; afterward my impression was that it had seemed to ignore the displayer.

This display seems to have had elements of both courtship—which would have been far out of proper season and latitude—and hostility. It somewhat resembles a display of the male *J. h. carolinensis* that Tanner (1958. *Migrant*, 29:62) presumed to be courtship: "It is usually performed on a perch near the ground when the female is nearby. He spreads and droops his tail, droops his wings, and frequently sings a quiet, Goldfinch-like warble which carries only a short distance. very different from the regular song." On the other hand, I have since found both the *tyou* notes and the head-up posture to denote hostility. As for the grass-carrying, Tanner (loc. cit.) found that the female *J. h. carolinensis* "does all the building," though Saunders (1938. "Studies of Breeding Birds in the Allegany State Park," *New York State Mus. Bull.*, 318:136) says of a nest of *J. h. hyemalis* that "In the building of this nest both birds took part." Perhaps the display I saw was an agonistic one with the grass-carrying a displacement component.—HERVEY BRACKBILL, *2620 Poplar Drive, Baltimore, Maryland, 16 May 1967.*

Yellow-headed Blackbird nesting in Southern Ontario.—The easterly range expansion of birds in the Great Lakes region has been reviewed by deVos (1964. *Amer. Midland Nat.*, 71:489–502). In this review the sporadic establishment of the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) in the large marshes at the western end of Lake Erie is discussed. Yellowhead nests have been reported from northern Ohio (Sandusky) and sightings have been reported from southern Ontario. In 1965, at a Lake St. Clair Marsh near the mouth of the Thames River (Bradley Marsh), three territorial adult male Yellowheads and one female were sighted. One suspected nest with nestlings was reported but the birds fledged before this could be confirmed. On 30 May 1966 a territorial sub-adult male and two females were sighted in the same marsh and one completed nest with two eggs was found. One of the eggs was collected and sent to the Royal Ontario Museum (Catalog Number 9336). Two additional eggs were laid, 1 June and 3 June. Another nest under construction was found nine meters distant from the first on 3 June. On 6 June the first egg was laid in this second nest and by 12 June there were four eggs. The first egg hatched in nest number one on 12 June and by 14 June all three eggs had hatched. All birds fledged by 25 June.

Of the four eggs laid in nest number two, three hatched and the fourth disappeared. Approximately every second day these three nestlings were weighed. Two fledged on 30 June and the third disappeared before fledging.

It is noteworthy that no adult male Yellowheads were observed in 1966, and since only one sub-adult male held a territory, immediate establishment of a breeding colony is perhaps doubtful. But if the trend of outward expansion continues and young birds continue colonization there is no reason known at the moment that will prohibit the Yellow-headed Blackbird exploiting the large marshes surrounding Lake St. Clair and Lake Erie.—Mark Sawyer and M. I. Dyer, *Department of Zoology, University of Guelph, Guelph, Ontario, 3 November 1966.*

Black-throated Gray Warbler and Virginia's Warbler banded in New Jersey.—Since the "Operation Recovery" banding program started in 1956 at the Island Beach State Park in Ocean County, New Jersey, several western species have turned up in the nets. Some have been collected; others have been banded, photographed in the hand, and released.

Two noteworthy captures which have not been reported and not collected are a Black-throated Gray Warbler (*Dendroica nigrescens*) caught on 29 September 1962 and a Virginia's Warbler (*Vermivora virginiae*) caught on 6 October 1962. The Black-throated Gray Warbler (Fig. 1) was captured by John Miller; it was seen and identified by Mr. and Mrs. Stanley S. Dickerson, Walter K. Bigger, James Richardson, and myself, as well as several visitors and assistants at the banding station. In our opinion it was most probably an immature female, the age being determined by the "skull-ageing" method.

Fig. 1. Black-throated Gray Warbler, Island Beach State Park, New Jersey, 29 September 1962.

The Virginia's Warbler was caught by James Richardson; it was seen and identified by Mr. and Mrs. Dickerson, Walter K. Bigger, and Mrs. Mabel Warburton. The age and sex of this bird were not determined. Both birds were photographed in color by Francis P. Hornick.

I would like to thank John Miller and Chandler Robbins for permission to use the banding data from the Island Beach project, and especially to Francis P. Hornick for the use of his photograph.—Bruce Adams, *40 Summit Road, Riverside, Connecticut, 15 March 1967.*

ORNITHOLOGICAL NEWS

The 1968 Annual Meeting

The Proceedings of the 49th Annual Meeting held at Carbondale, Illinois 2–5 May 1968 well be published in the September issue of *The Bulletin*, but it can be reported here that the meeting was a successful one in every way. The following items will be of interest at this time.

The Council confirmed that the 50th Annual Meeting will be held on 1–4 May 1969 at Williamsburg, Va. Dr. Mitchell A. Byrd will be chairman of the local committee. It is anticipated that housing will be in short supply at that time of the year in Williamsburg, and so persons planning on attending the meeting will be advised to make arrangements early. A notice to this effect will be mailed in early 1969.

A feature of the 1969 meeting will be a symposium on current and future ornithological research trends, and the Council voted to award a prize of $100 to the person, not holding a doctoral degree, giving the best paper at this meeting.

The Council also voted to increase the annual Fuertes Research Grant Award to $200. The meeting closed with the election of a new slate of officers, whose names appear on the inside front cover of this issue.

The Society owes a special debt of gratitude to C. Chandler Ross who has retired as Treasurer after five years of excellent service. It was Mr. Ross' fortune to preside over our treasury in a time of financial crisis, and after that had been solved, in a time of steadily increasing costs. He has given unstintingly of his time and effort to a difficult job during difficult times.

Brazilian Bird Recordings, including songs of the once thought legendary Uirapuru are now available. Contact Brazilian Bird Records, P.O. Box 5525, Washington, D.C. 20016 for further information.

The Cleveland County Bird Club of Norman, Oklahoma has organized a Committee for Quetzal Cloud-forest Preserves to alert citizen groups and conservation agencies on the threat to the habitat of this rare neotropical bird. Persons interested in obtaining further information, and in helping the cause should contact the Committee at P.O. Box 2666, Norman, Oklahoma 73069.

The South African Ornithological Society announces that the Third Pan African Ornithological Congress will be held on 15–19 September 1969 at Pretoriuskop in Kruger National Park, South Africa. Inquiries may be directed to: The Hon. Secretary, South African Ornithological Society, c/o Percy Fitzpatrick Institute, University of Cape Town, Rondebosch, Cape Town, South Africa. This constitutes a change in the date announced earlier.

Sadly, we report the death of Burt L. Monroe, Sr., Treasurer of the A.O.U. and Past-President of the Wilson Society on 17 May 1968.

ORNITHOLOGICAL LITERATURE

Oklahoma Birds. Their Ecology and Distribution, with Comments on the Avifauna of the Southern Great Plains. By George Miksch Sutton. University of Oklahoma Press, Norman, 1967: 6¼ × 9½ in., xlvi + 674 pp., 1 col. pl., 28 drawings, 2 maps. $9.95.

Professionals afar will pick up "Oklahoma Birds" to see how a distinguished ornithologist of cosmopolitan interests will treat the birds of his own (and well-known) region; and indeed they will find that Sutton's attention ranges far beyond the boundaries of the state. Students of the birds of the southern Great Plains will find here a meticulous account of the present and historical status of species. Admirers of Sutton as a person and a writer will relish the anecdotal flavor they have come to expect of him, a style that would infuse warmth and zest into a telephone directory. Only the people who think of Sutton primarily as an artist will be disappointed; the work is illustrated attractively with drawings of birds, but it is not a picture book. The one color plate, a frontispiece used also on the dust jacket, is a head portrait of a Harlan's Hawk with the gleam of life in its eye.

A feature of more than regional interest is Sutton's broad but brief treatment of each order and family of birds represented in Oklahoma. A chapter is devoted to each order and within it each family is introduced by a general discussion. It is here that Sutton expresses some taxonomic views dissenting from the Check-list of North American Birds. He separates the Ralliformes from the Gruiformes; places the Shoveler in the genus *Anas*; the Tree Swallow in *Tachycineta*; the Hermit, Swainson's, and Gray-checked thrushes and Veery in *Catharus*; and the Cardinal in *Pyrrhuloxia*. I will admit to being startled to see the Passeriformes designated "Sparrowlike Birds." This term is fully justified by derivation but it is with effort that I stretch the connotations of "sparrow" to cover all members of the perching order.

It is always debatable whether a regional report ought to restrict itself to political or ecological boundaries. Intuitively, many of us lean toward the ecological, but close study often reveals practical difficulties, such as the uncertainty of the limits of many ecological regions and the paucity of information on some parts. Sutton's way of dealing with this dilemma was to address himself primarily to the precise limits and subdivisions of a state, and then to comment in passing about other nearby areas when the information was available and when he deemed it pertinent. This treatment reminds us who think of Oklahoma as a Plains state that it actually contains a wide variety of habitats, ranging from desert through prairie to bottomland forest and comprising perhaps as many as 12 different kinds of areas.

Generally, the work is remarkably free of typographical errors, but Sutton has called my attention to two errors in the names of birds (not Oklahoma birds): the common name of the Short-toed Eagle (not Short-tailed) on page 94 and the generic name *Sarothrura* of the White-spotted Crake on page 159.

This scholarly work will be a landmark not only for Oklahoma but also for the southern mid-continent.—Harold Mayfield.

The Book of the American Woodcock. By William G. Sheldon. University of Massachusetts Press, Amherst, 1967: 7 × 10¼ in., xx + 227 pp., 58 figs., 30 tables. $8.50.

Oystercatchers, stilts, avocets, plovers, turnstones, sandpipers, phalaropes—practically all the shorebirds—are abroad by day and readily observed in open habitats. Not so the woodcock whose unorthodoxy in selecting the twilight for its principal activities and the daytime for seclusion in wooded habitats makes it observable only under the most difficult conditions.

I speak from personal experience because I elected to study the life history of the American Woodcock for my doctoral dissertation. One learns about the species, I realized eventually, by piecemeal observations. Anything like continuously watching the daily movements of individual woodcock through a breeding season is impossible.

Since the publication in 1936 of my three-year effort, many expert field men have investigated the American Woodcock, but none more intensively than William G. Sheldon who devoted 15 years to the species on its breeding grounds in Massachusetts and other New England states. In this book he has drawn upon the results of his own studies together with those of many fellow investigators including Howard L. Mendall and Clarence M. Aldous whose "The Ecology and Management of the American Woodcock" (1943. University of Maine, Orono) has constituted the only major publication on the species since 1936. Essentially the book is a compendium for it brings between two covers in concise yet readable form all the significant information gathered to date on the physical characteristics, breeding biology, feeding habits, populations, distribution, and migration of the American Woodcock. The wealth of data assembled on so elusive a species is most impressive.

In reading the book I could not help noting the extent to which my original, comparatively meager findings were later confirmed by ample evidence from many field workers through direct observations, banding, and the application of newer techniques. For example, I called attention to the greater abundance of wintering woodcock in Louisiana than anywhere else. Now we are shown conclusively that east-central Louisiana and extreme southwestern Mississippi actually have the greatest wintering density and that the population comes in part from all the northeastern states as well as from the states directly north. I guessed the maximum altitude of the woodcock's spiraling ascent in flight-singing to average 225 feet. Dr. Sheldon, using a precise method developed for measuring altitude of migrating hawks, found that three consecutive flights reached 275 feet. I discovered that two or more females may be attracted to a male's singing field and thus suggested that the woodcock is polygamous. Although Mendall and Aldous still considered the species monogamous, Dr. Sheldon and others have confirmed polygamy as a common trait. All the investigators, like myself, never once observed woodcock carrying young. Dr. Sheldon feels as I did that the several instances of this feat long ago reported in the literature were the result of a chick being accidentally caught between the legs of the brooding female when it flushed in alarm at the approach of the observer.

Some of the most important contributions to new knowledge of the species appear in the chapter on population dynamics. On the basis of hunter-kills, Dr. Sheldon makes the assumption that the continental population of woodcock totals approximately 5,000,000 birds. Banding recoveries continue to build evidence that female woodcock live longer than males. Discovering that it was possible to determine the difference between sexes by the width of the three outer primaries and the difference between juveniles and adults by the wear of these same feathers, Dr. Sheldon and other workers proceeded to examine thousands of wings donated by woodcock hunters. This yielded a rich variety of data and some tentative conclusions. Woodcock can sustain an annual loss of all sex and age groups of 52 percent and "still maintain a stable breeding population." The continental sex ratio was found to be 82 males to 100 females, while among adults only.

the ratio was even more unbalanced, being 63 males to 100 females. In accounting for this discrepancy, Dr. Sheldon speculates that males reach their northern breeding grounds earlier than females when the weather is unfavorable. Being smaller and "in poor flesh" when they arrive, they are more vulnerable to severe freezes and other weather hazards. Also, on their breeding grounds where they advertise their presence so conspicuously, they are more easily subject to predation. Banding recoveries suggest that most woodcock die of causes other than the gun. Adverse weather, obstructions in the migratory flight path, predation, nest destruction from fires, changes in habitat effected by man, and diseases—all are causes of mortality but none seems to be any greater than the others. As to the use of chemicals, which many of us have thought might be particularly detrimental to woodcock, "there is no evidence to date that aerial spraying is causing a decimation of the continental woodcock population. But results should be accepted with caution. Insufficient time has elapsed to be complacent about the status of woodcock. The harmful effects of chemicals may be accumulative over several years and may not be immediately apparent."

The final chapter is a comparative summary of the known information about European Woodcock. What emerges sharply from this is the paucity of data available for satisfactorily determining the extent to which the European and American species have diverged in habits. There are no precise descriptions of courtship flights or other breeding activities. The question of whether the species is normally single-brooded, like the American, or double-brooded has not been resolved. Reports on the European bird carrying its young are rare and conflicting—and tend to force the conclusion that the trait is more likely accidental, as in the American bird, than a behavioral adaptation. The only recent report on woodcock populations is from Denmark, in 1959.

"The Book of the American Woodcock" leaves me with only one wish, namely, that the author had systematically summarized his principal findings, either at the ends of the chapters or at the end of the book. In too many instances the main points and results of his endeavors and of others remain in the body of the text and are in a sense lost to anyone lacking the time to ferret them out. Otherwise I have nothing but high praise for the entire work, its format, the quality of the illustrations, and the excellent index, as well as the text itself.—OLIN SEWALL PETTINGILL, JR.

AVIAN MYOLOGY. By J. C. George and A. J. Berger. Academic Press, London and New York, 1966: 6¼ × 9¼ in., xii + 500 pp., 248 text-figs. $18.00.

Muscles constitute one of the most-studied organ systems in birds. This book attempts to give an overall summary of what is now known about them. Its first half deals with their histology, physiology, and biochemistry, concentrating on the chief muscles of flight, the pectoralis and the supracoracoideus. The morphological and cytochemical properties of the three types of fibers that have been found in avian skeletal muscles are discussed in detail. They are shown to determine the nature of contraction of a muscle fiber. On a wider scale, the types and relative abundance of fibers in a given flight muscle are seen to be related to a bird's manner of flying. An important chapter deals with the source and control of energy for sustained muscular activity such as migratory flight. It explains that at least certain muscles can synthesize their own fat and use it as fuel.

Much of this information has come from the research of George and his associates and students, performed mostly within the past ten years. It is astonishing to recall that in 1956 a study by Yapp (*Wilson Bull.*, 68:312–319) on the energetics of bird migration had to be largely theoretical because very little was then known about the muscular physiology of birds. Today, however, one of the best known of all skeletal muscles with respect to biochemistry and physiology, is the pectoralis muscle of the Common Pigeon (*Columba livia*).

By compiling and synthesizing findings in this new field, the first half of the book makes a notable contribution. Data are not only reported, but also their significance in muscular metabolism and locomotion is pointed out. This approach is commendably broad, but in places it suffers from too simple an evaluation of a bird's mode of flight. To characterize a species merely as a good or a poor flier does not go very far in giving meaning to biochemical data on its flight muscles.

Histological and histochemical features of muscles are illustrated with many photomicrographs of tissue sections. Material from several different muscles and from many species is shown, demonstrating that muscles are diverse in their properties. The pictures are much less valuable than they could be, however, because they are scarcely discussed in the text. Several of them are blurry and inadequately captioned or labeled. These illustrations will probably have little meaning for readers not familiar with cytology.

The second half of the book is largely a catalog of all the skeletal muscles in a bird. To the best of my knowledge it is the only such list that is complete and up-to-date. Non-skeletal muscles such as feather muscles are not mentioned. Gross morphology of every muscle is described and terminology is reviewed, often at length. The condition of specific muscles as found in various birds is reported in many cases. These statements are based on Berger's observations and the literature, though their source is sometimes not made clear. Several of the descriptions are very inadequate or contain errors. The accounts of the wing and the leg muscles are fuller than the rest because they also include detailed descriptions of these muscles in the Common Pigeon and the Red-winged Blackbird (*Agelaius phoeniceus*). This material is generally reliable and it will be a convenient reference for anyone seeking to identify the muscles of a dissected bird.

The many references to the literature of avian gross myology given in this chapter are a valuable introduction to the subject. As a matter of fact, readers will often have to turn to the literature because here the authors do not seem to have understood some of the papers they cite. Many studies on the musculature of the jaws and the neck, for example, are mentioned yet nothing has been passed on from them about the movements of these parts. Another example is the incredible statement (on p. 313) that there is little specific information in the literature on the supracoracoideus muscle: several important works dealing with this muscle are included in the list of references.

Nothing is said about the innervation or gross blood supply of muscles. The arrangement of muscular fibers in relation to tendons and aponeuroses is not discussed. Virtually nothing is said about the functions of any muscles. Inclusion of these topics would have helped to integrate the chapter on gross morphology with those on histochemistry and physiology. Also, the topics named have been subjects of much study. The fact that they have been omitted means that the book significantly fails to achieve the comprehensiveness for which it aims.

The accounts of gross myology give much attention to the use of muscles as indicators of phylogenetic affinities. It is hence ironic that without explanation of muscular functions, the comparative descriptive data have little meaning, either in themselves or as taxonomic clues. Muscles seem to be regarded here as blocks of tissue that have evolved without adaptation in birds.

Curiosity led me to compare the chapter on gross myology with its equivalent in A. J. Marshall's "Biology and Comparative Physiology of Birds" (1960. 1:301–344. Academic Press, New York and London) because the latter had been written by Berger. Choosing at random, I was surprised to find several paragraphs and shorter passages that were identical or almost so in the two chapters. The newer work offers more description than the older work, especially in regard to the non-appendicular muscles, and details of more birds, but no new insights on the study of avian gross myology.

The catalog of muscles is illustrated with many drawings of gross muscular anatomy. These are well suited for identifying and comparing muscles as they are found in dissection. There are no illustrations, however, that show details of attachment or the movements produced by muscular actions.

Virtually all the drawings have been taken from the literature. Jaw muscles, for example, are depicted from studies of certain species, syringeal muscles from studies of various other species, and limb muscles from still others. This treatment shows diversity among birds, but it fails to give an integrated picture of the entire skeletal musculature of any single species. I would like to see a revised edition of this book that includes drawings of all the muscles in either the Common Pigeon or the Red-winged Blackbird. These would complement both the descriptions of the muscles in these birds and the illustrations of those in other birds.

The labels and captions for many illustrations of gross myology have been seriously neglected. The abbreviations used for labels in drawings by Hudson and Lanzillotti (1955. *Amer. Midl. Nat.*, 61:1–67) and Sullivan (1962. *Australian J. Zool.*, 10:458–518) are not explained in any key. Sometimes the same muscle is designated by different names in illustrations by different authors. The digits in the wing tip are numberd 2-3-4 by Sullivan instead of 1-2-3 as done by many other anatomists. On seeing Sullivan's pictures here, a reader must recall that this topic was discussed 100 pages previously. I decry not these differences in terminology but the fact that they have not been pointed out in the captions.

One of Berger's contributions to avian anatomy has been his investigation of *M. expansor secundariorum*, a non-striated muscle in the upper arm. I am nevertheless puzzled by full-page photomicrographs of this muscle in three different species. Neither the text nor the captions make any comparisons among them. If there are no histological differences worth mentioning, I can see no purpose in showing all three, particularly at such size. Finally, the pictures lack labels and an indication of their scale.

The closing chapter deals with the origin of birds and the evolution of their capacity for sustained flight from a physiological standpoint. Its chief contribution is a review of adaptive radiation in the fiber composition of the pectoralis muscle from a reptilian pattern to diverse avian and mammalian patterns. Although presented too briefly, this is stimulating because it approaches the study of avian evolution at a new level, that of histophysiology.

Throughout the book one finds peevish criticism of avian anatomists and taxonomists. This is not only distasteful and unnecessary, but also it cuts with a double edge. The authors are guilty of some of the faults they find in others, such as misunderstanding anatomical evidence and overlooking important references. Their warning to beginners about reliance on Shufeldt's "Myology of the Raven" (1890) is, I believe, overdone. The true information in this pioneer work far outweighs the errors. Considering that it was written while Shufeldt was stationed at a remote army camp, it is a remarkably good book.

This book is far from being a complete reference on avian myology. It fails to portray muscles, singly or collectively, as dynamic parts of a living bird. Nevertheless, it is clearly the best single work in its field. Research workers will find it valuable as a compilation of information and an entrance to the literature. Students will find ideas in the many topics it suggests for future studies.—PETER STETTENHEIM.

THE BIRDS OF TIKAL. By Frank B. Smithe. Natural History Press, Garden City, New York, 1966: 4¾ × 7¾ in., xxix + 350 pp., 30 col. pls. by H. Wayne Trimm, 9 additional pls. (2 col.); 2 foldout maps. $7.50.

Frank Smithe has produced in this book an attractive guide to the identification and natural history of the birds at Tikal, a well-known archeological site in the Petén of northern Guatemala, Central America. Included are the 276 species recorded at Tikal (three known only from bones found in the debris and ceremonial caches about the Mayan temples), five others that have been found at nearby Uaxactun, and, listed in the appendix and mentioned occasionally in the text, 52 species that have been seen elsewhere in the Petén. Some of the non-Tikal birds are illustrated, including two, in fact, that have not even been recorded in Guatemala. With these inclusions the guide gives useful coverage of the birdlife of the Gulf and Caribbean Lowlands from southern Vera Cruz, Mexico, through Guatemala and British Honduras to at least northern Honduras.

The introductory pages in the book are brief but serve to locate Tikal and familiarize the reader with the climate, physiography, and vegetation of the area. A few paragraphs are devoted to the historical importance of Tikal as one of the major sites of Mayan Indian activity over a millennium ago and a summary is given of the ornithological work of the author and his co-worker, Raymond A. Paynter, Jr., and others starting in 1956. In 1963, Smithe and Paynter published an annotated list of the birds of Tikal (*Bull. Mus. Comp. Zool.*, 128(5)); see review in *The Wilson Bulletin* (1963, 75:467). Some additional records are included in the new book, most dating from the autumn of 1962. Since this season had not previously been studied at Tikal, many locality records and new migration dates are added, including a mass migration of Eastern Kingbirds (*Tyrannus tyrannus*) and three species new for the country, the White-rumped Sandpiper (*Calidris fuscicollis*), Veery (*Catharus fuscescens*), and Bobolink (*Dolichonyx oryzivorus*).

The species accounts are well thought out and interestingly presented. In addition to a brief but adequate description, information is given on the habitat, behavior, voice, nest, and eggs. In many cases useful syllables or symbols are used to represent the calls of the bird. Over half a page is devoted to the calls of the Common Potoo (*Nyctibius griseus*). An indication of relative abundance of each species is given. The terms used are generally meaningful, although I am not sure what distinction was intended by the expression, "Common and numerous," in reference to the Plain Antvireo (*Dysithamnus mentalis*). Specific data are included for some species on just where the bird might be seen at Tikal, mentioning perhaps a certain trail or *aguada* (pond). A valuable addition to each account is a list of references giving the location of illustrations, life-history studies, nesting data, and sound recordings. Cited frequently in the last category are the recordings of L. Irby Davis. Special notes are included at various places in the text, mostly where identification problems might arise with groups of similar species.

The sequence of species and the scientific and common naming are up-to-date, although some might question the retention of the family Coerebidae, which was probably done on the advice of Eugene Eisenmann. A second common or scientific name is given for some species. It is an interesting commentary of the state of flux of Middle American scientific nomenclature that Smithe lists 31 duplicate technical names and only 17 common ones. Since the new AOU Check-list Committee, headed by Eisenmann, has extended its coverage through Middle America, greater stability should be forthcoming. Spanish names, worked out with the help of Jorge Ibarra of the Guatemalan National Museum, and Mayan names are also included. Subspecific names are used where specimens have been collected and identified, although the nominate form of the Northern Waterthrush is included even though all collected specimens have been identified as *Seiurus noveboracensis notabilis*. Where more than one form occurs at Tikal each is given separate and full treatment, contrary to modern practice.

Thirty color plates depicting 107 species of birds are included. The species illustrated are reasonably well chosen, though the hawks, with 16 species on seven plates, might be overemphasized. On some of the plates, if the drawings were made a little smaller, many more species could have been included. Plate 6, the Black Hawk-Eagle (*Spizaetus tyrannus*), Plate 15, the Ocellated Turkey (*Meleagris ocellata*), and Plate 17, the Blue-crowned Motmot (*Momotus momota*) depict a single species. Two other plates, numbers 2 and 29, show only two species, one of which in each case has yet to be recorded in Guatemala. These plates are attractive and useful but uneconomical on space. By contrast Plate 22 shows six species of forest birds in nine poses and includes as well a good habitat background. Plate 13 includes eight species of hummingbirds in 11 poses with two extra tails added to show the dorsal surface. If all the plates had been handled this way—and I see no reduction in quality or loss of identification characters in the smaller drawings—all of the resident forms at Tikal could have been illustrated. Also, many of the forms depicted are rare at Tikal and unlikely to be observed by the casual visitor, further reducing the usefulness of the plates.

Mr. Trimm has done a good job with the illustrations though in a few the drawing is a little awkward and the placement and size of the feet do not seem correct. A few of the birds appear ready to fall one way or another. The colors are generally good although on Plate 19 the blue-backed kingfishers appear too blue and the green-backed forms too green. The artist has avoided one common error: he has counted the number of bones in a bird's foot and not put in the extra joint often depicted in the hind toe. Included on each plate is a scale line marked in inches and centimeters, a useful method of indicating the size of each bird. In a few cases, however, the markings are as much as 20 to 30 per cent off, as in Plate 8 where the adult female Double-toothed Kite (*Harpagus bidentatus*) measures less than 10 inches, using the scale on the plate, whereas a length of 13 inches is given in the text.

Plate 16 is a two-page color painting depicting the Great Plaza at Tikal as it might have appeared on a ceremonial day a thousand years ago. This striking illustration, painted by Alton S. Tobey and appearing originally in *Life* magazine, serves to maintain the mood and feeling of respect for the Mayan that Smithe builds throughout the book. Eight photographic plates in the closing pages show the ruins today, some of the buildings and habitats at Tikal, and the author at work on some specimens.

Seven appendices add data on climate, other Petén species, relationships with the Yucatán Peninsula as a whole, pensile nests, a check-list of Tikal birds, new Petén records, and a list of species accepted on the basis of sight records. The climatic data, which include rainfall and minimum and maximum temperatures for nearly every day over a four-year period, seem unnecessarily detailed for a work of this sort. The material on pensile nests could very well have been published as a separate study. An excellent bibliography, an index, and two maps complete the book.

In summary, Frank Smithe has produced a readable book that is far more than just a guide to the birds at Tikal. With his considerable field experience in the area he is able to give us many interesting behavioral notes, such as a Melodious Blackbird (*Dives dives*) "dancing" in sequence with the calls of a Laughing Falcon (*Herpetotheres cachinnans*). The author has avoided the deplorable modern tendency to remove all the minor but interesting details that make for enjoyable reading. This is a book that should prove useful to any student of Middle American ornithology, especially if he plans to be in the field in the Gulf or Caribbean Lowlands.—Hugh C. Land.

The Plains of Camdeboo. By Eve Palmer. Illustrations by John Pimlott. Viking Press, New York, 1966: 5¾ × 8⅝ in., 320 pp., numerous line drawings. $6.00.

The author writes in the foreword to her book: "This is not the story of the Palmer family—although they impinge upon it at times. It is the story of Cranemere, a farm—to some a ranch—twenty thousand acres in area on a great plain toward the southern tip of Africa. This is a countryside either completely overlooked or greatly slandered—few people visit it—and none has ever written of it." We can be grateful that she realized her childhood dream to write of this land—her Plains of Camdeboo—a Hottentot word meaning "thirst-land."

Eve Palmer seems to hold in her hands this eastern corner of the Great Karoo—a wide upland world 2,500 feet above the sea—with mountains rising steeply to the north, and like a blue rim to the east and west. From the free-drawn maps on the endpapers of the book, the reader quickly identifies the "dam" where in 1880 young George and Fanny Palmer, traveling the road between Pearston on the east to Graaff-Reinet on the west, stopped and said "this is it." The dam was to govern their lives and everything depended on it. The farm was named Cranemere for the blue cranes by the thousands and for the water they flocked to in the dusk. Here is one of their last strongholds in the world today. Two centuries ago along the old highway to the north traveled the first explorers, hunters, missionaries, botanists, ornithologists, and paleontologists. They were to know the bushmen who later disappeared with the coming south of the Bantu. The author writes vividly, with fine perception, of the excitement of discovery of the Bushmen paintings in the caves, of the plants, birds, animals, insects, snakes, and the fossils, such as the little lizard of 180 million years ago when "the Karoo was once a vast lake fed by a huge river, possibly larger than the Nile, which meandered across the country from the north, spreading a great sea of mud over the land." This is a captivating book, packed with scientific knowledge, stimulating and heart-warming, the story of a land where rain, however rare, makes life possible. "Within hours—it seems—the dust-dry soil is engulfed in succulence, every bare twig covered with leaves, the plains enamelled with flowers, the air filled with scents. The mountains cascade water, the rivers and pools brim over, frogs bellow, birds fill the trees and bees make honey all over the countryside. The great intricate web of Karoo life begins to function once again. Firm flesh covers the bones of the starving animals; and men, women and children cry, sing, and say their prayers."

The author has included a reference list of well over a hundred books. John Pimlott has done the charming line drawings and endpaper maps.—Marian McChesney.

PUBLICATION NOTES AND NOTICES

Reprinted recently by Dover Publications, New York, are five well-known works listed below. All are covered with stiff enameled paper embellished by illustrations in color.

Handbook of Birds of Eastern North America. By Frank M. Chapman. Second revised edition, published in 1932. $3.00. "Probably no book has had as much to do with developing ornithologists and an interest in birds . . . ." (from a review by Witmer Stone in *The Auk* 1932. 49:242–243). Today no less than years ago, an indispensible book for the identification of bird species close at hand.

The Watcher at the Nest. By Margaret Morse Nice. First published in 1939. $1.50. Reviewed by Helen Bates [Van Tyne] in *The Wilson Bulletin* for 1939 (51:128).

The Ivory-billed Woodpecker. By James T. Tanner. Originally published in 1942 as Research Report No. 1 of the National Audubon Society. $2.00. Reviewed by Josselyn Van Tyne in *The Wilson Bulletin* for 1943 (55:58–59).

The Roseate Spoonbill. By Robert Porter Allen. Originally published in 1942 as Research Report No. 2 of the National Audubon Society. $2.00. Reviewed by Carl L. Hubbs in *The Wilson Bulletin* for 1943 (55:59).

The California Condor. By Carl B. Koford. Originally published in 1953 as Research Report No. 4 of the National Audubon Society. $2.00. Reviewed by Joe T. Marshall, Jr., in *The Wilson Bulletin* for 1954 (66:75–76).

Birds of Australia. Illustrations by John Gould. Text by Abram Rutgers. Methuen & Co., Ltd., London (distributed in the United States by Barnes & Noble, New York), 1967: 7½ × 9⅞ in., 321 pp., 160 col. pls. $15.00.

This is a sequel to "Birds of Europe" which was reviewed in *The Wilson Bulletin* (1967. 79:255–256). All the criticisms apply equally well to this volume with one exception: The publishers have included a page of much-needed information about the illustrator and the author of the text.

History of the Birds of Kingston, Ontario. By Helen R. Quilliam. Kingston, Ontario, 1956:216 pp., 29 photos, foldout map. Privately printed; available from the author, Mrs. C. D. Quilliam, R.R. 1, Kingston. $2.50.

Area restricted to a 30-mile radius of Kingston. A commendably detailed, scholarly presentation that includes a description of the area and carefully organized accounts of each species, giving its known history in the area, specimens taken if any, and a concise summary of status.

The second (1956) printing of "Travels and Traditions of Waterfowl" by H. Albert Hochbaum has been reissued in paperback by the University of Minnesota Press, Minneapolis, and is available at $2.95. The first printing (1955) was reviewed in *The Wilson Bulletin* (1956. 68:339–340) by Frank C. Bellrose.

To replace its two previous series, *Occasional Papers* and *Wildlife Management Bulletins*, the Canadian Wildlife Service is publishing a *Report Series*, four of which have already appeared and are cited below. Large in format (8½ × 11 inches), paper covers embellished with striking color photographs, profusely illustrated throughout, and handsomely printed on paper of high quality, the new series is in all respects eye-catching. All four of the first reports are important contributions to technical knowledge. Although written in the language of wildlife experts, they nevertheless provide instructive reading for anyone. Copies may be purchased directly from the Queen's Printer and Controller of Stationery, or through the Canadian Wildlife Service, Department of Indian Affairs and Northern Development, Ottawa.

Whooping Crane Population Dynamics on the Nesting Grounds, Wood Buffalo National Park, Northwest Territories, Canada. By N. S. Novakowski. Report Series Number 1, 1966: 20 pp., 14 figs., 5 tables. 50 cents.

Bionomics of the Sandhill Crane. By W. J. Douglas Stephen. Report Series Number 2, 1967: 48 pp., 20 figs., 27 tables. 75 cents.

The Breeding Biology of Ross' Goose in the Perry River Region, Northwest Territories. By John Pemberton Ryder. Report Series Number 3, 1967: 56 pp., 29 figs., 20 tables. 75 cents.

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General Notes

Heads of HUDSONIAN GODWITS *(Limosa haemastica)*, male above and female below (Watercolors by George Miksch Sutton).

SEXUAL DIMORPHISM IN THE HUDSONIAN GODWIT

George Miksch Sutton

Many published descriptions of the Hudsonian Godwit (*Limosa haemastica*) read as if males were virtually indistinguishable from females. Of "adults in summer" Robert Ridgway (1919. *U. S. Natl. Mus. Bull.* No. 50, Pt. 8, p. 191) states flatly: "sexes alike." The caption for Robert Verity Clem's fine painting of a male in breeding feather in "The Shorebirds of North America" (G. D. Stout, Ed., 1967. Pl. 11, p. 89) states that the female is "quite similar." Yet bird observers who see the Hudsonian Godwit between mid-April and the end of May in central Oklahoma (see Sutton, 1967. Oklahoma Birds, p. 203) have no trouble distinguishing the richly colored males, whose underparts appear to be almost solid dark brick-red, from females with their comparatively pale, blotchy, almost piebald underparts.

Females are larger than males, too. The size difference is readily perceptible with specimens in hand, though not very noticeable in the field. Three carefully sexed males in the University of Oklahoma collection measure (in millimeters): wing 201–202 (201.4), tail 71–77 (73.6), culmen 73.5–75.5 (74.4), tarsus 55–56 (55.4); four females: wing 212–215 (213.5), tail 76–80 (78.0), culmen 88–90 (89.3), tarsus 60–64 (62.7). Ridgway's averages for four males (wing 203.5, tail 74, culmen 76.7, tarsus 57.5) and four females (wing 212.9, tail 77.9, culmen 79.5, tarsus 58.1) do not reveal this pronounced size difference, especially as regards the culmen and tarsus. Ridgway's statement that the sexes are "alike"; his comment (p. 192, footnote) that "some of the specimens measured doubtless have the sex incorrectly determined"; and especially his inclusion of the culmen length and tarsus length of 14 males and four females handled by G. S. Ageesberg in "Dakota" (see Coues, 1880. *Bull. Nuttall Ornithol. Club*, 5:60) convince me that some (perhaps several) of the eight specimens measured by Ridgway were, indeed, incorrectly sexed. The culmens of the males and females handled by Ageesberg averaged 74.9 and 87.4 respectively, the tarsi 57.1 and 63.2 respectively.

An aspect of the Hudsonian Godwit's sexual dimorphism that seems not to have received much attention pertains to bill-color at the height of the courting season. Note the following from "The Birds of Churchill, Manitoba" (Taverner and Sutton, 1934. *Ann. Carnegie Mus.*, 23:48): "It was noted during both 1930 and 1931 that after the courting season the orange color of the base of the bill in the male faded rapidly to dull fleshy. In field sketches made by the junior author from freshly killed specimens the base of the bill in the courting male is clear, rather bright orange; in females taken at the same time the base of the bill is purplish flesh-color of a distinctly different appearance. Fading of the bill in the male brings it to a color approximately that of the female's. In 1930 all specimens collected after June had dull, flesh-colored bills."

Our color-plate is based on the above-mentioned field sketches made by me in 1931. The sketch of the male was made on 12 June, that of the female on 3 July. A comment in pencil to one side of the latter indicates that the colors of the bill might have been a little brighter earlier in the season; but they were never, according to my recollection, either yellow or orange. Today I might call the color at the base of the bill of the courting male rich yellow rather than orange. I feel sure, however, that the colors of the sketch have not faded, for the drawing has been kept under cover.

Male Hudsonian Godwits that we see as they move northward through Oklahoma have bills that are somewhat yellow at the base, but the color apparently does not become intense until the birds reach their breeding ground.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF OKLAHOMA, NORMAN, OKLAHOMA, 29 AUGUST 1968.

COMPARATIVE ADAPTATIONS OF THE ALASKAN REDPOLLS TO THE ARCTIC ENVIRONMENT

William S. Brooks

Two species (by current definition) of redpolls are involved in the present study: *Acanthis hornemanni exilipes* (Coues), the Hoary Redpoll, and *Acanthis flammea flammea* (L.), the Common Redpoll. Redpolls breed circumpolarly in arctic and subarctic regions south to approximately 54°N latitude. Populations of *hornemanni*, in general, breed farther north than those of *flammea*. Most of the North American populations are migratory to some extent, and, probably depending on the availability of food. move irregularly into the northern one-third of the United States in winter. *Hornemanni* does not move as far south as *flammea* and is considered "rare" in the United States (Audubon Field Notes. 1947–1967 Christmas counts). Some overwinter the farthest north of any small North American bird except for the Black-capped Chickadee (*Parus atricapillus*). *Hornemanni* spends at least a part of the winter at Anaktuvuk Pass, Alaska, 68°N lat. (Irving, 1960) and possibly even on the Arctic Slope of the Brooks Range, within 100 miles (69°N lat.) of the Arctic coast in Alaska (Clayton M. White, pers. comm.). Both species can be considered arctic or subarctic permanent residents. They both (*flammea* more commonly) winter fairly abundantly at Fairbanks, Alaska (65°N lat.), which although it is subarctic, receives the lowest temperature extremes of the state, occasionally down to –60 C.

Survival of so small a bird (12–14 g) at such low temperatures is remarkable and merits study. Although certain behavioral and morphological aspects in the adaptations of the species were investigated, the present study deals primarily with the gross metabolic or bioenergetic relations of the birds to their arctic environment.

The taxonomy of the redpolls is by no means resolved. According to the 1957 A.O.U. Check-list, *hornemanni* and *flammea* are regarded as distinct species, but Salomonsen (1928, 1950–51), Williamson (1961), and others believe them to be conspecific. It is well known that they commonly interbreed, and that a wide range of plumage and bill-size intergradations is found in nature. From raw data for birds from Umiat, Alaska, kindly supplied by P. H. Baldwin, calculations made indicate that in 48 birds with *hornemanni*-type plumage, bill length (± SD) was 7.00 ± 0.37 mm; bill depth, 5.68 ± 0.22 mm; length/depth ratio, 1.228 ± 0.03. In 14 *flammea* types length was 7.50 ± 0.54 mm: depth, 5.61 ± 0.11 mm; length/depth ratio. 1.336 ± 0.02. Bill length and the length/depth ratio of *hornemanni* were both significantly less than those of *flammea* and bill depth for *hornemanni* was greater, but not significantly. Birds with intermediate plumage types were also intermediate in bill characters. Typical *hornemanni* specimens thus have a shorter and deeper bill than typical *flammea* specimens and in addition are much whiter and grayer (less brown), with little or no streaking on breast, abdomen, rump, and under tail coverts. Adult male *hornemanni* are also pink-breasted and rumped, whereas male *flammea* are red in these areas.

It was not the main purpose of this study to make any clear-cut decision regarding the taxonomy of these birds but the comparisons made between them may be of some use to taxonomists. Most of the birds available for research were intermediate in some morphological characteristics, but were close enough to one type or the other to be designated *hornemanni* or *flammea.*

MATERIALS AND METHODS

All redpolls were captured at two locations in Alaska and shipped to Illinois by air express. Fifteen birds from the breeding population were mist-netted during the latter half of August 1963 at Umiat, on the Arctic Slope of the Brooks Range, and 72 at Fairbanks, in central Alaska. One hundred fifty-seven birds were captured at Fairbanks at feeder traps during the latter half of March and first half of April 1964 by Heinrich K. Springer and sent in three shipments soon after capture. The birds were initially fed commercial bird seed but were gradually changed over to the experimental feed within a week. The experimental cages in which they were held measured 16 × 30 × 30 cm, and have been described in detail by Martin (1967). Metal perches were wound with masking tape in the low-temperature experiments. In approximately half the cages, activity was measured as recorded on an Esterline-Angus event recorder.

The University of Illinois No. 521 chick starter feed which was used was finely ground and homogeneous, but before being given to the birds it was put through a 1.5 mm mesh screen to take out foreign and insufficiently ground particles and to facilitate subsequent separation of waste food from excreta. The feed contains approximately 4.4 kcal/g and 21 per cent protein. Grit was not given to the birds. Water was supplied at above-freezing, and snow at below-freezing temperatures.

Molt was determined by sorting and counting all loose feathers in the cage at the time of cleaning. Molt intensity values were obtained by summation, with an index value of 1 for each remex or retrix, each five body feathers or coverts, or each 15 head or neck feathers (adapted from West, 1958).

At the end of each 3-day experimental period birds were weighed on a Torsion balance to the nearest 0.01 g and were rated according to the following fat classification (modified from Weise, 1956):

1. no visible fat;
2. little fat (no fat visible between the intestinal folds, fat lining the furcula);
3. moderate fat (fat visible between the intestinal folds and filling the furcula);

4, fat (fat visible subcutaneously on the abdomen and bulging from the furcula);
5, very fat (fat bulging from the abdomen and furcula).

Subclasses were also recognized here, especially among the higher categories, for example, 3.00, 3.25, 3.50, 3.75, 4.00, etc.

For lipid analysis the birds were dried for 24 hours at 68 C in a vacuum oven and weighed. They were then macerated and ground in petroleum ether until the largest particles were less than 5 mm in size, and the lipid was extracted in a modified Soxhlet apparatus and weighed.

Gross energy intake was determined for individual birds during each 3-day experimental period by subtracting the weight of unconsumed food from the weight of the food given and multiplying this by the caloric value of the food. *Excretory energy* was calculated by multiplying the weight of the excreta by its calorie value. Subtracting excretory energy from gross energy intake gave the *metabolized energy.* During a sequence of periods when a bird maintained constant weight (did not vary more than 0.25 g, approximately two per cent of body weight), metabolized energy was designated *existence energy.* This is defined as the energy required by a bird under caged conditions to maintain life, with only a limited number of activities such as feeding, preening, etc. Any metabolized energy above the existence level would be available for molting, reproduction, fat deposition, migration, etc. and can be termed *productive energy.*

Caloric values for food and excrement were obtained by bomb calorimetry. The samples and their weights were obtained in the following manner. Between consecutive 3-day periods each cage was cleaned and provided with fresh water or snow and a known weight of fresh food. Excreta and waste food were oven-dried together at approximately 65 C for 3 days, then separated by brushing through a 1.5 mm mesh screen (fecal pellets did not go through), and weighed to 0.01 g. An amount of food, equal in wet weight to and taken from the same supply as that given the birds, was dried and weighed at the same time to determine the dry weight of food given the birds. All samples were then stored at below-freezing temperatures until the caloric determinations were made. With the excreta these determinations were made only for periods in which the bird maintained a constant weight, and thus were presumably in energy balance.

Experiments, for which birds were always randomly chosen, were done both in controlled temperature cabinets or rooms and in an outdoor aviary protected from wind and precipitation. For all experiments (see Table 1) the birds were given previous photoperiodic and temperature conditioning, similar to the experiment, for one to three months. Examination of plumage, bill color, vocalization, and cloacal and gonadal development indicated that this conditioning period successfully put the birds in the proper phase of their annual cycle.

The cages were always cleaned and the birds weighed at the same time of day to minimize differences caused by the daily feeding cycle. Ambient temperatures were measured at 24-minute intervals with copper-constantan thermocouples placed near the birds and connected to a Leeds and Northrup recording 24-pen potentiometer. Means were calculated from all recordings in each 24-hour period. Humidity was not measured.

The outdoor experiment was run to determine whether the annual physiological cycle would be greatly altered by keeping the birds as permanent residents in Illinois. In addition, a group of birds was placed in a cabinet under a regime of simulated outdoor conditions for Fairbanks, Alaska. This group was first subjected to the daily changes in temperature and photoperiod that occurred from 2 December 1963 to 26 January 1964, and then to those from 20 November 1964 to 8 January 1965. Daily minimum, maximum,

TABLE 1

SUMMARY OF EXPERIMENTS AT DIFFERENT PHOTOPERIODS AND TEMPERATURES[1]

Experiment	Time	Species[2]	Sex	Initial age class	When caught
24-hour, high-temp. (32 to 38 C)	19 June–10 Aug., 1964	H	3m	3 imm.	March, 1964
		F	7m, 2f	7 ad., 2 imm.	
24-hour, medium-temp. (9 to 11 C)	14 Aug.–4 Sept., 1964	H	2m, 1f	3 ad.	March, 1964
		F	2m	2 ad.	
24-hour, low-temp. (–5 to –31 C)	12 Aug.–16 Nov., 1964	H	3m	3 ad.	March, 1964
		F	6m, 1f	7 ad.	
7-hour, high-temp. (31 to 39 C)	3 April–5 June, 1964	H	1m	1 ad.	March, 1964
		F	6m, 5f	9 ad., 2 imm.	
7-hour, medium-temp. (9 to 10 C)	3–29 March, 1964	H	3m	3 ad.	March, 1964
		F	2m	2 ad.	
7-hour, low-temp. (–10 to –38 C)	22 April–13 July, 1964	H	3m	1 ad., 2 imm.	March, 1964
		F	4m	3 ad., 1 imm.	
10-hour, low-temp. (–7 to –32 C)	27 Jan.–12 March, 1964	H	0	0	—
		F	3f	3 imm.	Aug., 1963
Varying-photoperiod, approx. 25 C	18 June–29 Oct., 1964	H	1m	1 ad.	
		F	5m, 2f	5 ad., 2 imm.	March, 1964
Varying-photoperiod, approx. –2 C	2 May–13 Sept., 1964	H	1m	1 imm.	
		F	6m, 1f	4 ad., 3 imm.	March, 1964
Outdoors, Illinois	10 Oct., 1963–11 Oct., 1964	H	3m, 1f	1 ad., 3 imm.	
		F	2m, 3f	3 imm., 2 juv.	Aug., 1963
Simulated Fairbanks outdoors	2 Dec., 1964–17 March, 1965	H	2m, 2f	4 ad.	April, 1964
		F	4m, 1f	5 ad.	March, 1964

[1] All birds captured at Fairbanks except the four *hornemanni* used in the outdoor experiment, which were captured at Umiat.

[2] H = *A. hornemanni*; F = *A. flammea*.

and mean temperatures, obtained from U.S. Weather Bureau reports, were established manually in the temperature cabinet each day for the approximate times and durations that they had occurred in Fairbanks. Photoperiods included the time from sunrise to sunset plus the percentage of civil twilight that the birds in the outdoor experiment had utilized. These percentages agreed well with data given by Franz (1943, 1949).

Daylengths (including utilized twilight) of 7 and 24 hours were considered to be most representative for redpolls during winter and summer respectively, therefore most constant-temperature experiments were run at these two photoperiods. At each photoperiod groups of birds were subjected to high temperatures (31 C to the upper limit of tolerance), medium temperatures (9 to 11 C), and low temperatures (–5 C to the lower limit of tolerance). A low-temperature experiment was also run with a 10-hour photoperiod. The birds were maintained at a constant temperature until they reached a constant weight, then the temperature was lowered or raised approximately 3 C to the next level.

A group of birds held at approximately –2 C was given a varying photoperiod schedule of 7, 3, 7, 10, 18, 24, 18, and 10 hours of light per day in that order, each period lasting at least nine days. Another group at approximately 25 C was given a schedule of 24, 18, 10, 7, 3, and 10 hours of light. Three hours was estimated to be close to the shortest daylength encountered by redpolls wintering in central Alaska. Data for 7-, 10-, and 24-hour photoperiods at these temperatures were incorporated into the analysis of temperature effect.

After determining gross, excretory, and existence energies in the various experiments, regression lines of energy on temperature were calculated for all groups of birds. Those for the constant-temperature birds were done in the IBM 7094 computer at the University of Illinois with the help of personnel from the Statistical Service Unit.

Statistical methods used in this study were taken from Jacob and Seif (mimeo) and Steel and Torrie (1960). Unless otherwise stated, simple F tests were used in comparing values. The level of significance set for all comparisons is $P = 0.05$.

RESULTS

Redpolls under Constant Temperatures and Controlled Photoperiods

Energy relations.—The relation between gross, existence, and excretory energies is shown separately for *hornemanni* and *flammea* in Figures 1–3. In no case in Figure 3 were the slopes or any values along corresponding curves at any one photoperiod significantly different between species. The curves show a more-or-less linear increase of energy with decreasing temperature. Temperature differentials at various locations within the low-temperature cabinet, and the inability of all cabinets to hold a set temperature within 1 or 2 C for extended periods have resulted in data being used for temperatures closer together than the 3 C interval mentioned above. For this reason the curves were calculated using values for individual birds rather than means of several. Goodness-of-fit tests for the regression lines (Table 2) were significant, indicating that the lines are good representations of the numerical data.

Exponential regressions were calculated from quadratic through quintic because it seemed obvious that the data contained other than linear components. Quintic curves are shown in Figures 1 and 2 because they best fitted the points, statistically and visually. Quintic curves for 24-hour birds are not shown but they were quite similar in shape to those for 7-hour birds. Although these lines are similar in general shape, suggesting that the variations were not random, there are certain differences between them, and it is very possible that their deviations from a straight line are not actually or always of the magnitude or direction indicated in these experiments. West and Hart (1966) found a somewhat similar curvilinear relation at night but a linear relation during the daytime with the Evening Grosbeak (*Hesperiphona vespertina*). Therefore, linear regressions, representing the more general trends in the data, have mostly been used in comparing the two species of redpolls. It should be recognized, however, that the actual relation seems to be curvilinear.

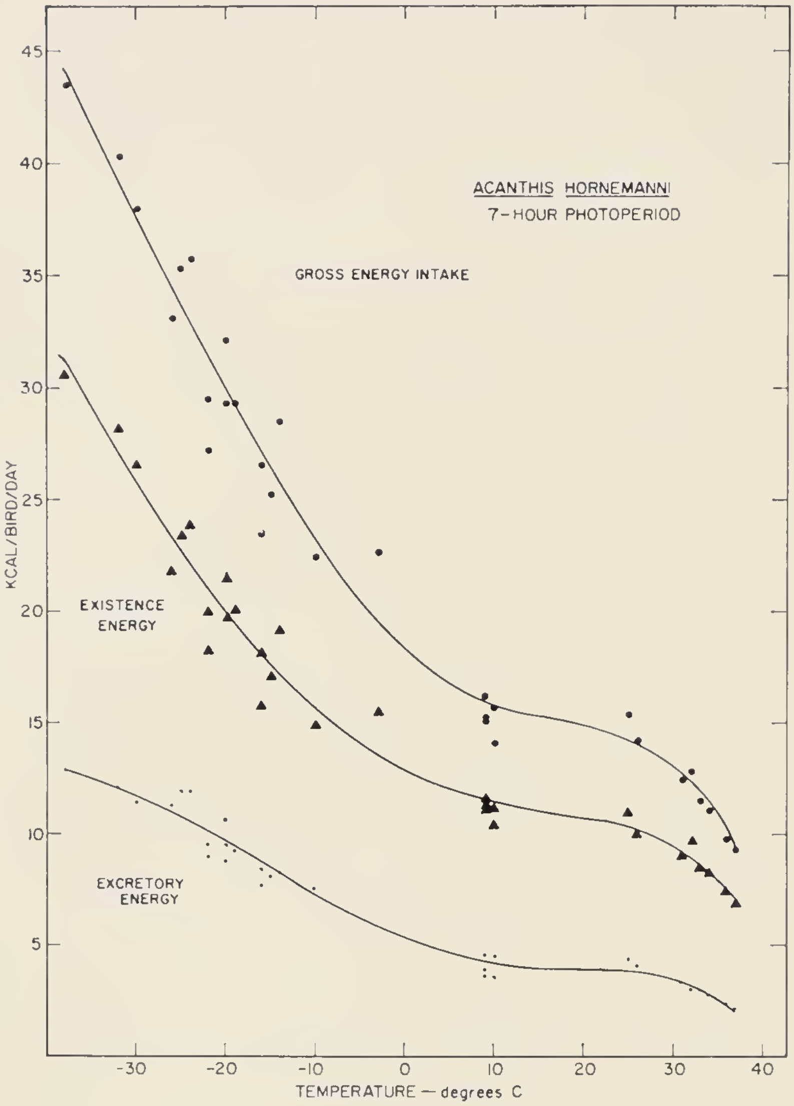

FIG. 1. Quintic regressions of energy on temperature for *A. hornemanni* at a 7-hour photoperiod.

The 24-hour gross and existence energy lines (Fig. 3) are significantly different in slope from the corresponding 7-hour lines for each species. Values on these two sets of lines for *hornemanni* are significantly different at all temperatures but for *flammea* are different only below about 20 C. Excretory energy lines are not different in any respect, although 24-hour values are somewhat higher. Values on these lines at –2 and + 25 C came from the birds held at varying photoperiods.

At photoperiods of 7 hours and lower most birds at less than 0 C fed during total darkness, as did the 3-hour birds at 25 C. Seven-hour birds at extreme high temperatures also drank at night, but the amount was not determined. The amount of food consumed at night was measured at the 3-hour photoperiod, both at –2 and at + 25 C. At these respective temper-

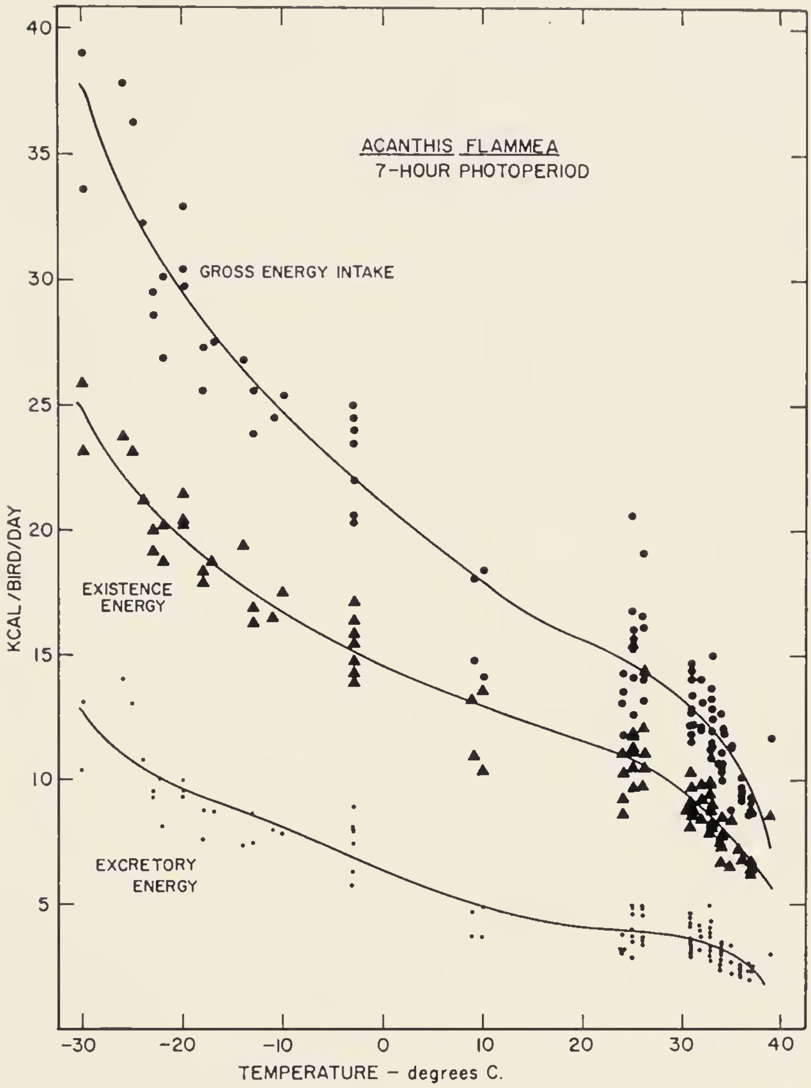

FIG. 2. Quintic regressions of energy on temperature for *A. flammea* at a 7-hour photoperiod.

atures the birds at night consumed a mean of 42 and 58 per cent of their total gross intake, although there was considerable individual variation.

The coefficient of metabolic utilization or digestive efficiency (per cent assimilated of the total calories ingested) was calculated by dividing metabolized energy by gross energy. The efficiencies shown in Figure 4 are the means calculated from constant-weight periods, and thus are comparable at any temperature or photoperiod.

Hornemanni was significantly more efficient (Chi square) than *flammea* at the extremes of temperature, otherwise the two species were essentially similar. Efficiencies increased significantly with increasing temperature at 7 hours of light but not at 24 hours. This and the fact that the 7-hour values at low temperatures were significantly lower than those at 24 hours may be

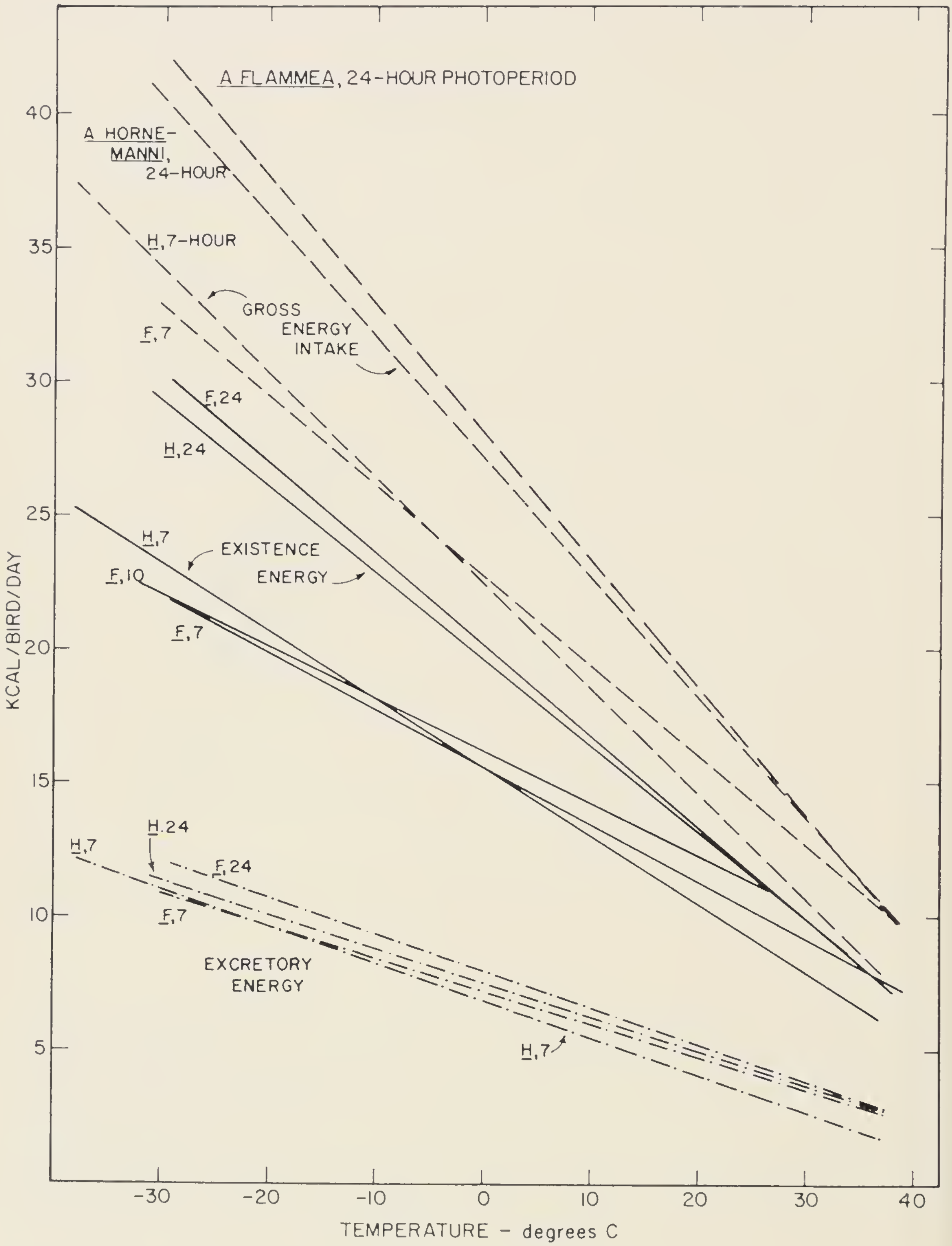

FIG. 3. Linear regressions of energy on temperature for *A. hornemanni* (H) and *A. flammea* (F) at 24- and 7-hour photoperiods. The existence energy line for *flammea* at a 10-hour photoperiod is also shown.

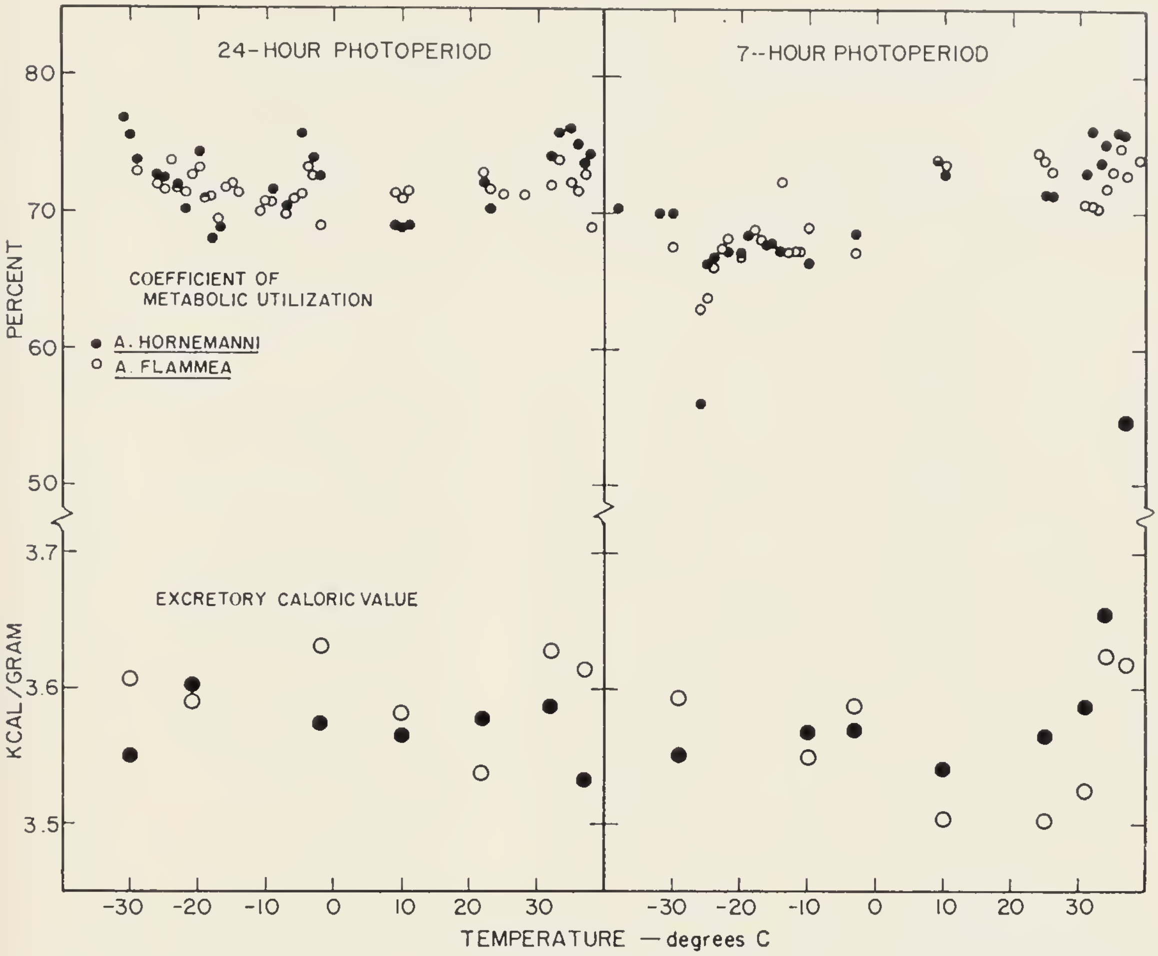

FIG. 4. Excretory caloric value and coefficient of metabolic utilization (digestive efficiency) in relation to temperature for redpolls at 24- and 7-hour photoperiods.

explained by the lower feeding rate per light hour and presumably longer retention of food in the gut of 24-hour birds. Efficiencies at high and intermediate temperatures were not different between 7- and 24-hour birds, where the feeding rates were more alike. There was also a significant increase in efficiency for *hornemanni* at temperatures of –30 C and lower at both photoperiods, but not for *flammea*. The explanation for this increase at extreme low temperatures seems to be that *hornemanni* was somehow able to retain food in the gut longer than was *flammea*, reflected in the relatively lower excretory caloric value for *hornemanni* at these temperatures (Fig. 4).

There were no significant or consistent differences in excretory caloric values between the two species or between birds at different photoperiods. However, except at high temperatures on a 24-hour photoperiod, the differences shown in efficiency are roughly inversely correlated with the caloric values per unit weight of excreta, as expected. At extreme high temperatures large amounts of fluid in the excrement made separation from waste food, with its higher caloric content, difficult and inaccurate. It should be

TABLE 2

QUINTIC AND LINEAR REGRESSION EQUATIONS OF GROSS (GE), EXCRETORY (EE), AND EXISTENCE (ExE) ENERGY ON TEMPERATURE FOR REDPOLLS UNDER CONTROLLED TEMPERATURE CONDITIONS AT DIFFERENT PHOTOPERIODS[1]

	Quintic $y =$	Linear $y =$
A. hornemanni		
24-hour, GE	$25.217 - 0.435T + 0.0127T^2 - 0.308 \times 10^{-3}T^3 - 0.134 \times 10^{-4}T^4 + 0.370 \times 10^{-6}T^5$	$27.224 - 0.450T$
EE	$7.244 - 0.091T + 0.575 \times 10^{-2}T^2 - 0.210 \times 10^{-3}T^3 - 0.739 \times 10^{-5}T^4 + 0.256 \times 10^{-6}T^5$	$7.587 - 0.126T$
ExE	$17.973 - 0.344T + 0.697 \times 10^{-2}T^2 - 0.977 \times 10^{-3}T^3 - 0.600 \times 10^{-5}T^4 + 0.144 \times 10^{-6}T^5$	$19.637 - 0.324T$
7-hour, GE	$18.154 - 0.364T + 0.012T^2 - 0.781 \times 10^{-5}T^3 - 0.458 \times 10^{-5}T^4 - 0.461 \times 10^{-7}T^5$	$22.506 - 0.394T$
EE	$5.388 - 0.164T + 0.465 \times 10^{-2}T^2 + 0.603 \times 10^{-4}T^3 - 0.231 \times 10^{-5}T^4 - 0.338 \times 10^{-7}T^5$	$6.884 - 0.139T$
ExE	$12.766 - 0.199T + 0.750 \times 10^{-2}T^2 - 0.681 \times 10^{-4}T^3 - 0.227 \times 10^{-5}T^4 - 0.123 \times 10^{-7}T^5$	$15.621 - 0.255T$
A. flammea		
24-hour, GE	$26.346 - 0.548T + 0.699 \times 10^{-2}T^2 + 0.214 \times 10^{-4}T^3 - 0.545 \times 10^{-5}T^4 + 0.674 \times 10^{-7}T^5$	$28.177 - 0.477T$
EE	$7.717 - 0.158T + 0.126 \times 10^{-2}T^2 + 0.832 \times 10^{-5}T^3 - 0.149 \times 10^{-5}T^4 + 0.288 \times 10^{-7}T^5$	$7.989 - 0.136T$
ExE	$18.628 - 0.389T + 0.573 \times 10^{-2}T^2 + 0.131 \times 10^{-4}T^3 - 0.396 \times 10^{-5}T^4 + 0.385 \times 10^{-7}T^5$	$20.187 - 0.341T$
7-hour, GE	$20.910 - 0.358T + 0.324 \times 10^{-2}T^2 + 0.112 \times 10^{-3}T^3 + 0.194 \times 10^{-5}T^4 - 0.174 \times 10^{-6}T^5$	$22.804 - 0.337T$
EE	$6.405 - 0.179T + 0.258 \times 10^{-3}T^2 + 0.151 \times 10^{-3}T^3 + 0.203 \times 10^{-5}T^4 - 0.131 \times 10^{-6}T^5$	$7.211 - 0.122T$
ExE	$14.505 - 0.180T + 0.298 \times 10^{-2}T^2 - 0.388 \times 10^{-4}T^3 - 0.893 \times 10^{-7}T^4 - 0.428 \times 10^{-7}T^5$	$15.593 - 0.215T$
10-hour, ExE		$16.195 - 0.196T$

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[1] T = temperature, degrees Celsius; y = energy in kcal/bird-day.

TABLE 3
LETHAL TEMPERATURES FOR INDIVIDUAL REDPOLLS[1]

7-hour photoperiod		10-hour photoperiod	24-hour photoperiod	
H	F	F	H	F
37 C	37 C		38 C	35 C
	37		2 survivors, > **38**	35
	37			37
	37			38
	37			**38**
	3 survivors, > 37			4 survivors, > 38
–26	–20	–32	3 survivors, < **–33**	–17
–43	–24	–32		–24
($\bar{x}$ = **–34**)	–32	–36		–26
	–32	($\bar{x}$ = **–33**)		**–26**
	($\bar{x}$ = **–27**)			–29
				–33
				1 survivor, < –33

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[1] Best estimates (mean or median) of limits of tolerance are in boldface for *A. hornemanni* (H) and *A. flammea* (F).

emphasized, though, that this error is cancelled out in the calculation of metabolized energy, so that the existence energy values in Figures 1–3 are not biased at any temperature on this account.

Temperature tolerance.—The temperature at which half the birds die should approximate the mean limit of tolerance for a population. Because so few *hornemanni* were available, their exact limits of tolerance could not be accurately determined in all cases (Table 3).

The lower limits of tolerance for 7- and 24-hour *hornemanni* were respectively –34 and lower than –33 C, and for *flammea*, –27 and –26 C. This did not support the expectation that birds with only 7 hours of light would not withstand lower temperatures than birds with constant light. The insulative value of the plumage was probably decreased in summer-plumaged (24-hour) birds due to an apparently normal loss of fair numbers of body feathers which was observed. White (pers. comm.) has found that wild birds had a 31 per cent heavier plumage in November than in July. The increase in caloric intake (Fig. 3) was apparently almost completely offset

TABLE 4

LIVE BODY WEIGHT AND FAT CLASS OF REDPOLLS AT CONSTANT TEMPERATURES[1]

Photo-period	Temp. (C)	N		Body weight (grams)[2]		Fat class	
		H	F	H	F	H	F
7 hours	–38	1	–	17.41	–	3.0	–
	–32	1	1	17.12	13.57	3.0	1.8
	–29	2	2	16.56 ± 0.32	15.22 ± 0.66	3.1	2.9
	–25	2	3	16.26 ± 0.24	15.07 ± 0.39	3.0	2.6
	–21	3	4	15.65 ± 0.76	15.02 ± 0.40	2.9	2.9
	–15	3	4	15.42 ± 0.60	15.50 ± 0.14	3.2	3.5
	–10	3	4	15.20 ± 0.66	15.52 ± 0.40	2.9	3.3
	– 2	1	7	15.57	15.53 ± 0.46	3.0	3.6
	10	3	2	13.78 ± 0.42	16.10 ± 1.33	3.5	4.4
	25	1	7	13.05	14.93 ± 0.44	2.9	4.3
	31	1	11	13.33	14.34 ± 0.42	2.8	4.0
	33	1	11	13.18	14.18 ± 0.45	2.9	4.0
	34	1	11	12.88	13.71 ± 0.43	2.9	3.8
	37	1	10	10.93	12.31 ± 0.25	2.4	3.3
24 hours	–31	3	3	15.39 ± 0.43	15.50 ± 0.19	3.9	3.3
	–25	3	6	15.45 ± 0.34	15.38 ± 0.53	3.7	3.6
	–21	3	6	14.98 ± 0.35	15.46 ± 0.53	3.6	3.6
	–17	3	6	14.41 ± 0.34	15.56 ± 0.46	3.3	3.8
	– 5	3	7	14.03 ± 0.47	15.51 ± 0.44	3.3	4.0
	– 2	1	7	15.92	15.65 ± 0.18	4.6	4.8
	10	3	2	13.89 ± 0.73	15.39 ± 1.83	4.2	4.3
	25	1	7	12.71	14.06 ± 0.41	4.2	4.1
	32	3	9	14.03 ± 0.24	14.48 ± 0.31	4.5	4.5
	35	3	9	13.24 ± 0.18	13.51 ± 0.31	4.3	4.3
	37	3	7	11.97 ± 0.59	12.65 ± 0.42	3.8	4.0
	38	2	6	12.21 ± 0.65	11.96 ± 0.37	3.8	3.9
10 hours	–32	–	3	—	14.08 ± 0.15	–	2.9
	–26	–	3	—	14.69 ± 0.42	–	3.2
	–20	–	3	—	14.78 ± 0.52	–	3.3
	– 7	–	3	—	14.75 ± 0.63	–	3.4
	– 2	–	7	—	15.92 ± 0.32	–	4.2
	25	–	7	—	15.36 ± 0.82	–	4.6

[1] Different groups of birds were used at low, intermediate, and high temperatures, as indicated by the spacing. H = *A. hornemanni*, F = *A. flammea*.

[2] Means ± SE.

by the increased heat loss and by energy expenditure for the greater amount of locomotor activity (Fig. 5). The lower limit for 10-hour (winter-plumaged) *flammea* was –33 C, significantly lower than for 7-hour birds.

This was to be expected, since the former had more time available for intensive feeding and for maintenance of insulation (preening).

The upper limits for 7- and 24-hour birds were respectively 37 C and probably 38 C or greater. This difference may be significant. The 24-hour birds not only had reduced plumage but, probably of most importance, were able to see and to drink freely at all times, and thereby were able to withstand a slightly higher temperature.

Activity.—Activity data (Fig. 5) were combined for all birds because no significant differences could be distinguished between the species. Changes in total activity at different temperatures were very similar at both 7- and 24-hour photoperiods, with a peak between 25 and 30 C, a sharp decrease above 30 C, a more gradual decrease from 30 to –20 C, then a small increase to about –30 C. Inactivity at low temperature conserves energy and heat loss is retarded. At very high temperatures, on the other hand, inactivity reduces the amount of heat that must be lost from the body.

Body weight and fat class.—Females and males were of equal weight. In general, decreasing temperatures were correlated with increasing weight (Table 4). However, separate groups of birds were used at the intermediate temperatures and their weights do not fall exactly into place in the table. In the low-temperature experiments at both 7- and 24-hour photoperiods, *hornemanni* increased significantly in weight but *flammea* remained about the same. At the end of the 7-hour experiment *hornemanni* had become significantly heavier than *flammea*, and at the 24-hour photoperiod, had equalled *flammea* in weight, whereas it had been significantly lower at the beginning. In the 7-hour low-temperature experiment (–10 to –38 C) *hornemanni* did not change appreciably in fat class with a drop in temperature, but at 24 hours (–5 to –31 C) it increased significantly (Chi square), and in both cases its fat class at the end of the experiment was significantly higher than that of *flammea*. *Flammea* decreased significantly in fat class at both photoperiods. Both species decreased significantly in weight and fat class at temperatures above 31 C.

Outdoor Redpolls

Energy relations.—Linear regression lines of existence energy on temperature for *hornemanni* and *flammea*, using mean values obtained during constant-weight periods at various temperatures within the range of –15 to + 30 C, are fitted respectively by $y = 16.920 - 0.228T$, and $y = 16.878 - 0.237T$, where y is existence energy in kcal/bird-day and T is the Celsius temperature. The mean photoperiod for these birds was about 13 hours. The lines for the two species were not significantly different. Values for all months, except September and October 1964, did not deviate significantly

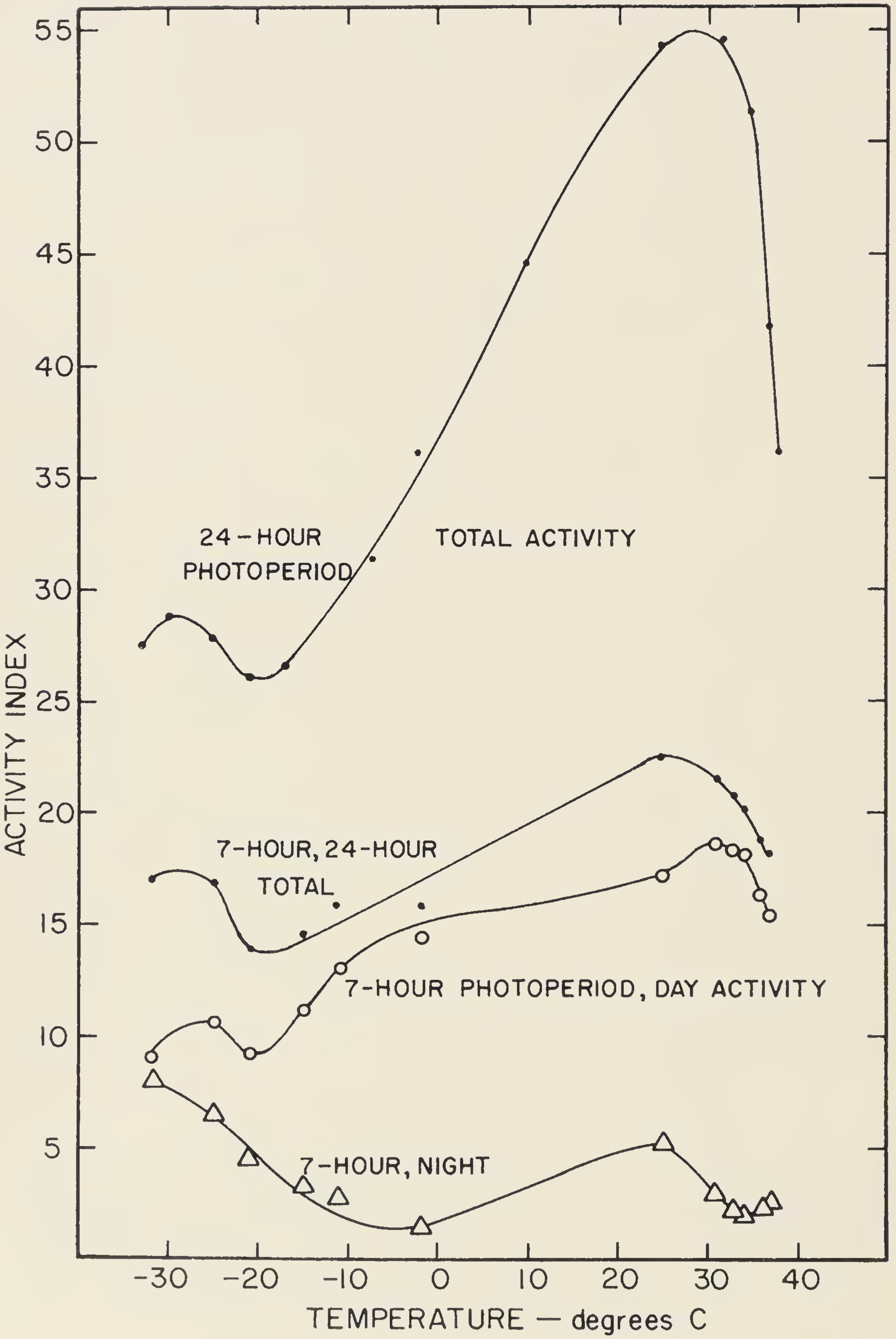

FIG. 5. Combined recorded cage activity at various temperatures. One activity index unit equals approximately 15 minutes of activity. Lines drawn by eye.

from these lines. Values for these two months, however, were significantly lower (1.5 and 2 kcal, respectively), apparently as a result of increased insulation due to the completion of molting. It appears that in the entire range of about 7 to 24 C ambient temperature there was a uniform saving of about 2 kcal/bird-day (13–17 per cent) due to having molted.

The exceedingly high productive energy values obtained during the first half of October 1963, shown in Figure 6, are not reliable because the technique of separating waste food from excreta had not yet been perfected and excrement was lost due to over-vigorous screening. Otherwise, peaks of productive energy were well correlated with temperature, fat deposition, and molt. It is evident that peaks and lows of productive energy were exactly synchronized between the two species when energy was only temperature dependent (December), but that synchrony was less perfect at other times, when this energy was correlated with fat deposition or molt. The total productive energy for the year was higher for *hornemanni*, but not significantly.

Metabolic efficiency was almost always about one per cent higher for *hornemanni*, but the differences between species were never significant. Fluctuations in efficiency were small in both species.

Activity.—Diurnal activity indices (Fig. 6) were essentially identical for *hornemanni* and *flammea.* Nocturnal activity, however, was somewhat different. Peaks of nocturnal unrest came slightly, but probably not significantly, earlier in spring and later in autumn for *hornemanni* and this species exhibited a higher intensity than *flammea.*

The hourly pattern of diurnal activity was bimodal throughout the year: higher values from just after awakening to midmorning, lower values in early afternoon, and higher values again just before activity ended. Differences between the highs and lows were of greater magnitude in summer, indicating that a more constant volume of activity per hour was maintained in the colder months. Nocturnal activity (*Zugunruhe*) in autumn was spread throughout the night but diminished somewhat in the hours around midnight. Spring *Zugunruhe*, however, was concentrated in the hours after midnight, perhaps indicating that redpolls are more often night migrants in autumn. Palmgren (1936) reports night migration of redpolls in autumn, and I infer from his paper that it is uncommon in arctic finches.

The duration of diurnal activity was generally somewhat greater for *hornemanni* than for *flammea* (Fig. 6). The difference can be attributed to greater utilization of civil twilight (earlier arising and later retirement) by *hornemanni*, to the extent that it was active an average 6 minutes per day longer than *flammea* for the year.

Body weight and fat class.—The mean bimonthly changes in weight and fat class were generally well correlated with each other (Fig. 6). However,

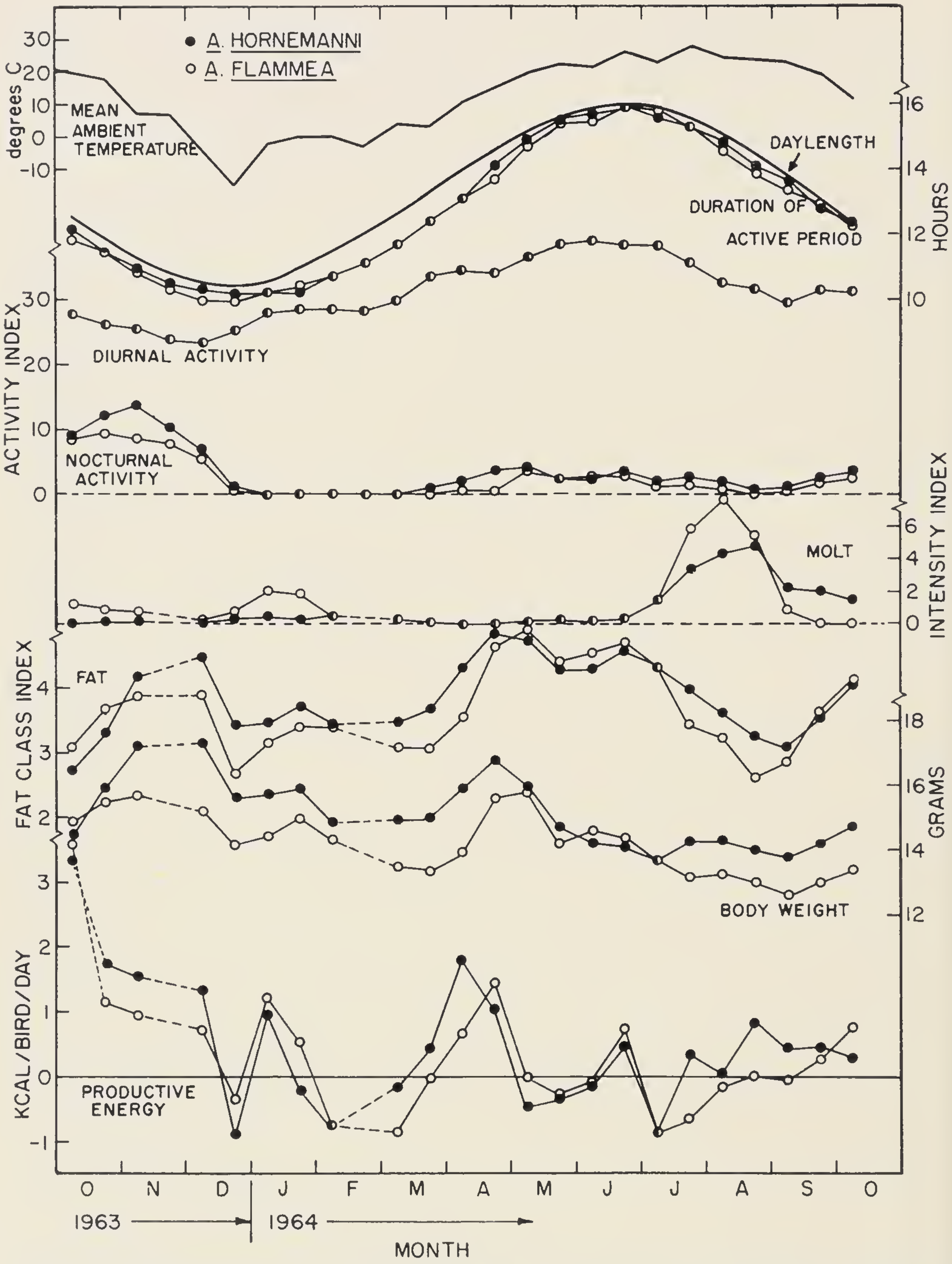

FIG. 6. The annual cycles of *A. hornemanni* and *A. flammea* held outdoors in Illinois. Values are bimonthly means. Daylength includes civil twilight.

the birds were of equal or lower weight in October 1964, yet had a higher fat class than in October 1963. This might be explained by the birds having relatively more muscle, with its higher specific gravity, than fat at the beginning of the experiment. Caging obviously causes a significant reduction in flying, and there may be atrophy of the pectoral musculature.

Changes in fat class were closely synchronized between the species only in December and January, when they were influenced by temperature alone. The other peaks and lows were associated with migration and molt, and were not as exactly synchronized between species, but the differences were probably not significant. In general *hornemanni* was significantly heavier than *flammea* and had a higher fat class (not significant), but at certain times of the year there was no difference in weight (October 1963 and May to July 1964).

Molt.—The peak of postnuptial molt was reached later in *hornemanni* than in *flammea,* was more prolonged, and of lower intensity (Fig. 6). Molt extended over a period of 114 days for *hornemanni* but only about 65 days for *flammea,* each as a group. The mean length for individual birds was 80 days for *hornemanni* and 61 days for *flammea.* The sequence of feather loss in their molts was similar and apparently normal with respect to wild birds.

Redpolls under Simulated Fairbanks, Alaska, Temperature, and Photoperiod Conditions

Energy relations.—Existence energy was calculated from periods when the birds maintained constant weight. Regression equations for existence energy on temperature within the range of –45 to –7 C, were for *hornemanni* and *flammea* respectively, $y = 15.575 - 0.308T$ and $y = 15.079 - 0.314T$. They were essentially similar both in means and slopes. When plotted, the points appear to merge with the points obtained for the outdoor birds between –15 and –7 C (Brooks, 1965), and the curvilinear relation suggested by the points for the birds held at constant temperatures (Figs. 1 and 2) again becomes apparent. No combined regression lines were computed, however.

Temperature tolerance.—Although these birds under fluctuating conditions were at a shorter photoperiod, their low-temperature tolerance was greater than that of those under constant conditions. The lethal temperatures for individual birds, calculated as the mean temperature for a period of 3 days prior to death, were, for individuals of *hornemanni,* –42, *–44,* –44, and –45 C, and for individuals of *flammea,* –21, –33, *–34,* –35, and –41 C. The italicized values are median estimates of the lower limit of temperature tolerance. *Hornemanni* was better able to withstand low temperatures, except for one *flammea* individual which lived through all the "cold spells" that were lethal to *hornemanni,* but died at a higher temperature almost one month later. This bird was noticeably less excited by handling than any other bird in all the experiments and may have been able to withstand lower temperatures because it was less stressed by caging and handling.

General

The weight of total body lipids was not directly proportional to fat class but rather was related curvilinearly (Fig. 7). The curve is fitted by the equation: $y = 1.3235 - 0.256x + 0.1451x^2 - 0.301x^3 + 0.1147e^x$, where y is grams of total lipids and x is fat class. The difference in weight of lipids between classes 1 and 4 was only about 1.0 g, while the difference between 4 and 5 was about 2.5 g. The fat classes can be used to estimate roughly the total lipids of a bird by using the values on this curve.

It became apparent during the experiments that the head and body feathers of *hornemanni* were longer and fluffier than those of *flammea*, but no size measurements were made. However, the dry weights of the plumage of 7 *hornemanni* and 7 *flammea*, randomly chosen from winter-plumaged birds which died soon after capture, gave the following results (means ± SD):

hornemanni;	total plumage, 1.0258 ± 0.10 g; head and body, 0.8386 ± 0.09 g; flight (remiges and rectrices), 0.1871 ± 0.03 g.
flammea;	total plumage, 0.9506 ± 0.08 g; head and body, 0.7472 ± 0.05 g; flight, 0.2034 ± 0.03 g.

Only head and body plumage weights were significantly different between the two species, with *hornemanni* having the heavier plumage, and consequently, a better body insulation. The *hornemanni* and *flammea* specimens used here had respective mean fresh body weights of 13.22 and 13.58 g (not significantly different), indicating that the differences in weights of feathers were not due to size differences of the birds.

DISCUSSION AND CONCLUSIONS

Redpolls under Constant Temperatures and Photoperiods

Birds at low temperatures.—As expected, *hornemanni*, and to a lesser extent, *flammea*, tolerated lower temperatures than any passerine yet investigated at the University of Illinois, from tropical permanent residents to arctic summer residents (Cox, 1961; Zimmerman, 1965*b*; Olson, 1965; Kendeigh, 1949; Davis, 1955; West, 1960).

Heat production and retention are the major problems of birds at low temperatures. The main source of heat production is shivering, according to West (1962) who worked with redpolls and Evening Grosbeaks. By increasing energy intake, not only is more energy available for shivering, but specific dynamic action (SDA) also increases and contributes to the total heat production. In the present study and in those by Kontogiannis (1965), Olson (1965), Williams (1965), and Zimmerman (1965*a*) an

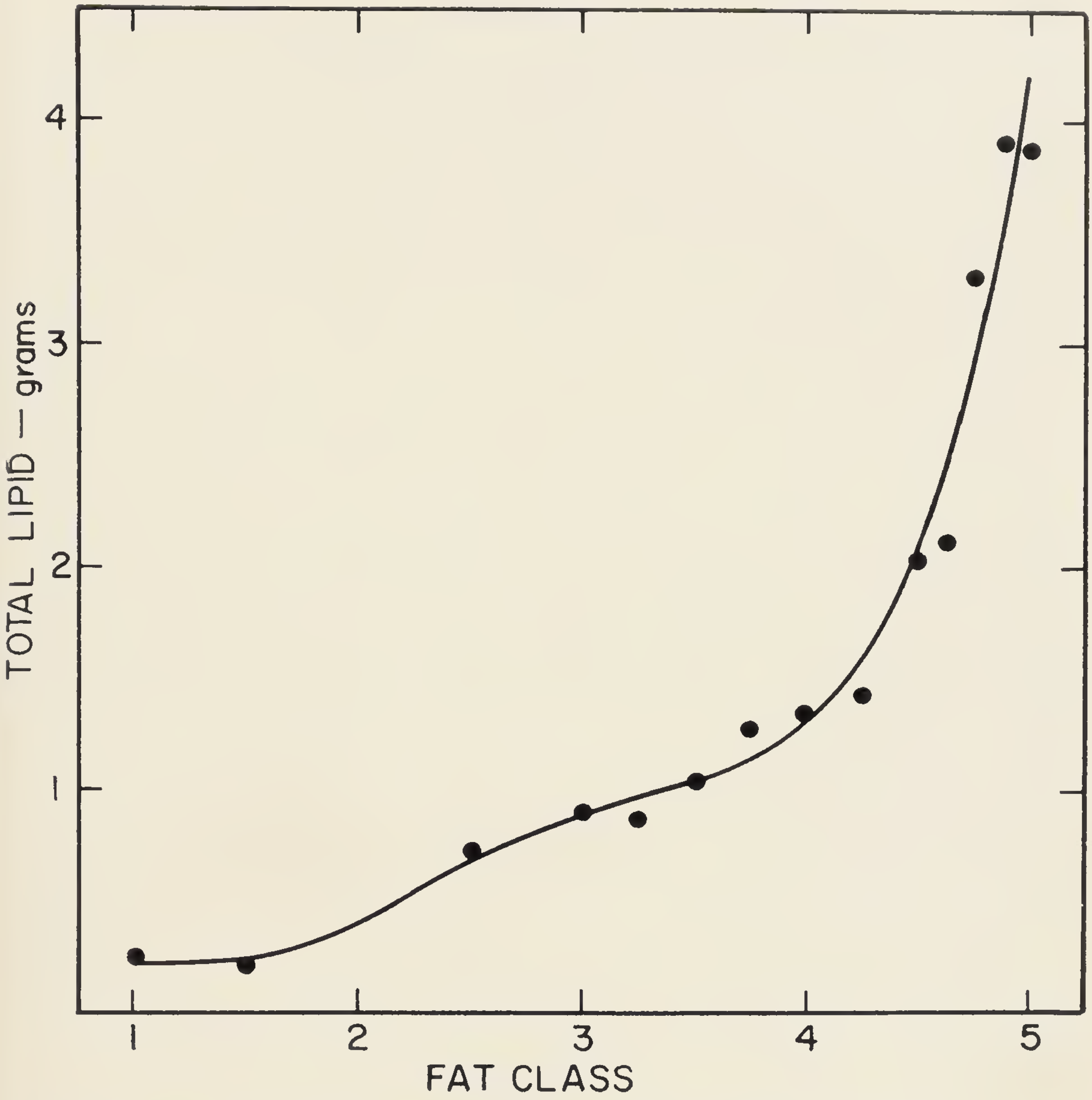

Fig. 7. Relation of total body lipids (dry weight) to fat class of redpolls.

increase in lean dry weight or protein with decreasing temperatures below about 0 C was shown (redpoll data given in thesis, Brooks, 1965). The increase in muscle mass (protein) and shivering are probably interrelated.

Retention of heat is facilitated by fluffing the feathers, by becoming inactive, by seeking shelter, and according to West (1962), by peripheral vasoconstriction. Reduction of locomotor activity, shown rather well in this study (Fig. 5), was necessary for obtaining maximum insulation from the fluffed-out plumage of the redpolls.

The most beneficial shelter would probably be a cavity of some sort, since there is a considerable saving of energy in these circumstances (Kendeigh, 1961). The dense foliage of white spruce (*Picea glauca*), which redpolls often utilize at Fairbanks, is almost as good as a cavity, in that the birds are not radiating to the night sky. Cade (1953) has reported redpolls entering and feeding in holes in the snow formed either by protruding vegetation or by the birds themselves, and Irving (1960) writes that Eskimos at Anaktuvuk Pass have also seen this behavior. Whether it is primarily to obtain shelter or food is not known, nor is the extent to which it is done. I have observed redpolls held in flight cages in Illinois burrowing through piled snow given to them for drinking purposes, but their actions indicated that they were bathing or dusting rather than finding shelter or food.

The breeding distribution of *flammea* is very well correlated, according to Peiponen (1962), with the distribution of dwarf birch (*Betula nana*, *B. tortuosa*, and others). Having been snow-covered through the winter, seeds of these small "trees" are readily available in the spring when the seeds of larger trees have been blown away. He also found that these birds are "largely specialized" in feeding. Birch seeds, when available, make up over 80 per cent of the diet in northern Finland, even for young birds in the nest. Indeed, the German common name for this species is "*Birkenzeisig*," literally, "birch siskin." White (MS) determined that for redpolls in the vicinity of Fairbanks the proportion of birch and alder (*Alnus*) seeds in the diet was 88 per cent.

From the linear regression equations in Table 2 it can be calculated that gross energy intake at the lower limit of temperature tolerance in the 7-hour experiments was 35.9 kcal/bird-day for *hornemanni* and 31.9 for *flammea*. On the experimental diet having a caloric value of 4.4 kcal/g, the corresponding weights of food ingested would be respectively 8.2 and 7.3 g. The caloric value of unhusked birch seeds, however, is about 5.5 kcal/g (White, MS). Assuming the same metabolic efficiency, substitution in the regression equations indicates that weights of birch seeds equal to the weights of experimental feed ingested would permit tolerance of temperatures to about –57 C by *hornemanni*, and to about –51 C by *flammea*. If, rather than using calculated weights (from the regression equations), the actual weights of feed ingested by the birds (these values were somewhat higher) are used in this computation, it is found that the extrapolated lower limit of temperature tolerance is then somewhat lower than –62 C for both species. These values are all fairly close to the lowest temperatures that wild redpolls are subjected to near Fairbanks (–57 C:Johnson, 1957; –60 C:Pewe, 1964). It should be kept in mind that these are average limits for the redpoll population, and that about half the population can be expected to withstand considerably lower temperatures. The seeds of birch are substantially higher in caloric value than most types which have been measured (Kendeigh and West, 1965; Turček, 1959), thus the adaptive value of the redpolls' selectivity of birch seeds in the wild is self-evident.

The esophageal diverticulum of the redpolls, absent in most fringillids but present in several northern forms (e.g., crossbills, *Loxia* spp.), is a partially bilobed ventro-lateral outpocketing located approximately halfway between head and body (Fisher and Dater, 1961). White (MS) has found this structure to contain a maximum of 1.3 g of birch seeds in wild birds, or about 7 kcal of energy. Without this "extra" food resource the extrapolated lower limit of temperature tolerance for *hornemanni* would be reduced to about –40 C, and for *flammea*, to about –30 C. In the present study the birds at low temperatures were observed to fill their "crop" just prior to the lights going off.

Feeding in total darkness by the experimental birds at low temperatures probably depended on their having a ready food source and knowing exactly where it was. Johnson (1957) and Heinrich Springer (pers. comm.) never observed feeding during the dark near Fairbanks, although Brina Kessel (pers. comm.), at the same location, reports that during the winter redpolls were active earlier in the morning than other birds, when, to her eyes, it was still dark. Palmgren (1936) noted that redpolls caged indoors were different from other small birds in being active even under very dim light conditions. Palmgren also mentions that redpolls have been heard in migration at night, and outdoor birds in the present study showed *Zugunruhe*, but, of course, this activity is far different from searching for and feeding on small seeds. The Gray Jay (*Perisoreus canadensis*) manufactures and caches pellets of food for later consumption (Dow, 1965), and it would seem to be very advantageous for a bird like the redpoll, which can be active during darkness, if it were to cache food in or near its roosting place. However, redpolls are not known to do this. Perhaps the advantage in being able to be mobile at very low light intensities is that in the morning redpolls can fly out to the feeding area in near-darkness and be ready to feed as soon as light is sufficient to see the small seeds. In the evening they can remain at their feeding until the last light, and then make their way back to the roost again in near-darkness. Such a capability would extend considerably their actual feeding period in the long Alaskan twilight. Further observations of wild birds are required on the question of nighttime feeding before it can be stated definitely that its occurrence was a laboratory artifact, since redpolls are suspected of wintering above the Arctic Circle where there are no daylight hours during the winter.

Concerning body insulation, in addition to the "normal" body plumage, redpolls have numerous down-feathers in the apterylae during the winter, unlike a large number of other small birds. Irving (1960) ranked 12 species of fringillids in order of the "apparent usefulness for insulation" of their contour feathers. Only the Pine Grosbeak (*Pinicola enucleator*) was higher, *hornemanni* and *flammea* ranking second and third respectively. His criteria for better insulation were, feathers "having less rigid terminal barbs with softer barbules containing extended fine processes." Retention of air within the plumage is presumably greater with these feathers. The apparent greater fluffiness of the body feathers of *hornemanni*, and the demonstration that the dry weight of the winter plumage on the head and body of *hornemanni* was significantly greater than that of *flammea*, have already been mentioned, both facts pointing to the correctness of Irving's ranking of these species.

At 7 hours of light *hornemanni* exhibited a higher rate and capacity of energy intake below 0 C than *flammea* (Fig. 3). It gained weight and did not decrease in fat class with temperatures decreasing below –5 C, while *flammea* did not gain weight and its fat class decreased. *Hornemanni* presumably, then, was able to spend more time with activities such as preening, which is, of course, very important in maintenance of insulative value of the plumage.

Steen (1958) has suggested that small arctic birds in the wild, including redpolls, undergo marked hypothermia at night at low ambient temperatures. He was able to show this only in newly caught birds, not in birds that had adjusted to caging. West (1962) suggests that these newly caught birds were subnormal. Redpolls, studied by West, that dropped more than 4 degrees in body temperature during their first nights after capture "lost weight or ultimately did not survive." There was no evidence that birds were hypothermic at any time in the present study. If it were true, one would expect to see a leveling off or a dip in the low-temperature regions of the curves in Figures 1 and 2. There is indeed the hint of a leveling off at the extreme low temperatures in all curves but this is at or beyond the lethal point for most of the birds, and since the birds here were rapidly becoming moribund, they would be expected to be subnormal.

Birds at high temperatures.—The problems here, in direct contrast to those at low temperatures, are in reducing heat production and increasing the rate of heat loss from the body. Redpolls employed the only two major methods of reducing heat production, the most important being a reduction in activity (Fig. 5), since most of the body heat is produced by muscular contraction. They also consumed less food, thus reducing the heat from SDA.

Evaporation of water from respiratory surfaces in birds is of major importance for heat dissipation as long as water is available. It has already been mentioned that redpolls drank copious amounts of water at high temperatures, no doubt for this purpose. Reduction in the insulative value of the plumage by wear or loss of feathers, and sleeking down the feathers to decrease the thickness of insulation and expel trapped warm air were also methods employed by redpolls. Birds in winter plumage (7-hour photoperiod), when subjected to the high-temperature regime, were observed to pluck out body contour and down-feathers. Birds in summer plumage (24-hour photoperiod) had already reduced their plumage in the normal spring feather loss, and started their postnuptial molt during the experiment. Nevertheless, self-plucking was observed here, also. This plucking out of feathers may be an adaptation to the relatively rare occurrence of high temperatures in the arctic, when they must quickly reduce their insulation. Since the time of year when high temperatures occur is shortly before the birds' normal molt, the period of reduced insulation against cold would not last long.

The upper limit of temperature tolerance for *flammea* is lower than that for other passerines similarly studied, and may also be lower for *hornemanni*, although this was not determined exactly. For central Alaska the highest recorded temperature is 37.8 C (Pewe, 1964), almost exactly the same as the upper limit of temperature tolerance determined for redpolls.

Redpolls under Outdoor Fluctuating Temperatures and Photoperiods

The composition of the Umiat redpoll population is a matter for debate, some workers (Bee, 1958) referring all birds to *flammea*, some (Baldwin, 1955) to *hornemanni*, and others (White, pers. comm.) to both species plus intergrades. The outdoor birds used in this study from Umiat were rather typical *hornemanni* and those from Fairbanks, typical *flammea*. For convenience they have been referred to as these species in the present study, but it may be more correct to regard them simply as representing two different breeding populations of *Acanthis* from northern and from central Alaska.

Hornemanni, representing the northern population, showed *Zugunruhe* and reached a peak in this and fat deposition slightly earlier in spring and somewhat later in autumn than *flammea* (Fig. 6). This is a common relation in migration between northern and southern populations among other species (Lincoln, 1950). Fat deposition times of the outdoor birds correspond fairly well with those given by White (MS) for Fairbanks and for northern Russia by Blyumental (1961). Blyumental has also shown that postnuptial molt, autumn fat deposition, and migration overlapped in arctic *flammea* as they did for the other arctic species she studied. There was little overlap in the present study for *flammea* (subarctic) but considerable overlap for *hornemanni* (arctic).

The postnuptial molt in *hornemanni* began slightly later and reached a peak considerably later than in *flammea* (Fig. 6). The time of beginning molt for *hornemanni* coincides with that in wild birds at Umiat, but the duration of 80 days was approximately twice as long as in wild birds

(Baldwin, 1955). Possibly this was due to the stress of caging and handling, and perhaps the more rapid decline of photoperiod at Umiat, compared with Illinois, was also involved.

Productive energy for *flammea* increased during the molt but the birds were still in negative energy balance. However, they lost considerable fat during this time, indicating that this was a supplementary energy source. By using 9.5 kcal as a rough estimate of the energy gained from one gram of dry fat, and estimating, from Figure 7, the grams (dry weight) of fat used, the deficits of July and August are accounted for.

It is of interest that during the molt *hornemanni* continued to meet most of its energy needs by feeding and did not reduce its body fat reserves as much as did *flammea.* This behavior may have definite survival value in the far north where it is colder in summer and more subject to early and sudden periods of cold.

Regression lines for existence energy of outdoor birds paralleled but were higher than those for birds at constant temperatures and a 7-hour photoperiod. These higher mean daily values for the outdoor birds were due to the longer photoperiods (averaging 13 hours), because the birds' hourly values were lower than those of the constant-temperature birds, although not significantly. The slopes and means for the simulated Fairbanks "outdoor" birds' existence energy lines, however, were significantly steeper and higher (except at temperatures near 0 C) than those of the 7-hour birds, even though the simulated birds were exposed to shorter photoperiods (averaging 6 hours). West and Hart (1966) determined that the metabolism of Evening Grosbeaks was not significantly different under either constant or fluctuating temperature conditions in the range of about –10 to + 20 C, although the values for fluctuating conditions were somewhat higher throughout. This was contrary to the findings of others, and their explanation was that in both cases the birds had been either acclimated or acclimatized to the respective conditions, whereas they had not in other studies. In the present study the redpolls were also acclimated to constant conditions or acclimatized to fluctuating conditions. It therefore appears that in these considerably smaller birds with their higher intrinsic metabolic and heat-loss rates, low fluctuating temperatures are correlated with relatively higher metabolism than are low constant temperatures, but at less severe temperatures the relation is similar to that in the grosbeaks. If this is the case, the low-temperature metabolic rates and lower limits of tolerance determined for the simulated birds in the present study are probably more indicative of those of birds under natural conditions than are those of the low-temperature 7-hour birds. At temperatures above –10 C or so this does not hold, and here the constant-temperature birds' values are as good as any.

Assuming this interpretation to be correct, substitution (into the respective regression equations) of the caloric value of birch seeds and the weight of feed ingested at the lower limit of temperature tolerance, as was done earlier with the constant-temperature birds, indicates that the estimated lower limit of tolerance in the wild for *hornemanni* would be about –67 C, and for *flammea*, about –54 C (using the simulated birds' values). These figures, in relation to the absolute Fairbanks minimum of –60 C indicated earlier, show better agreement than do those of the constant-temperature birds.

In the outdoor experiments *hornemanni* averaged 6 minutes per day greater utilization of civil twilight throughout the year than *flammea.* The bimonthly mean difference varied considerably but *hornemanni* was generally active at lower light intensities. This may be another adaptive difference between the two species. Since civil twilight lasts about four times as long in central Alaska as in Illinois, *hornemanni* should average from 20 minutes to one-half hour longer activity than *flammea* each day there. This, however, needs corroboration from studies on the wild population.

A brief comment on the taxonomic status of the redpolls may be in order at this concluding point. In the present study *hornemanni* has been shown to be better adapted to the arctic environment than *flammea*, particularly by its significantly greater tolerance of low temperature, attributable to the cumulative effects of several small and often nonsignificant differences. Apparently, due to interbreeding between *hornemanni* and *flammea*, a complete gradient of morphological types occurs. It would not seem unreasonable to assume that a physiological gradient exists as well, with typical specimens of *hornemanni* and *flammea* occupying different positions on it. In view of this and the fact that natural interbreeding occurs, the only logical answer seems to be that there is but one species of *Acanthis* here, *hornemanni* and *flammea* being, at best, subspecies adapted to slightly different environments.

SUMMARY

Inverse linear as well as curvilinear correlations of metabolized energy (kcal/bird-day) with temperature were demonstrated under both constant and fluctuating temperatures between –30 and + 38 C for *Acanthis hornemanni exilipes* (Hoary Redpoll) and *A. flammea flammea* (Common Redpoll) at winter and summer photoperiods. Digestive efficiency generally decreased initially with a drop in temperature but increased after a long duration at low temperature, especially at extreme low temperatures, and particularly with *hornemanni.*

The lower and upper limits of temperature tolerance determined for birds held at constant temperatures were respectively: *hornemanni*, –34 to + 38 C or higher; *flammea*, –27 to + 38 C. Both upper and lower limits were lower than for any other passerine species similarly studied. These limits were established using feed with a caloric content of 4.4 kcal/g. By substituting the higher caloric value of birch seeds (the major natural food) these estimated lower limits drop to –57 C for *hornemanni* and –51 C for

flammea. The lower limits for birds held under fluctuating temperatures and photoperiods, simulating actual periods of winter weather occurring at Fairbanks, Alaska, were probably closer to those for wild birds. These limits were for *hornemanni*, –44 C, and for *flammea*, –34 C. Again substituting the caloric value of birch seeds the respective values are –67 and –54 C.

The most important adaptations of the redpolls to the arctic winter, in comparison to non-arctic passerines, are:

1. Relatively higher rate and quantity of gross energy intake at low temperatures, owing in part to the possession of a croplike esophageal diverticulum which is filled with "extra" food just prior to the onset of darkness.
2. Selection of high-calorie foods (primarily birch seeds) over foods containing fewer calories per unit weight.
3. The ability to increase digestive efficiency at extreme low temperatures.
4. Plumage with probable greater insulative value.
5. The ability to continue activities at very low light intensities.

Hornemanni is better adapted than *flammea* by being slightly more extreme in each of these adaptations (excepting diet selection) and, in addition, this species may not decrease its food intake during the autumn molting period to the degree that *flammea* does, thereby maintaining fat reserves for use during early, sudden cold periods in its more northern environment.

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REALLOCATION OF THE EOCENE FOSSIL *PALAEOPHASIANUS MELEAGROIDES* SHUFELDT[1]

JOEL CRACRAFT

In 1913 Shufeldt described a new fossil bird, *Palaeophasianus meleagroides*, from the early Eocene of Wyoming. Shufeldt considered the relationships of *Palaeophasianus* to be within the Galliformes, more particularly with the Tetraonidae and Meleagrididae. On the basis of Shufeldt's published figures Brodkorb (1964:303) placed *Palaeophasianus* in the subfamily Cracinae of the Cracidae with the remark "The shapes of the cotylae and the proximal inner margin of the shaft [of the proximal end of the tarsometatarsus] are reminiscent of *Penelope*, although the large size recalls *Crax*." Brodkorb also suggested that since the type was imbedded in matrix, more preparation of the fossil would be necessary before its relationships could be determined with any certainty.

During the course of other paleontological work on Oligocene birds I had occasion to examine the type of *Palaeophasianus*. Through the courtesy of Dr. Malcolm C. McKenna of the Department of Vertebrate Paleontology of the American Museum of Natural History the type was further prepared, thus allowing a more complete study of the fossil. Subsequent examination has revealed that the relationships of *Palaeophasianus* are not with the galliforms but with the gruiform birds of the family Aramidae. The fossil appears to represent a heretofore unrecognized genus and species of that family. Because the fossil was covered with matrix, Shufeldt's description was incomplete; therefore, it is necessary to redescribe the type material (see Fig. 1).

MATERIAL

American Museum of Natural History No. 5128, Department of Vertebrate Paleontology; the distal end of left tibiotarsus, proximal and distal ends of left tarsometatarsus, and seven or eight broken pieces of one or more long bones; collected by the American Museum expedition of 1910, Willwood Formation, Elk Creek, east of Dry Camp 2, Bighorn Basin. N. W. Wyoming; age: early Eocene (Gray Bull fauna).

Tarsometatarsus.—The proximal end of the tarsometatarsus is similar to the living *Aramus guarauna*, but with (1) the anterior metatarsal groove deeper (may be due, in part, to crushing); (2) intercotylar prominence more horizontal, not projecting upward as much (when viewed from the side); (3) intercotylar prominence well developed but less well defined; (4) internal cotyla larger than external cotyla; (5) intercotylar area more elevated, ridges on inner sides of external and internal cotylae more developed;

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[1] Dedicated to Dr. George M. Sutton on the occasion of his 70th birthday.

FIG. 1. Stereophotographs of the type of *Palaeophasianus meleagroides.* Upper left, proximal end of tarsometatarsus; upper right, distal end of tibiotarsus; lower left, anterior view of tarsometatarsus; lower right, internal view of tibiotarsus.

(6) slope of anterior margins from the top of the intercotylar prominence to the external and internal cotylae more gradual (from an anterior view); (7) shaft decidedly more triangular in shape (possibly due, in part, to crushing), the sides of the hypotarsus and shaft being more planar; (8) external cotyla somewhat less open anteriorly and posteriorly; (9) internal and external cotylae more round and cup-shaped; and (10) hypotarsus more developed, projecting more posteriorly.

Tibiotarsus.—The fossil is similar to living *Aramus guarauna*, but (1) from anterior view the internal condyle more elevated relative to external condyle (may be partially the result of crushing and displacement of bone); (2) internal condyle thicker basally, more triangular in shape (when viewed from distal end); and (3) rim of external condyle elevated more posteriorly relative to posterior rim of internal condyle (when viewed from distal end).

Measurements.—Tarsometatarsus: greatest breadth of head 18.5 mm; greatest depth of head (measured from tip of intercotylar prominence to most posterior portion of hypotarsus) 19.0 mm; width of shaft 30 mm below top of intercotylar prominence 12.3

mm; tibiotarsus: greatest breadth across condyles 16.5 mm; width of shaft 30 mm from top of internal condyle 9.6 mm; depth of shaft 30 mm from top of internal condyle 7.5 mm; greatest width of external condyle (measured from anterior to posterior) 16.0 mm.

DISCUSSION

The hypotarsus of the tarsometatarsus is badly damaged, but portions of several canals are still present. A well marked canal is found on the external side of the hypotarsus, but it is impossible to say whether or not the canal was open or closed posteriorly. In addition, a larger, medial canal and a smaller, internal canal are present, but again, one cannot be sure whether they were grooves (i.e., open) rather than canals (i.e., closed).

Taken by itself a positive identification of the fossil tibiotarsus is difficult. The bone was considerably damaged in preservation and portions of it were probably displaced as fossilization was taking place. Consequently, the above description, especially of the topographical relationships of the condyles to each other, may possibly be somewhat misleading. The fossil tibiotarsus superficially resembles that of tetraonids in some respects, for instance in the more developed, more triangular internal condyle. Unfortunately. the area of the supratendinal bridge is still covered by a very hard matrix and further preparation does not appear possible. The fossil does, however. resemble the Aramidae in general features, and there is no good reason for doubting its inclusion along with the tarsometatarsus in this family.

The distal end of the tarsometatarsus included in AMNH No. 5128 still remains imbedded in matrix on one side, and the shaft and trochleae are so broken up, that if more matrix were removed, the fossil would break apart. Because of this situation, the distal end of the tarsometatarsus cannot be identified in itself. It is also not possible to identify the remaining fragments of the long bones.

Three fossil aramids have been described from the early Tertiary:

Badistornis aramus Wetmore
  White River series, Upper Oligocene, South Dakota
Gnotornis aramiellus Wetmore
  White River series, Upper Oligocene, South Dakota
Aramornis longurio Wetmore
  Snake Creek Beds, Middle Miocene, Nebraska

Palaeophasianus appears to resemble *Badistornis* in certain features. but when compared with Wetmore's description (1940), *Palaeophasianus* differs in the following characters: (1) internal cotyla is not as high relative to the external cotyla; (2) internal cotyla is more round; (3) external cotyla is apparently not as open anteriorly or posteriorly; and (4) comparison with

Wetmore's Figure 7 indicates the anterior margin from the intercotylar prominence to the external cotyla is much less vertical (from an anterior view). All of these characters, along with geologic age differences, suggest that *Palaeophasianus* is generically distinct from *Badistornis.*

Gnotornis is represented by the distal end of a left humerus. The measurements given by Wetmore (1942) indicate *Gnotornis* was approximately one-third the size of either fossil or living limpkins. On the basis of certain characters of the humerus, Wetmore considered *Gnotornis* to be a distinct genus. Because only the humerus of *Gnotornis* is preserved, a comparison with *Palaeophasianus* cannot be made.

Aramornis is represented by the distal end of a left tarsometatarsus. According to the measurements (Wetmore, 1926) *Aramornis* was slightly larger than the Recent genus *Aramus.* A comparison of size between the type of *Aramornis* (AMNH No. 6292) and the damaged tarsometatarsus of *Palaeophasianus* shows that the latter is considerably larger. The tarsometatarsus of *Palaeophasianus* is badly damaged, hence a comparison with *Aramornis* cannot be made.

Shufeldt (1915) placed another fossil (distal end of right tarsometatarsus) from the Bridger Formation of the middle Eocene of Wyoming in the genus *Palaeophasianus.* The fossil (Yale Peabody Museum No. 896) was compared to the types of *Palaeophasianus* and *Aramornis* and to skeletons of *Aramus.* This second specimen is so badly damaged—the trochlea for digit 2 is gone, the posterior side of the trochlea for digit 3 is lacking, and the trochlea for digit 4 is slightly broken—that comparison is difficult. However, there is little doubt that the Yale specimen is larger than *Palaeophasianus meleagroides.* Moreover, certain characters suggest this bone is not a limpkin: the distal foramen is farther removed proximally from the base of the trochlea for digit 3 and the external intertrochlear notch than in *Aramus,* and the base of the trochlea for digit 2 appears not to be directed posteriorly as it is in *Aramus.* The Yale specimen may possibly be an aramid, but because the bone is greatly damaged, positive identification is nearly impossible.

Wetmore (1940:33) believed the differences of *Badistornis* from the Recent genus *Aramus* "tend to ally it to the cranes, the Gruidae, so that it appears ancestral to the modern limpkins. As it gives a closer approach to the cranes than does living Aramus it indicates more certainly the presupposed line of ancient connection between the Aramidae and the Gruidae." *Palaeophasianus* also resembles the Gruidae in some characters but no more so than it does several other families. The resemblances seem better explained on the basis of characters inherent in the tarsometatarsus and tibiotarsus themselves and appear not to be a reflection of relationship.

Included with the Aramidae and Gruidae in the superfamily Gruoidea is the Eocene family Geranoididae (Wetmore, 1933). The type species, *Geranoides jepseni*, is based on the fragmentary remains of the distal ends of a tarsometatarsus and tibiotarsus. The tarsometatarsus is distinctly different from that of the Aramidae. The tibiotarsus of *P. meleagroides* shows some differences from the tibiotarsus of *Geranoides*, notably in the shape of the external condyle. Due to the fragmentary nature of the type material of *Palaeophasianus*, comments about its relationship with *Geranoides* are probably best kept at a minimum at this time.

The placing of *Palaeophasianus* in the Aramidae extends the known occurrence of that family back to the early Eocene and indicates that the family had attained a remarkable diversity by the early Tertiary.

SUMMARY

After further preparation and study, the early Eocene fossil *Palaeophasianus meleagroides* Shufeldt is found not to be a member of the Cracidae but is instead representative of the Aramidae.

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REPRODUCTIVE BEHAVIOR OF HAIRY WOODPECKERS
II. NESTING AND HABITAT

Lawrence Kilham

The nesting period of Hairy Woodpeckers (*Dendrocopos villosus*) is of interest for a variety of reasons, one being that selective pressures are intensive at this time, and thus serve to bring out sexual differences in foraging, agonistic, and other behavior. Individuality appears to be well developed or at least observable in this species, as discussed in three previous reports. The first of these (Kilham, 1960) described a female which took the lead in an unusual courtship lasting through fall and winter months, and a second discussed sexual differences in feeding habits (Kilham, 1965). A third communication (Kilham, 1966*a*), reported observations on early breeding behavior, from pair formation in mid-winter to completion of nest excavations in early May, as well as a tabulation of the various vocalizations, drummings and other displays observable throughout the year. The present report, like the preceding one, is based on nearly twenty pairs of Hairy Woodpeckers observed in Tamworth and to a greater extent in Lyme, New Hampshire, from 1958 to 1966.

INCUBATION

Hairy Woodpeckers are subdued and silent while incubating eggs in the middle weeks of May and members of pairs usually make no more than a few intimate *teuk, teuk* notes when relieving each other at the nest. Pair H in Tamworth in 1958, however, was exceptional in the liveliness of its behavior. I was below the nest in an aspen on 19 May, when I heard *speaks*, then saw the two woodpeckers perched close together exchanging *joick, joick* notes before one flew off and the other entered the hole. Similar greetings accompanied all change-overs observed over the course of four days. Since the male, MH, spent the night on the nest, change-overs at the extremes of the day required a special timing. When I entered the woods before dawn on 20 May, for example, the first Yellow-bellied Sapsucker (*Sphyrapicus varius*) drummed at 4:45 AM and the first Yellow-shafted Flicker (*Colaptes auratus*) at 5:10, but there was no activity at the nest of the Hairy Woodpeckers until the female, FH, arrived with a medley of *joicks* to relieve her mate at 5:35 AM. It seemed probable that she needed half an hour to feed before settling down to her turn at incubating. Events took place in reverse in the evening, when MH came to relieve her at 7:30 PM which gave her about thirty minutes to feed before twilight. MH was late in arriving, however, on 20 May. FH was obviously nervous for she would emerge from the nest, feed hastily on a nearby birch, then re-enter the nest only to emerge 5 minutes later for a similar performance. MH finally arrived for the night and took her place at 7:45 PM.

The members of Pair B in Lyme in 1965 contrasted with Pair H in having been exceedingly quiet during the incubation period. Incubation appeared to begin on 7 May when the drummings and vocalizations associated with the copulatory behavior of a few days before (for description of methods of communication, see Kilham, 1966*a*) tapered off rather abruptly. MB emerged from his nest hole at 6:30 AM as his mate arrived silently. He gave a Whinny, then flew to the far end of the wood and drummed a single burst before flying elsewhere. Throughout the next few weeks, I heard almost nothing from the pair, on visits paid nearly every morning. On entering the pasture woodland on 21 May, however, I realized almost immediately that the eggs had hatched by the behavior of MB who flew from his nest hole at 6:35 AM, did some quick, nervous preening on a nearby tree, then drummed at what for a Hairy Woodpecker was a very rapid rate of 16–20 bursts a minute. I had rarely heard him drum at a rate of over 5 bursts during the early breeding period from January through April. His behavior on 21 May was obviously unusual.

NESTLING STAGE

Table 1 presents uniformities of behavior observed among Hairy Woodpeckers during the nestling period. In retrospect, however, it was rather the diversity and adaptability of the species, not only between adjacent pairs but also within the same pair in successive years, which impressed one. These situations were well exemplified by Pairs A and B, which bred in adjacent territories in 1964 and 1965.

Pair B.—The members of Pair B were closely adapted to each other and to their territory, or so it appeared from their quiet behavior, prolonged courtship (Kilham, 1966*a*), and close cooperation in successful nesting during 2 successive breeding seasons. The situation where I observed the nesting activities in 1965 was optimal in a number of ways. It was located in an open woodland which did not attract Starlings (*Sturnus vulgaris*), which can be effective competitors for nest holes, and the nest cavity was four meters up in the rotten center of an aspen (*Populus tremuloides*) of which the living outer inch of wood provided protection against predators.

At 6:30 AM on 22 May, the day after hatching, FB alighted below the nest hole with food in her bill, then entered to remain on the nest after MB had wriggled out from the tight-fitting entrance, giving low conversational notes as he did so. This close brooding of the young continued for the next five days. FB alighted on the sixth day with a few *teuk* notes, but her

TABLE 1
GENERAL DIFFERENCES IN NESTING BEHAVIOR OF MALE AS COMPARED WITH FEMALE HAIRY WOODPECKERS

Type of Behavior	Male	Female
1. *Foraging*		
a. foraging areas	away from nest	close to nest
b. prey sought	mostly in trees	trees, brush, ground
c. location of prey	deep in wood	superficial; under bark, etc.
d. size of prey	larger; bill fails to close	smaller; bill closes
e. manner of hunting	deliberate; works one place	keeps moving; restless
f. number visits to young	relatively few	3 to 4 × as many as M
g. care of young	less concern	more attentive
2. *Guarding of Young*		
a. general surveillance	little	maintained during day
b. special danger	remains close to nest	less involved
c. night	roosts in nest	never
d. reaction to danger	calm	hyperexcitable
3. *Other*		
a. nest sanitation	does most of it	infrequent
b. plumage, end of nesting	good condition	frayed and soiled

mate was not there. She entered to feed, then emerged with a mass of feces in her bill and flew 100 m with peculiar short, rapid wing beats before discarding it. This was one of the relatively few occasions on which I observed performance of nest sanitation by a female of *D. villosus* (see Table 1). Both sexes exhibit the same type of flight when carrying feces.

A number of other patterns of behavior observed for Pair B were ones common to various pairs of Hairy Woodpeckers. On 28 May, for example, FB made 5 visits at close to 5-minute intervals between 6:15 and 6:40 AM carrying insects so small that they barely protruded from her bill. It was apparent from watching and listening that FB was foraging for prey on bark and other locations located not far from the nest and always within hearing distance of the steady *pee-urp, pee-urp, pee-urp* vocalizations of the young. These calls are doubtless a stimulus driving females to incessant activity. The attentiveness of the female in care of young at this and other nests was reflected in their plumages, which became increasingly sooty and disheveled as the season progressed while those of the males, which had come to nests less frequently, remained as well-preened and sharply black and white as in early spring.

Male B took life in a more leisurely fashion than his mate. On 2 June, for example, when she made four visits with small insects between 6:40 and

6:50 AM, he came only once, but with a grub so large that he could not close his bill. He was about to enter when FB alighted close by. She greeted him with *chewk, chewk* notes, then moved to his place and entered as he gave way and flew to a tree 30 feet away to wait until she emerged. On this and other occasions, it appeared as if females of *D. villosus* were often dominant in the particular situation of feeding the young. On 2 June MB returned to the nest after his mate had left, fed the nestlings, then flew off carrying a fecal mass in his bill.

Although MB was generally away from the vicinity of the nest more than FB, he remained close when there was any danger to put him on guard. On 6 June 1965, for example, I found him giving an uninterrupted series of loud *speaks* near the nest tree. By searching neighboring trees I discovered a gray squirrel (*Sciurus carolinensis*) resting on a level with the nest hole and seven m away. These squirrels are a threat to the nest cavities of larger woodpeckers. Within a few days after the young had flown from the nest of Pair B, for example, a squirrel had gnawed and largely destroyed the entrance.

MB appeared to do little and FB nearly all of the feeding of the young in the last few days of the nesting period. The volume of vocalizations made by the nestlings had become considerable by 10 June. Two days later the nest was silent. Thinking it empty, I knocked hard on the tree trunk below and thus precipitated an alarm vocalization which I had not heard before, a harsh *scree* as a well-feathered nestling looked out, then dropped back out of sight to become silent again. When a parent approached and pecked nervously on a tree on seeing me, the young began a clamor of begging notes. All of them had flown by the following morning.

The 1965 nest of Pair B was in an optimal location and the woodpeckers experienced no serious interference from nest-hole competitors. Their 1964 nest, however, presented a more complicated situation. Although it also was within the rotten center of a living tree, a butternut (*Juglans cinerea*), the tree was between two fields on an aerial highway of Starlings which came to rest on it many times a day. In the few moments of their stay, they often edged over toward the nest hole of Pair B with evident interest and curiosity. On 5 June when an especially inquisitive Starling approached the nest hole, MB faced it in threat display, with bill raised and wings outspread. Both birds held frozen positions momentarily. Then FB joined her mate and the advance of the two of them together frightened the Starling away. Other birds of similar size, such as Catbirds (*Dumetella carolinensis*) and Brown Thrashers (*Toxostoma rufum*) which occasionally perched even closer to the nest hole, aroused no reaction on the part of the woodpeckers. It thus appeared that the Starlings were their chief concern.

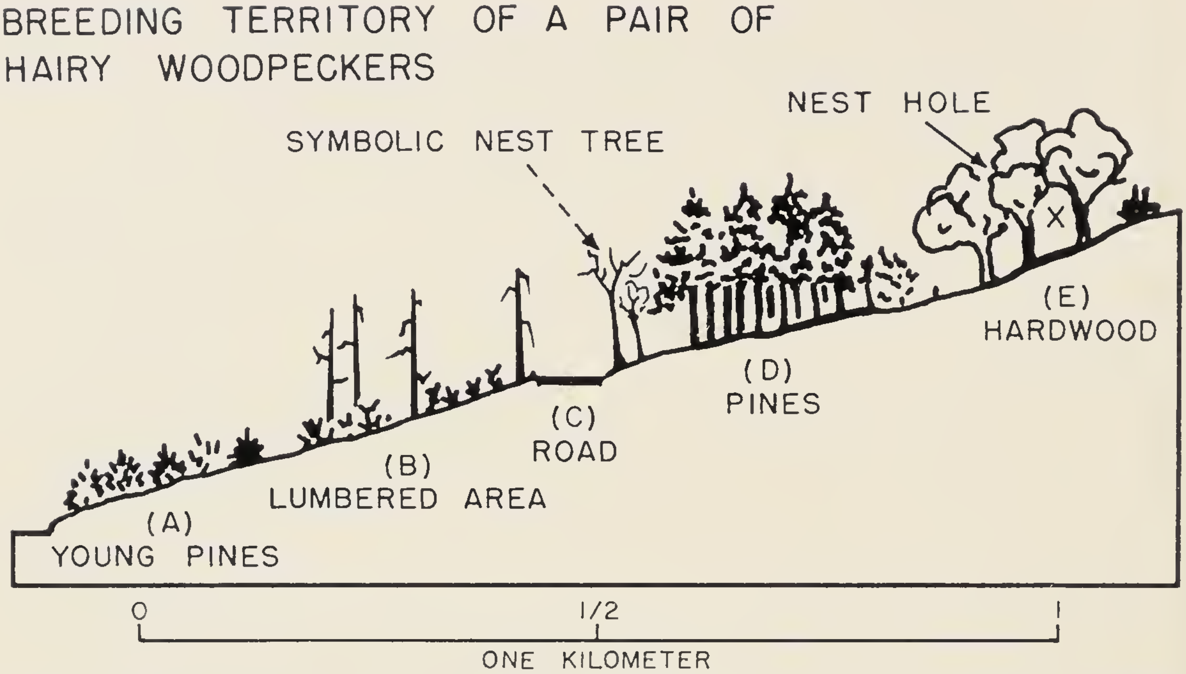

Fig. 1. Diagrammatic cross section of breeding territory of Pair A, 1964. Activities noted for each part of the territory were: A. Cover of juveniles in weeks after nest-leaving. B. Early courtship in open area of drum trees and symbolic nest hole (see Kilham, 1966*a*). C. Section of territorial boundary; scene of conflicts between Male A and Male B in late winter. D. Foraging area of Female B, at distance from E, the location of nest hole.

The striking behavior of the woodpeckers in this year, 1964, as compared with 1965 was that one or the other of them was always on guard, presumably due to the Starlings. MB might fly in from the woods with food in his bill and FB leave as he arrived, but never before. He would go directly to the nest hole, feed the young, then ascend the same limb in a leisurely fashion, drumming here and there as he did so. His next move might be to drum a few loud bursts on a special resonating limb. While on guard duty for the next five or ten minutes he might shift idly from one neighboring tree to another, pick an insect from the bark, carry it to the nest, then pause for a rest below the entrance. As soon as FB returned, however, he would take off immediately. On some few occasions he would raise his bill and greet her with *chewki, chewki, chewki* notes before doing so. FB was by far the more active and restless of the two woodpeckers. She seldom either drummed or remained quietly in one place, but spent her time on guard duty hitching hurridly over limbs and trunks of adjacent trees, even though insect prey became scarce on these over-worked locations. She occasionally flew to a dying elm 60 m from the nest, where her search for prey was more rewarding (Kilham, 1965). While on the elm she was still within full view of her nest.

In summary, one might say that (1) in the presence of a threat by Starlings, the two woodpeckers cooperated closely in guarding their nest daily and at all times of day. (2) The same pair when nesting 250 m away in the following year and without any Starlings in the vicinity always left their nest unguarded while foraging for prey, except for the one special occasion when MB faced a gray squirrel. (3) As with other pairs of *D. villosus*, the greater activity and attentiveness of the female was generally apparent. (4) In spite of, or possibly because of, the differences of temperament of FB and MB, the two woodpeckers were never antagonistic but always appeared closely paired and devoted to each other, as had been the case throughout the early breeding seasons of two successive years (Kilham, 1966*a*). (5) MB was an unusually tame and leisurely individual. Neither parent, however, took much notice of me, even when I stood directly below their nest hole which was only six meters above the ground. Two of the offspring of Pair B which I kept under observation for several months in my aviary were quite tame. This tameness offered contrast to the rather different behavior of neighboring Pair A described below.

Pair A.—In 1964 this pair had an excellent nest hole, seven meters up in a living white birch (*Betula papyrifera*) in an open wood of red oak (*Quercus rubra*), birch, and hornbeam (*Ostrya virginiana*) (E in Fig. 1). The parent woodpeckers, however, seemed to find little prey in the area and took long flights away from their nest after feeding the young (for example to area B in Fig. 1).

MA was unusual in starting an almost uninterrupted series of vocalizations if I were within 20 or even more meters of the nest as he alternately approached, then circled away, making loud ruffle noises with his wings. His excitement was considerable. Aside from *speaks* given in a shrill fashion that made them resemble the *peek, peek* notes of a neighboring pair of Robins (*Turdus migratorius*) he gave sputters of his own variety. These had a quality of harsh laughter, of which a common sequence was *speak - chrr - charr - jer-jer-jer, charr - jer-jer.* FA was also excitable but less so than her mate. Her sputter was a more even *speak-ha-ha-ha-ha.* The young of this pair also seemed to be unusually excitable, and as they grew older they gave similar explosive sputters from within the nest. I had never heard such noises from the young of Pair B in two successive years. This hyperexcitability of MA, appeared to be one manifestation of a general eccentricity, evident not only in the prolonged courtship with FA (see Kilham, 1966*a*) but also by his rather extreme lack of aggressiveness whenever MB invaded his territory, a subject to be described in a subsequent report.

FA acquired a new mate, MA′, in 1965. This new male had a calmer disposition, more similar to that of other males which I had observed. Pair A in both 1964 and 1965 showed a marked preference for seeking white birches as nest trees. The 1964 tree was an excellent choice, since it was tall and vigorous with a nest entrance 7 m from the ground, made through living wood. If it could be considered at one end of the scale of suitability for nesting, the 1965 nest, located 3 m up in a rotten, fungus-grown birch stub, could be considered at the other, in regard to safety from predators. The stub stood in an open, lumbered area, where FA found insect prey without going beyond ear shot of the begging cries of her young (as I judged by the distance of 50 m at which I could still hear them). She was far more attentive than MA′ in looking after the nestlings. On 3 June, for example, she brought small amounts of prey to the nest eleven times between 6:23 and 6:53 AM, at intervals of approximately two and one-half minutes, a rate far greater than that observed at any time for MA′.

In contrast to FA's mate of the year before MA′ was a leisurely individual. He would stop to drum a few bursts, then take a long flight over the tree tops to some foraging area of his own. On many days he only made a sixth as many feeding visits as FA, but he nearly always brought in a large grub which protruded from his bill and after poking it into the bill of a young one, would help arrange the morsel in proper alignment for the nestling to swallow it.

Observations made on the feeding activities of FA in two successive years were, by chance, comparable for the middle of the nesting periods and can thus be summarized as follows. In 1964 with mate MA and poor foraging near the nest, FA made sixteen and MA, eleven, feeding visits to the young, in a total of two hours of observation time, while in 1965 with mate MA′ and good foraging in the vicinity of the nest, she made twenty-three visits to the young as compared with only four by her mate. This amounted to 5.8 times as many feeding visits by the female as by the male.

The possibility that Pair A was nesting in a stub too rotten for safety was substantiated on 10 June. As I approached early in the morning I could tell by her vocalizations that FA was excited. She was still carrying insects in her bill as she moved excitedly two meters above a skunk (*Mephitis mephitis*) which was pushing its way through nearby vegetation. The skunk turned when I called to it, coming right to my foot with FA following closely and giving loud, repeated *chip - ha-ha-ha* notes as she did so. I now saw that the entrance to the nest in the rotten birch stub had been largely chewed away. The fledglings had survived, however, for one of them looked out through the ragged hole giving a series of vigorous sputters similar to those of its mother. I was also able to locate MA′ in the distance by his steady succession of *speak*. Closer inspection of the nest stub revealed a few gray hairs caught on a rough place as well as a cluster of wide-spreading claw marks left on the birch bark below where a raccoon (*Procyon lotor*) had embraced the

FIG. 2. Direct view of Hairy Woodpecker defending nest hole showing disruptive color pattern. (Drawn by Cornelia Wood.)

stub. The proximity of the skunk at the time of my arrival had thus been a coincidence. It was remarkable that the raccoon had not been able to chew the nest out completely. My supposition was the MA′, while roosting in and guarding the nest at night, had struck back at the raccoon in an effective manner, as illustrated by Figure 2, which is an imaginative reconstruction. This close encounter, if such took place, may have explained why MA′ appeared to be particularly timid about approaching the nest on the early morning of 10 June. The two fledglings left their disrupted nest hole on 12 June when fully fledged.

Other aspects of nesting behavior.—Patterns of behavior common to Pairs A and B in two successive years as well as two other pairs observed during the nestling period in New Hampshire are summarized in Table 1. A few additional observations were as follows: (a) Nestlings could be quiescent at times, become vociferous as parents approached, then quiet down gradually after being fed. (b) Although adults entered the nest to feed smaller nestlings, they might rest on the outside and poke food to young, clinging within the entrance even sixteen days before nest-leaving. The open bills of parent and young met at angles to each other in the transfer of food. (c) After giving food, an adult might spend some moments poking back to aid a nestling arrange prey for swallowing. (d) If one Hairy Woodpecker arrived while its mate was still feeding young, there was often an exchange of *teuk, teuk* notes as the first bird flew away. (e) Although hand-raised nestlings occasionally formed fecal sacs, parents engaged in nest sanitation usually

Fig. 3. Vigorous feeding reaction of young Hairy Woodpecker, taking food from forceps at estimated thirteen days old.

appeared to be carrying irregular masses of fecal material. Whether sacs are formed or not, may be related to the type of diet at the time.

Pair G. 1966.—The nest of this pair was 7 m up in a dead beech (*Fagus grandifolia*) stub. The openness of the surrounding beechwood and its freedom from low vegetation enabled me to observe the flights of the parent birds to and from the nest to excellent advantage. What was striking under these circumstances was the amount of time spent by female FG on the ground. She appeared to be little disturbed by my presence 20 m from her nest and might alight as little as 10 m from me to forage. She tossed leaves aside in vigorous fashion, uncovered partially buried dead limbs of beech and other trees and sought prey from rotten wood, while moving rapidly and not pausing long in any one place. It would take her about five minutes on an average to find enough prey for a visit back to the nest. Her activities, however, might vary with climate and other conditions. The woodland floor, for example, had become relatively dry by mid-June but a heavy rain on the 16th made dead logs and branches soft and soggy. FG was especially active under these conditions, making as many as 7 visits to her nest in 23 minutes, all to and from an oak log which had been relatively hard in dry weather.

FG appeared to be much at home on the ground. She not only preened there in leisurely fashion on some occasions before foraging but, as I had observed on 6 May she even copulated there.

Very few other species of birds fed at the lower levels in the beech woods. Such birds as thrushes were all in mixed woods at the periphery of the wood leaving the female Hairy Woodpecker as seemingly the only one that could find prey efficiently on or near the ground under the beeches.

On 18 June after feeding the young from the outside MG paused to tap, then drum-tap, just within the entrance. I had observed similar behavior for Male F in 1964. It seemed in both situations as though these drummings might be a way for the growing young to learn the displays of their species, or to have their innate proclivities for doing so reinforced.

I kept the captive young of Pair G in an aviary, the floor of which simulated the conditions of a woodland floor. Under these conditions the female, both as a juvenile and an adult spent much time foraging about on the ground. The young male, however, limited himself largely to a number of upright logs. Thus, a sexual difference observed in the field was duplicated to some extent in captivity. The significance of this difference of feeding habits may be in that female Hairy Woodpeckers have increased chances of finding food for their young, while remaining close to their nests.

OBSERVATIONS ON NESTLINGS

The principal observations on the nestling stage of Hairy Woodpeckers were made on two sets of young obtained in Maryland. In 1960 I studied three young from one nest which were of different sizes and stages of development. The feathers of the smallest were just emerging while the largest one had well-developed tracts of feathers. They had probably hatched on different days. The nestlings responded well to artificial feeding, making vigorous sucking motions on a small pair of forceps used to insert food into their throats (Fig. 3), and producing fecal sacs when probed after being fed. They were shut in a dark cabinet between feedings. Here they made low peepings which reminded me of a chorus of frogs in the swamp from which they had come. When I opened the cabinet door in the morning, all three heads shot out with necks outstretched begging for food.

The nestlings began to preen each other and to stretch their wings in a both-wings-up stretch at an estimated age of fourteen days. The gradation in size remained marked. At an average of eighteen days the largest was well-feathered and twice the size of the smallest, which was equally healthy and vigorous. The ivory white tip of the upper mandible (Fig. 4) as well as the fleshy knobs at the corners of the bill which aid parents in feeding their young, were still discernible at this age.

Several unplanned situations brought on vigorous defense reaction. On one of these, a fledgling Blue Jay (*Cyanocitta cristata*), caused the three young woodpeckers to crouch low, the fore parts of their bodies pressed down, and their heads elevated with bills wide open. In this position they made a harsh, pulsating noise, not unlike that of a young Starling. The reaction was brought on a second time when some new born suckling rats were placed in the same cabinet. It was a unique performance, for we saw nothing like it at other times.

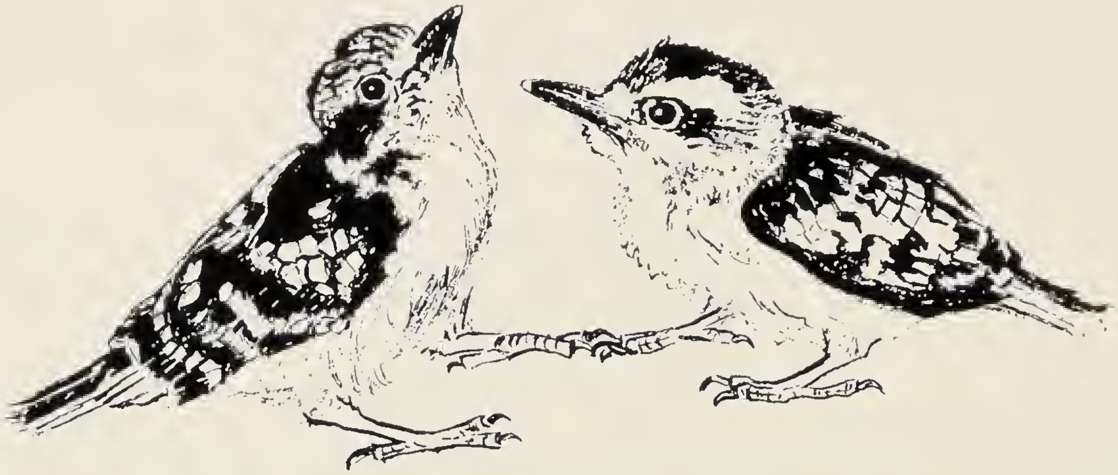

Fig. 4. Nestling at estimated eighteen days old still retaining white tip of upper mandible.

Another set of nestlings was obtained on 21 May 1957 when about half way through the nestling period or an estimated age of twelve days. Both were kept in a hollow log nest-cavity. They became upset if removed from it, as evidenced by efforts to climb upward and their settling down immediately when returned. The female was the larger of the two and she not only seized food in an aggressive manner but also pecked so hard at the smaller male, with fierce, persistent jabs, that he cowered as if in fright much of the time. On 24 May I put in a partition in an effort to ameliorate this situation. On 27 May, however, the female climbed over it to attack the male who did not defend himself on this or other occasions. Aggressiveness ceased at the time of nest-leaving, so completely that the two woodpeckers were able to rest together peacefully. Sielmann (1958) has described a situation closely similar to the above, in which he had to separate the smallest and weakest nestling in order to rescue it from attacks of the largest and fiercest of a brood of the Great Spotted Woodpecker (*Dendrocopos major*) which he raised in captivity from the time they were ten days old.

Time of Nest-Leaving Under Natural Conditions.—When I made my first visit to Nest B in Lyme at 6:15 AM on the day of nest leaving, 12 June 1964, two of the young had already flown and a last one was still chittering within the nest hole. I attempted to locate the fledglings which had left. One of them gave away his position by making *speak* notes in a small pine tree, close to the ground. While I was looking at him MB, who had been preening in a leisurely fashion close by the nest tree, came within 3 m, making *jeek* notes to the young one, and seemed unconcerned by my proximity. His mate, on the other hand, was full of activity as she hitched up a dying elm, prying out larvae from the bark and feeding them to a second fledgling who was following her up the trunk, jerking his body, half-starting his wings, and making a sputtery whinny as he did so.

FB flew back to the nest hole some minutes later with prey in her bill. The third and last fledgling, however, had already flown. FB bowed in and out of the entrance as if aware that another young one was to be accounted for, but uncertain where it might be. She flew about the nest tree for several minutes, swinging her head to look about and giving excited Speaks. She then flew to the trunk of a neighboring tree as the lost fledgling started upward from the ferns at its base, possibly in response to her vocalizations.

I interrupted these events by capturing two of the fledglings for further observations in the aviary. Under usual circumstances Hairy Woodpeckers cease to share the job of feeding their young after nest-leaving and are followed about in succeeding weeks by a particular offspring which is cared for entirely by one parent. I had thus created something of an experiment. With only a single young one remaining, which parent would care for it? There was actually little question, however, as I observed on the following morning when FB, who had been the more attentive in caring for the nestlings, was taking full care of the surviving juvenile. The latter made Speaks, Whinnies, and a *quare*, tree-frog like note, when she came to feed it. This was in a wood 200 m from the old nest. Vocalizations were even more lively on the following day when I came to the thicket of young pines. FB on this occasion flew to where her juvenile was lurking with a loud ruffle of wings, then burst into a series of exuberant *joick, joick* notes such as she had used earlier in the year in greeting her mate (Kilham, 1966*a*).

Comments on agonistic Behavior of Nestlings.—The harsh noises made by the nestling Hairy Woodpeckers on sudden threat were startling performances and comparable in this respect to the hissing vocalizations of nestling flickers, even though not snake-like. On 29 June 1957, I put an arm down into a flicker's nest. The nest was dark and silent beforehand, and the sudden, explosive, snake-like hisses of the young flickers, which were an estimated twelve to fourteen days old, were both unanticipated and frightening. According to Sherman (1910) flickers make hissing vocalizations steadily from the time they are a day old. She does not, however, describe the startling effects of sudden hissing as being a probable defense reaction. Sibley (1955) has described this type of behavioral mimicry for titmice (Paridae) and other birds.

Sherman (1910) noted in her observations of nestling flickers that some broods were more "quarrelsome" than others, a situation which may also be true for *D. villosus,* since the set of nestlings which I raised in 1960 were peaceful in contrast to the brood of 1957. A number of factors may be operative in determining the extent of agonistic behavior among nestling woodpeckers. One is that the nestlings hatch on different days so that some are more developed and larger than others. The relative weakness of a small sibling may serve to initiate aggressiveness of older nestlings, which in turn may serve a biological function in survival if we consider the ways in which the attacks may take place under natural circumstances. Thus Sherman (1910), speaking of nestling flickers as fighting like "little demons at times," states that "Their battle-ground is in the vicinity of the hole. The one in possession of the hole maintains his supremacy there by occasional withdrawals of his head from the hole in order to deliver vigorous blows on the heads of all within his reach, causing them to shrink downward. This is the case with the stronger ones, the weaker ones frequently are driven from the vantage place." One can imagine that in adverse circumstances, such as poor foraging conditions in unseasonable weather, there could be survival value for the species in reducing the number of nestlings. The combination of varied ages of nestlings and fierce aggressiveness of the first to hatch, would thus provide mechanism for adaptiveness to environment, operative not only in regard to food supply, but also to space within the nest hole, if such were limited. This latter point can be a problem of consequence. If woodlands where woodpeckers nest have few suitable nest trees, the birds may be forced to excavate holes in nest trees that are below optimum in size. Not all of the young hatched could possibly reach the full size of fledglings under such circumstances. Hence survival of only two out of four, for example, would insure adequate space for the smaller number. This relation of brood size to adequacy of the nest tree is worthy of continued study. The situation first became apparent to me among Casqued Hornbills (*Bycanistes subcylindricus*) (Kilham, 1956), large hole-nesting birds which always lay two eggs, three or four days apart. Only one of the hatchlings, however, survives. The size of the bird combined with the general destruction of forests in Africa has made it very difficult for this species to find nest holes adequate in size.

While raptors such as eagles are not troubled by living space, they furnish parallels to woodpeckers and hornbills in several respects. As stated by Brown (1955) "eagles lay their eggs several days apart, and since they begin to incubate the first egg at once, the first eaglet hatches several days earlier than the second. As soon as this first eaglet is sufficiently active it starts to attack the other weaker eaglet with a viciousness which is hardly paralleled in the bird world." Brown is unable to explain this situation, in which "one eaglet generally kills the other."

NEST-HOLE COMPETITORS

While most pairs of Hairy Woodpeckers were little disturbed by my standing within 20 m of their nest trees in making observations, a few pairs were more difficult of approach. As shown in examples below, this disturbed behavior appeared to be less a matter of chance variation than of stress carrying over from earlier competition with Starlings.

Pair Y, 1966.—This pair nested on a farm on the outskirts of Lyme and, as seemed inevitable, were dispossessed by Starlings from two successive holes excavated in exposed situations. By 10 May Pair Y was working on its third and successful nest hole. This was located on the under side of an arching limb of a butternut (*Juglans cinerea*), with an entrance pointing toward the ground and partially concealed by leafy branches, a type of location unattractive to Starlings in my experience. Both the male and female of Pair Y were highly excited and difficult to observe. During the incubation period, for example, Male Y made many *speak* notes, pecked on bark, or hastily preened in a quick, nervous, ineffective manner as he moved about the nest tree in the course of frequent change-overs at the nest. Neither he nor his mate were able to remain on the nest for very long. If he came to the entrance, he would bow in and out repeatedly, before swinging inside. His mate, FY, exhibited a similar type of nervousness throughout the nesting period. What was surprising, however, was that in Male Y this nervousness appeared to cease by the time the eggs had hatched, as was shown by his behavior on 5 June. On this occasion two juvenile red squirrels (*Tamiasciurus hudsonicus*) had begun to leave their nest in a limb above the one occupied by the Hairy Woodpeckers and were crawling about the nest tree. FY, when alone, was too excited to take effective action. She would pop into her nest hole, come out, fly to a neighboring tree, return, jerking her body about in exaggerated swings with head feathers bristling and while making almost incessant *chip* notes. Male Y, in contrast, flew quietly to the nest tree at 6 PM. He alighted to one side of the nest, surveyed the two squirrels within only a few feet of where he clung motionless. Then he entered the hole and rested immediately with bill out, as if on guard. As with other pairs of Hairy Woodpeckers observed, this male appeared to have a temperament different from that of the female and one that made him a more effective guardian of the nest in the face of disturbing circumstances.

Pair E, 1965 and 1966.—The territory of this pair remained the same in two successive years. It consisted of a wooded slope of oaks and beeches terminating in an open beaver swamp, providing favorable habitats for flying squirrels and for Starlings respectively.* In 1965 Pair E had a first nest-hole eight m up in the straight bole of a beech tree. Female E entered the hole on 2 May and remained quietly inside as if incubating. On subsequent visits,

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* There are two species of flying squirrels in central New Hampshire (*Glaucomys sabrinus* and *G. volans*) which are much alike in size and color and I made no attempt to differentiate between them under field conditions.

however, I found that the members of Pair E had abandoned this completed excavation, and had made a second one in another beech farther along the same slope. I watched them here without difficulty in June as they carried on nesting activities in quiet fashion. Their young left the nest successfully on 19 June. Subsequent observations indicated that the first nest cavity had been taken over by flying squirrels.

Starlings were the nest-hole competitors of Pair E in 1966. On 10 April, I found the two woodpeckers working on two excavations simultaneously, one in the straight bole of a beech tree, such as flying squirrels had taken over the year before and a second one in a dead elm, standing in the open swamp. Only the latter excavation was completed. I observed copulations of the pair near this cavity on 22 April, but Starlings, of which there were many about the chain of open beaver swamps below, had taken over from the woodpeckers by the end of the month. The woodpeckers returned to the wooded slope and nested in a tall white birch. I found that they had now become timid and excitable to an extent that I could only see them coming to the nest by approaching with care, then hiding at some distance. The behavior of the two birds thus exhibited a change, not only from what it had been earlier in the same spring, but also from that of the nesting period of the year before and one which persisted until the day of nest leaving.

Flying squirrels may slip into a nest hole when it is momentarily unguarded, thus presenting the woodpeckers with a *fait accompli* on their return. There is probably little they can do about it. When Starlings take over a woodpecker's excavation at the moment of its completion, however, it is by a hard, relentless struggle in which the teamwork and aggressiveness of the intruders always wins, or so it would seem from earlier (Kilham, 1960) and present observations, as well as those of Howard (1920), Löhrl (1957), and Shelley (1933) among others. Stickel (1963) has described a rather surprising lack of interest taken by a pair of Hairy Woodpeckers in a flying squirrel occupying the same nest tree.

DISCUSSION

Tinbergen's remark that "only a few workers recognize the amazingly high degree of adaptiveness to be found in numerous behavioural characteristics" (1955) is particularly pertinent to the present studies. The fact that the members of a pair of Hairy Woodpeckers are beautifully adjusted to each other, in most cases, as well as to the woodlands in which they nest is due in large measure, it would seem, to their preceding period of courtship (Kilham, 1966*a*). There are various expressions of this adaptiveness. Among these, one of particular interest to this observer is the separation of nesting duties between the male and female and the question of why these duties should come to be divided in the way they are. Why is the male, for example, the one to spend the night on the nest, whereas the reverse is true among most species of passerine birds? Answers to these and other problems are sought below on a basis of observations made not only on woodpeckers but also on other species of unrelated hole-nesters including the Red- and the White-breasted nuthatches (*Sitta canadensis*) and (*S. carolinensis*) and Casqued Hornbills (Kilham, 1956).

An explanation of the male spending the night in the nest may lie in the fact that the nest-holes of such species as Hairy Woodpeckers are defensible fortresses under usual circumstances, as can be imagined by viewing a male resting inside, facing a predator (see Fig. 2). Its bill in this position becomes an effective weapon, as I have tested with individuals defending their roost hole in an aviary. Hairy Woodpeckers strike fast, hard blows and these should be enough to fend off a raccoon, especially when nest holes are built through living wood as they usually are. That a male may be able to protect its nest under even less favorable conditions is suggested by the account given of Male A′ in 1965. Here a raccoon had been unable to reach the nestlings even though it had greatly enlarged the nest entrance built in rotten wood. A point to be made in these considerations, is that the defending woodpecker has to be aggressive to hold its position. The question then is which member of a pair of woodpeckers would be most likely to exhibit these qualities and strike back at a raccoon if necessary?

Field observations suggest that male Hairy Woodpeckers are not only the more aggressive, as is also true of many species of passerine birds in the breeding season, but also have the temperament needed in the presence of danger. This was well shown by Male Y, for example, when facing red squirrels within a few feet in 1966. Since female Hairy Woodpeckers have appeared to be overly excited and ineffective under such conditions, one may wonder whether males among woodpeckers have not come to replace them on the duty of night-on-the-nest, because of a premium put on their natural aggressiveness in terms of survival of the species. The bill as a weapon within a fortress has thus come to be associated with a behavior pattern making it effective. This is a situation which Waddington (1956) summarizes well in his analogy of the target-following gun.

The distribution of duties among the members of pairs of nuthatches differs markedly from that among woodpeckers, for here it is the females which not only spend nights on nests but also stay there during the day while incubating their eggs alone. The task of the males becomes limited to bringing food to the entrance to feed their mates at least in the earlier stages of nesting. In these connections, one might note that nuthatches do not have defensible nest-holes. Red-breasted Nuthatches usually nest in rotten stubs where their small size and slender bills would offer unlikely protection against a raccoon, which could chew the nest open with little difficulty. White-breasted Nuthatches, on the other hand, have stronger bills and do nest in natural cavities within living trees, which might be likewise considered as natural fortresses. Their preference, however, is for cavities with large entrance holes. It would seem improbable that a nuthatch only partly filling such a hole with its body could fend off as common a predator as the raccoon, which could easily reach in behind it. Nuthatches actually have other ways of protecting their nests without reliance on meeting intruders head on. Their various methods of nest hole defense, including bill-sweeping, are reported elsewhere (Kilham, 1968).

According to Haartman's classification (1957) nuthatches are secondary hole-nesters, since they have spotted eggs and have probably acquired hole-nesting habits more recently than species such as woodpeckers which lay white eggs. Could it be that given more time, nuthatches might also evolve the habit of having males replace females on their nests at night? There would appear to be little indication of evolution in this direction at the present time. It is here that the habits of hornbills appear curiously parallel to those of nuthatches. Hornbills are primary hole-nesters, laying white eggs like those of woodpeckers but the females do all the incubating and rearing of the young, with the male having only a single duty of feeding his mate at the entrance (Kilham, 1956). The female hornbill is within a fortified nest and she has a powerful bill to defend it. This way of breeding depends on the female having a maximum of protection by laying eggs and incubating them without ever leaving the nest. The curious thing is that these habits are not altogether dissimilar from those of present-day nuthatches. The European Nuthatch (*S. europaea*), for example, even walls in its nest entrance, (see Löhrl, 1958) and is the only bird to do so outside of the group of hornbills, as far as I can determine.

The color patterns of the heads of Hairy Woodpeckers are strikingly disruptive if one is facing a roosting or nesting individual with its head drawn-back, ready to strike, from within a darkened entrance. This effect is only partly shown in Figure 2. In dimmer light, the black and white lines radiating from the base of the bill give the appearance of some snake-like creature, especially since the true eyes are concealed in black bands while the front portions of the white bands above them stand out as prominent false ones. This effect is increased when feathers on the top of the head are raised, as they may be in excitement. The sudden enlarging, or changing in shape of the two visible white patches gives an effect not dissimilar to the false eyes revealed on the unfolding of wing spots among certain moths.

Color patterns of hole-nesting birds may have adaptive significance and this may be especially true of black patches concealing eyes. These patches are found in a variety of hole-nesters such as Red-breasted Nuthatches and Chickadees (*Parus atricapillus*) which resemble Hairy Woodpeckers in having nest entrances which exactly fit their head and body size. The black is absent. however, where head and entrance size are disproportionate. White-breasted Nuthatches and Tufted Titmice (*Parus bicolor*) which are without such patches, for example, nest in natural cavities with large irregular entrances. European woodpeckers of the genus *Dendrocopos*, however, present an exception difficult to explain. It would be of considerable interest to know if the species of woodpecker involved are exposed to different types of selection pressures or nest in a different fashion than their American counterparts. Photographs assembled by Blume (1963) help to visualize the appearance and nesting activities of Great Spotted Woodpeckers, which are similar to those described for Hairy Woodpeckers in many respects. The white patches around the eyes, however, are strikingly different.

Nest sanitation is another task performed by males among Hairy as well as Black-backed Woodpeckers (*Picoides arcticus*) (Kilham, 1966*b*) which are two species I have studied at the same time and in a similar manner. One can only hypothesize as to why females of the two species should take a much lesser interest in the performance, when they are in general the more active partner in the care of the young. A nest hole, however, is also a male's roosting hole. He is thus, in a sense, more the true proprietor and hence may be more concerned in keeping it free of fecal contamination.

The almost feverish activity of female Hairy Woodpeckers in foraging for their young, their hyperexcitability, and the soiled, frayed appearance of their plumages as the nesting season progresses, all suggest that the vocalizations of their young are constantly impelling them on their round of duties. Their mates on the other hand, spend much of their time beyond the range of these noises and this may account, in part, for their more leisurely demeanor. Some situations, however, tend to obscure the fact that females are the more attentive of the two partners in care of the young. One of these is the nature of the woodland habitat. If this is unfavorable for local foraging as illustrated in Figure 1, the female may have to travel farther away. beyond earshot of the young, and will visit her nest less often in consequence. A second situation concerns an observer standing too close to a nest hole so that only the male may continue to feed the young while his mate. being the more timid, stays away, a situation which I have also observed for Black-backed Woodpeckers (Kilham, 1966*b*) and which Steinfatt (1937) has described for the Great Spotted Woodpecker.

It is difficult to understand the *Umwelt* of Hairy or other species of woodpecker in any degree of completeness, "The *Umwelt* of any animal" being "only a section carved out of the environment" (von Uexküll, 1957). Figure 1 is an attempt at such a section for a single pair. It shows that different parts of the territority were used by the Hairy Woodpeckers for different purposes over a long breeding period which began when the bare woods was filled with snow in mid-winter and ended when juveniles left their parents in mid-summer. Each phase of a breeding season interrelates with others. In many ways the period of actual nesting is the one of most interest, since it is here that selective pressures exerted by the environment are most acute.

SUMMARY

Observations on Hairy Woodpeckers indicate that males forage away from nests, making fewer feeding visits but with larger prey, whereas females forage within earshot of their young, making frequent visits as well as maintaining general surveillance. Variations in local ecological conditions may upset patterns of nesting behavior. Among varying factors observed were the suitability of the nest tree in terms of security from predation, the closeness of foraging areas, and the presence or absence of such nest-hole competitors as flying squirrels or Starlings. Hairy Woodpeckers are able to adapt to a wide range of conditions. Sexual differences in feeding and agonistic behavior as well as the closeness of pair bonds may account, in part, for this adaptibility.

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CLUTCH SIZES, HATCHABILITY RATES, AND SEX RATIOS OF SPARROW HAWKS IN EASTERN PENNSYLVANIA

Donald S. Heintzelman and Alexander C. Nagy

Within recent years many biologists, including Clement (1965) and Broun (1966), have expressed alarm over the possibility that a rapid and serious decline is occurring in the population of birds of prey of the United States and Canada. If objective evaluations of the population levels of our raptors are to be made, detailed information is required, from many areas, on the success, failure, and rates of reproduction of each raptor species. Relatively little detailed information of this type is currently available. This paper presents data obtained from a study of clutch sizes, hatchability rates, and sex ratios of Sparrow Hawks (*Falco sparverius*) living on Charlex Farm in Albany Township, Berks County, Pennsylvania. From 1959 through 1966, 21 active Sparrow Hawk nests were located on the study area. The positions of 11 of these nests during the years 1960 through 1963 have been shown in a previous paper (Heintzelman, 1964). In order to limit human disturbances at nests, only 14 of the available 21 active nests were studied in varying degrees of thoroughness.

During this investigation, Heintzelman was active in the field from 1959 through 1963, and Nagy was active from 1961 through 1966. Previous papers have been published dealing with the population changes of these Pennsylvania falcons (Nagy, 1963; Heintzelman, 1964), their food habits (Heintzelman, 1964), and their aerial capture of prey (Heintzelman, 1966*b*).

METHODS

Our field methods were routine. All nests were in man-made boxes placed at favorable sites in trees along secondary roads and hedge-fence rows. Nest boxes were assigned permanent letters. Thus box B, for example, was the same box during all years of the investigation. Contents of nest boxes were determined by climbing to a particular box and examining its interior. Eggs were numbered with an ordinary soft lead pencil in the order in which they were deposited. This enabled us to determine the exact egg hatching sequence at certain selected nests. Data were recorded on printed field data forms designed for use on this research project.

EGGS

None of the Sparrow Hawks observed during our investigation made any attempt to construct a nest. Our falcons deposited their eggs directly on the bottoms of nest boxes. Sometimes debris from previous nesting seasons

FIG. 1. Sparrow Hawk nest 1962-B, showing a completed clutch of falcon eggs which were deposited upon materials remaining in the nest box as a result of a previous nesting attempt by Starlings.

littered the bottom of a box, and eggs were placed on this old material. In other cases, we placed sawdust on the bottoms of the newly constructed boxes and eggs were deposited on this. One nest, 1962-B, contained plant material remaining from the nesting activities of a pair of Starlings (*Sturnus vulgaris*), and the Sparrow Hawks deposited their eggs directly upon this material (Fig. 1).

Early in this investigation, Heintzelman attempted to determine the actual date on which the first egg was deposited in each of three nests. The exact date, 23 April 1960, was determined for nest 1960-B. In the literature, Bent (1938:120) lists 86 egg dates for New Jersey and Pennsylvania. For 57 records, they range between 17 April and 3 June, and for 29 records between 28 April and 14 May. Our egg dates (although not necessarily first dates) for the years 1959 through 1963 range from 15 April (1961) to 4 July (1959). The latter date is extremely late and may be the result of a second nesting attempt. It is later than any record which we find recorded in the literature.

TABLE 1
CLUTCH SIZES, HATCHABILITY, AND SEX RATIOS

Nest Number	Number Eggs in Completed Clutch	Number Eggs Hatched	Per Cent Eggs Hatched	Number Females	Number Males
1959-B	2	2	100	1	1
1960-A	5	0*	0	0	0
1960-B	5	5	100	3	2
1961-A	5	5	100	3	2
1961-B	6†	5	83	1	4
1961-E	No Data	No Data	—	2	1
1961-F	3	3	100	1	2
1962-B	4	3	75	0	3
1962-E	3	3	100	0	3
1962-F	6	6	100	4	2
1963-B	5	5	100	3	2
1964-J	5	2	40	2	0
1965-B	5	4	80	3	1
1966-B	1	0	0	0	0
Totals	55	43		23	23

* Eggs disappeared before hatching.
† One egg accidentally destroyed while being numbered.

During 1960 and 1961, Heintzelman attempted to determine the interval between egg laying at three Sparrow Hawk nests. Each nest was visited at least once each day. During the period of oviposition, two and three visits were made each day. In the three nests which were intensively studied, all eggs were deposited on alternate days (that is, if an egg was laid on a Monday the next egg was laid on a Wednesday, etc.) except for nest 1961-B which followed this pattern up to and including the fifth egg. A sixth egg was deposited on a different time schedule, and we were unable to determine exactly when it was deposited. However, we know that it was not laid on a schedule of alternate days. It probably required an extra day which is in disagreement with the findings of Sherman (1913).

The clutch sizes of these nests ranged from one to six eggs (Table 1). The mean clutch size for 13 of these nests was 4.23 eggs. The mean clutch size for 13 Sparrow Hawk nests recorded on Cornell University Nest Cards is 4.69 eggs. In experimental, captive Sparrow Hawks, Willoughby and Cade (1964:77) state that 12 clutches of Sparrow Hawk eggs averaged 3.66. The range was three to four eggs per clutch.

It is difficult to determine the period of incubation of wild birds. Sherman (1913) states that the incubation period for the Sparrow Hawk eggs in the nest which she had under observation was 29 and 30 days, Roest (1957) recorded 30 to 31 days, and Willoughby and Cade (1964) recorded an average of 28.4 days with a range of 27 to 33 days. The eggs in our nest 1960-A were destroyed during the incubation period due to unknown causes. However, in nest 1960-B, the first three eggs hatched on the same day. If we assume that incubation began with the laying of egg number three, then the incubation period for eggs number one, two, and three was 30 days when the day egg number three was deposited is considered as day 0 of incubation. On the other hand, if we follow the method used by Nice (1954) in which the incubation period is calculated from the time that the last egg is deposited to the time that the last egg hatches, where the day the last egg was deposited is considered as day 0, then the incubation period for this last Sparrow Hawk egg (number five) was 28 days. Egg number four in this clutch required 30 days of incubation.

Six eggs formed the full clutch in nest 1961-B. We do not know the exact dates when the first two eggs were deposited, and the sixth egg was broken as it was being numbered. Of the remaining eggs, number three required 35 days of incubation, number four required 33 days, and number five required 32 days. The mean period of incubation, in days, for eight marked eggs from two Sparrow Hawk clutches on Charlex Farm was 30.9 days.

HATCHABILITY RATES AND SEX RATIOS OF NESTLINGS

We were particularly interested in the hatchability rates of our Sparrow Hawk eggs because this species is one which is widely exposed to a variety of agricultural chemicals which might have adverse effects on the species' reproductive capacity. Table 1 shows that the hatchability rate of specific clutches varied greatly, but the over-all rate of the 55 eggs which were deposited was about 78 per cent. This seems to be a fairly high rate in view of the ecology of the species.

On Charlex Farm, the sex ratios of nestling Sparrow Hawks varied from nest to nest and from year to year (Table 1). However, the ratio of males to females during the eight years of this investigation was exactly 50 per cent males to 50 per cent females. In contrast, other studies have generally shown that a population of Sparrow Hawks contains more males than females. Roest (1957:16–18) sampled the sex ratios of Sparrow Hawks during late summer, fall, and winter, and found that 67 (63 per cent) of 107 birds observed were males. Broun (1949:171) states that about 65 per cent of migrant Sparrow Hawks passing Hawk Mountain are males. The sample size is not given. At Bake Oven Knob, Lehigh County, Pennsylvania, observations on migrant hawks were conducted from 1961 through 1966. During this time, 665 Sparrow Hawks passed Bake Oven Knob (Heintzelman and Armentano, 1964; Heintzelman, 1966*a*; Heintzelman, unpublished data).

Sexes were recorded for 177 of these birds, with 107 (60.4 per cent) being males. An exception to this is the population of Sparrow Hawks which Cade studied in southern California (Willoughby and Cade, 1964:78). Of 728 Sparrow Hawks which were identified to sex, 277 were males. This is a ratio of one male to 1.62 females, or about 38 per cent males.

Cade was unable to explain the significance of the difference between the sex ratio composition of the southern California Sparrow Hawk population as compared with other areas where males predominate. Likewise, we do not know why our Charlex Farm population of nestling Sparrow Hawks deviated so far from other populations in respect to sex ratios. Perhaps it was a somewhat atypical population, perhaps female Sparrow Hawks have a higher mortality rate than males over a given period of time, or perhaps there is a difference in the migration pattern of the two sexes.

ACKNOWLEDGMENTS

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NEW LIFE MEMBER

A recent addition to the roster of Life Members of the Wilson Ornithological Society is Mr. J. de Navarre Macomb, Jr. of Chicago, Illinois. Mr. Macomb holds degrees from Princeton University and Illinois Institute of Technology. At present he is Assistant to the Director of Public Relations of Inland Steel Company. He is a member of the AOU, Cooper Society, several Audubon Societies, as well as the Explorer's Club of Chicago, and several professional engineering societies. His interests in ornithology have centered about bird photography and he has specialized in tropical and subtropical birds. The photograph shows him in a Flamingo colony on Bonaire, N.W.I., examining some eggs which having fallen from the nest have become cooked in the high temperatures prevailing there. On his photographic expeditions Mr. Macomb is usually joined by his wife Marjorie.

MAINTENANCE BEHAVIOR OF THE COMMON RHEA

Robert J. Raikow

The many detailed studies of avian behavior which have appeared during the last few decades have concentrated on the carinates, and relatively little attention has been paid to the more primitive ratites. Schneider (1949) studied the Ostrich (*Struthio*) in captivity, and Meise (1963) summarized and evaluated the behavior of the ratites with reference to their phylogeny. One of the least studied ratites is the Common Rhea (*Rhea americana*) of South America. Field studies of this species, such as those of Darwin (1955), Adams (1908), Hudson (1920), and Wetmore (1926) are short, and largely anecdotal. Studies of captive birds are also few in number. Portielje (1925) briefly described some reproductive activities, Brito (1949) provided data on nesting and egg production, and Faust (1960) described the brooding biology of captive rheas.

The present study, undertaken to provide more detailed information about the behavior patterns of the Common Rhea, was carried out during 1962–63 at the Detroit Zoological Park. The subjects were a group of about twelve Common Rheas, half of them of breeding age and half subadult. They were maintained in an outdoor enclosure of approximately two acres, most of it flat except for the edges which sloped downward to prevent escape. The soil was bare in places but most of the area was covered with grass and a few patches of large trees. The area contained a drinking trough and a small, shallow pool of water. Other animals in the enclosure included llamas and Jabirus (*Jabiru mycteria*).

A few observations were also made at the San Diego Zoo. The first part of this study is concerned with the maintenance behavior of the rhea. A subsequent paper will deal with agonistic and sexual behavior.

POSTURES

Standing.—When standing the rhea generally holds one foot about twelve inches behind the other. One leg is directed backward at a slight angle and apparently supports less weight than the other, which is held vertically. Probably the bird is more stable with the feet placed at two points along the longitudinal body axis than at one point (Fig. 1).

Crouching.—In this position the rhea rests its weight on its heels and, to a lesser extent, on its toes. The tibiae are almost vertical and converge downward so that the heels are in contact, or nearly so. The toes are generally held together and pointed downward, resting on the ground, so that the distal ends of the tarsi are lifted an inch or two off the ground (Fig. 2).

Sitting.—Both the knee and heel joints are completely flexed, with the

FIGURE 1

FIGURE 2

FIGURE 3

FIG. 1. Standing position of the Common Rhea.
FIG. 2. Crouching position of the Common Rhea.
FIG. 3. The common sleeping position of the rhea.

tibiae and tarsi being approximately parallel to each other and to the ground. This is the common resting and brooding posture. The neck may be held vertically, folded in an S-curve, or extended straight out on the ground. The crouching position is an intermediate stage in the process of sitting down or standing up, and usually lasts only a few seconds. Occasionally it is maintained for several minutes or more, during which the rhea may preen or dust-bathe.

Sleeping Postures.—Most commonly the rhea sits with its wings folded over its back, its neck folded in a tight S-curve, with the nape resting on the back or on the base of the neck, and its head held horizontally with the bill resting on the throat (Fig. 3). Occasionally the rhea extends its neck, places its bill against the ground, and slides its head forward so that the neck is stretched straight out in front of the body with its entire ventral surface on the ground.

Immelman (1959) noted that the Ostrich (*Struthio*) utilizes the latter position during deep sleep at night. It is possible that the rhea also uses some such position at night, as distinct from that used in light sleep during the day. However, this is uncertain, as rheas were not observed at night during this study.

During light, intermittent sleep, the neck is held up vertically and the eyes are opened and closed every few seconds. This may precede a period of deeper sleep as described above.

LOCOMOTION

With their long, powerful legs rheas are well adapted to roam about on the plains in search of food. Darwin (1955) states that rheas are capable swimmers. In the zoo there is a pool about two and one-half feet deep, in which they might wade, but they were never observed to enter the water.

As the rhea walks there are slight back-and-forth movements of the head in the sagittal plane. Such movements are common among birds and probably give mechanical assistance to the walking movements; they may also aid in visual fixation of the surroundings (Daanje, 1950).

The posture assumed in running varies with the rhea's motivation. In non-social situations, as when a bird runs to be fed by spectators, the neck is held vertically, the wings are raised only slightly above the back, and the plumage is not conspicuously ruffled. In contrast, the running postures assumed during sexual or agonistic activities involve crouching, wing and neck movements, and ruffling of the plumage. These postures will be described in another paper.

FEEDING BEHAVIOR

Feeding Movements.—The rhea spends much of its time wandering about in search of food. The neck is bent downward at the shoulders and curves up again to the head, giving a U-shaped curve. The rhea moves slowly, raising and lowering its head slightly, or looking from side to side. When food is located the bird extends its neck and picks up the object in the tip of its bill, then jerks its head back a few inches, releases the food, and thrusts its head forward again with its bill open so as to catch the food in the back of its mouth. After taking a few bits of food the rhea raises its neck vertically and holds it up for a few seconds, looking from side to side. This probably facilitates swallowing while the bird keeps an eye out for possible danger.

Types of Food.—Rheas in the wild feed primarily on vegetable material such as grasses, seeds, and berries (Stejneger, 1885), as well as insects (Adams, 1908) and snakes and rodents (Peterson, 1963:179). In captivity they feed mainly on a mixture of corn, lettuce, and other items provided by the keepers.

On two occasions rheas were seen feeding on fecal material deposited a few minutes earlier by other rheas. One pecked at the feces, then walked away to wipe its bill in the grass. Bill-wiping is a common activity of passerines, but this was the only time it was observed in a rhea.

Occasionally a rhea will peck at flies on another's folded wings while following it about for several minutes. The other bird ignores this activity.

On two occasions the rheas attempted to catch small birds. Once an adult captured, killed, and ate a Common Grackle (*Quiscalus quiscula*). The capture was not observed. The rhea was first seen holding a struggling grackle in its bill. It then ran about the enclosure, stopping often to rub the grackle vigorously in the dust, sometimes dropping it and picking it up again. This continued even after the grackle had ceased to move. Another rhea tried to pick up the dead bird several times when the first dropped it. but the captor quickly ran off with its prey. During this time the rhea was extremely excited, and glanced about alertly. After about fifteen minutes it swallowed several pieces of meat which it had torn from the grackle by pecking at it and shaking it in the air. Then it picked up the remainder of the grackle's body, and by vigorously shaking its head back and forth, managed to swallow it. When it had finished the rhea walked about slowly, occasionally searching the ground, but did not resume feeding for about five minutes. The entire incident took about 20 minutes.

DRINKING BEHAVIOR

A rhea usually stands while drinking. Gaping slightly, it extends its neck and vigorously dips its bill into the water, pulls it out about six inches. and snaps its head forward again so that the water pulled into the air by the backward movement is caught in the mouth by the forward movement. This "pecking" of water is rapid, and similar in appearance to pecking at food. It is rather different from the more passive dipping movements by which most birds drink, though the rhea may also do this at times.

Quick drinks may be taken at any time but prolonged drinking periods of five to ten minutes most often occur after the rhea has been actively feeding, or soon after it awakens and before a period of prolonged feeding. After drinking the rhea will commonly wander about for a few minutes, often dipping its head as though to feed, but stopping with its bill a few inches above the ground. Apparently the presence of water in the digestive tract inhibits feeding for a few minutes.

TABLE 1
PERCENTAGE OF PREENING IN VARIOUS BODY AREAS IN *RHEA AMERICANA* (276 MOVEMENTS) AND THE AMERICAN GOLDFINCH. (1457 MOVEMENTS)[1]

Area	Rhea	Goldfinch
Wing	43.9	28.0
Head and Neck	14.8	28.0
Breast and Abdomen	10.5	17.0
Sides and Flanks	7.2	4.0
Back and Shoulder	6.9	13.0
Rump and Tail region	2.2	7.0
Feet and Legs	14.5	3.0
Total	100.0	100.0

[1] From Coutlee, 1963.

PREENING BEHAVIOR

Preening Movements.—A rhea may pause briefly to preen while feeding, resting, etc., but prolonged preening bouts are most common when the bird is settling down for a nap or arising from one. The wing is extended laterally to be preened, and although only one can be preened at a time, both wings may be spread simultaneously. The wing is held differently than by most birds. The humerus is extended laterally and the radio-ulna directed downward, so that the elbow points upward and the dorsal wing surface is directed anteriorly. This is also seen in the Wing Display of the male, which is apparently derived from this preening posture. In most other birds the elbow is pointed downward so that the ventral wing surface is directed anteriorly. In preening, the neck is bent back over the humerus and the bill is inserted among the bases of the plumes from the undersurface of the wing, presumably because this surface is bare, while the dorsal wing surface is covered with small feathers which might make it difficult to reach the bases of the larger plumes.

Preening Frequencies.—The rhea preens its wings more frequently than any other part of the body (Table 1). The number of feathers here is large, and many of these are primaries and secondaries whose long shafts are easily disarranged by the wind or by contact with the body. Also, the wings are moved about vigorously during running and display, and also during the preening of body areas which the wings cover when folded. All of these movements lead to disarrangement of the feathers. Wing preening also occurs as a displacement activity during courtship and aggressive behavior.

The neck is the second most frequently preened area, and again, is a region which is apt to be disturbed by frequent movements. The same is true for the tibiae, which are preened almost as often as the neck (13.4 per cent or 92 per cent of all preening movements on the legs). The remaining areas of the body surface, such as the back, rump, and flanks are moved relatively little, or are only sparsely feathered, and therefore require only occasional preening. The rhea occasionally nibbles at its unfeathered tarsus (1.1 per cent), and is probably picking at loose pieces of scaly skin.

Coutlee (1963) has described the preening behavior of the American Goldfinch (*Spinus tristis*), and her data provide an opportunity to compare the preening frequencies of the rhea with those of an advanced, flying species. In both forms the wings and neck received the most preening, but in the rhea the wings were preened three times as often as the neck (Table 1) while in the goldfinch the rate was the same for both areas. Perhaps this can be explained by the relatively loose arrangement of feathers in the rhea, or by the disturbing effect of movement on the loose-vaned ratite feathers as compared to the goldfinch whose feathers, being equipped with barbules, have stiffer, more tightly arranged vanes.

The breast and abdomen received the next highest rate of preening in the goldfinch (17 per cent), while the corresponding area in the rhea was fourth. The rhea preens its tibiae with the third highest frequency, while in the goldfinch the feet and legs receive only three per cent of the preening movements. This difference is probably due to the fact that in the rhea the relatively large tibiae are exposed, while in the goldfinch they are more hidden in the body plumage. Also, the rhea moves its legs much more than the goldfinch during locomotion. In both forms the general body surface was preened relatively infrequently as compared to the neck and limbs.

Thus there is a close similarity in the frequencies with which the various parts of the plumage are preened in birds at opposite ends of the phylogenetic scale. The major difference is correlated with a major difference in morphology and behavior associated with the primary method of locomotion in each form.

DUST-BATHING

Dust-bathing most often occurs at the beginning of a rest period. It may begin while the bird is crouching and continue while it is sitting. The rhea extends its neck and picks up some dust or dirt with its bill from directly in front of it, draws its neck back into an S-curve, and swings its head around to one side to throw the dust onto its wings, which are folded over its back. Sometimes, under what is apparently a less intense drive, the dust is merely dropped beside the rhea instead of onto it. After several minutes of intermittent dust-bathing and preening, the rhea settles down to sleep. It may awaken a few times in the next several minutes to perform a few listless and incomplete movements in which the dust is picked up and then dropped in place, before finally falling asleep.

Dust-bathing is usually regarded as a means of removing external parasites. In many birds, including Ostriches and many passerines, the activity involves extremely vigorous thrashing of dust between and through the feathers, compared to which the rather quiet movements of the rhea appear to be of little value. It may at times function as a displacement activity in relieving restlessness caused by broodiness or mild aggressiveness. It is performed mostly by males, which tend to rest in nest-like concavities in the ground, apparently nests dug by males who subsequently fail to brood. Once a male was observed sitting in this way when another approached and poked about curiously. Ordinarily this would elicit head-forward threat movements from the sitting rhea. This time, however, it merely dust-bathed listlessly, ceasing as soon as the other rhea departed. Such incidents were not uncommon. From the context these ineffective dust-bathing movements appeared as displacement movements, occurring in place of an insufficiently activated agonistic response.

MISCELLANEOUS MAINTENANCE ACTIVITIES

Defecation most often occurs during feeding, and sometimes during drinking.

To scratch its head while standing, the rhea stretches its neck straight forward and downward so that its head is just a few inches above the ground, then extends one leg forward and scratches vertically eight or ten times with its foot.

A standing or walking rhea often jerks its wings slightly, several times in succession. Occasionally it stretches the wing on one side laterally and slightly downward, while simultaneously stretching the other leg straight backward. In addition, there are innumerable slight twitches or jerks of the head, wings, body, and skin, which may occur at any time without interfering with the activity of the moment.

SUMMARY

The behavior of *Rhea americana* was studied at the Detroit Zoological Park. The usual form of locomotion is walking, with running generally restricted to social activities. The common sleeping posture is with the neck in an S-shaped loop, with the bill resting on the throat. The rhea is largely herbivorous, but occasionally captures small birds or other animals. It may sip water in the manner common to most birds, but usually pecks at it. Prolonged drinking inhibits feeding for a few minutes. The frequeney with which various body areas are preened is similar to that in a passerine, *Spinus tristis*. Dust-bathing frequently precedes a period of sleep and may be used as a displacement activity.

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VEGETATION USED FOR NESTING BY THE RED-WINGED BLACKBIRD IN FLORIDA

Jacob F. Stowers, Donald T. Harke, and
Allen R. Stickley, Jr.

The versatility and adaptability of the Red-winged Blackbird (*Agelaius phoeniceus*) in nesting in diverse habitats and different species of vegetation has been noted by several ornithologists (Beer and Tibbitts, 1950; Campbell, 1948; Case and Hewitt, 1963; Meanley and Webb, 1963). Some of these authorities (Campbell, 1948; Meanley and Webb, 1963) have listed the plant species used by Redwings to support nests in certain study areas. However, other than a few species mentioned by Bent (1958) and Sprunt (1954), the multiformity of habitat types and species of vegetation in which the Redwing nests in Florida has not been documented.

The diversity of Redwing nesting sites impressed the authors while collecting Florida Redwings for a U.S. Bureau of Sport Fisheries and Wildlife taxonomic study. During May and June 1966, a list of the various habitat types and species of vegetation used by Redwings for nesting was compiled from breeding areas scattered throughout the state (Fig. 1). These areas included the major habitats in Florida and afford a good indication of the diversity of Redwing nesting in the state.

A total of 30 genera of plants was found to contain Redwing nests in marsh and upland habitats. In Table 1 the vegetation is categorized into eight subdivisions under three main habitat headings: inland freshwater areas, coastal saline areas, and upland field areas. These three general habitats are the primary ecological types that are important Redwing nesting sites in the state. The vegetative types under the habitat subdivisions are listed in descending order of frequency in which they were found to contain Redwing nests.

Common and scientific names in Table 1 are taken from Hotchkiss (1950) and Small (1933). We wish to acknowledge the assistance of Dr. E. S. Ford, Department of Botany, University of Florida, in identifying some of the plants.

RESULTS

Predominant nesting sites used by Redwings are small shrubs or grasses in marshy areas or upland fields. The plant found to be used most frequently by nesting Redwings was buttonbush (*Cephalanthus occidentalis*), a very common shrub indigenous to both shallow and deep freshwater marshes in Florida. Of the 177 nests found, 50 (28 per cent) were in buttonbush, and it

FIG. 1. Areas in Florida where nesting vegetation data were collected during May and June, 1966.

was a major nesting site in three of eight habitat subdivisions listed in Table 1.

Other plants in which Redwings were found to nest were *Baccharis halimifolia* and *Salix* sp.; 25 (14 per cent) of the 177 nests were found in *Baccharis*, while 14 (8 per cent) were in *Salix*. *Baccharis* is commonly found in wet areas along roadsides and in uncultivated fields, and *Salix* is often found in marshy areas, especially in roadside ditches

Redwing nests were found in experimental sweet corn plots in May at the University of Florida Experimental Station at Belle Glade. They occasionally have been found in abandoned cornfields in south Florida, but only after the corn was harvested, and spraying and cultivation had ceased. One three-fourths-acre-plot contained two nests, while 14 (of which nine were active) were found in another. These plots had not been cultivated for at least two weeks before the nests were found. Nests in corn were either supported by two adjacent cornstalks (Fig. 2), or were placed on a single stalk in the angle between the top ear and the stalk.

In south Florida Redwing nests also were found in another cultivated crop, sugarcane. Nesting density did not appear to be high; but because of the large acreage, the crop should be considered as a major nesting site in the Belle Glade area.

TABLE 1
SUPPORTING PLANTS AND HEIGHTS OF 177 NESTS OF THE RED-WINGED BLACKBIRD, LISTED BY HABITAT TYPE[1]

Supporting plant	Number of nests	Height of nests (feet)	
		Average	Range
Inland freshwater areas			
Shallow or deep freshwater marshes			
Buttonbush (*Cephalanthus occidentalis*)	14	3.1	2–5
Silverling (*Baccharis halimifolia*)	5	3.4	1–6
Panicum (*Panicum* sp.)	4	3.0	2–6
Pigweed (*Amaranthus* sp.)	3	2.6	2–3
Willow (*Salix* sp.)	1	3.0	—
Sweet bay (*Magnolia virginiana*)	1	15.0	—
Bitter-weed (*Ambrosia elatior*)	1	3.0	—
Dock (*Rumex* sp.)	1	2.0	—
Deer's tongue (*Trilisa odoratissima*)	1	2.0	—
Open freshwater (edge)			
Buttonbush (*Cephalanthus occidentalis*)	26	2.0	1–3
St. Johnswort (*Hypericum* sp.)	1	2.0	—
Gum (*Nyssa* sp.)	1	6.0	—
Pine, (dead) (*Pinus* sp.)	1	2.0	—
Seasonally flooded basins (roadside ditch)			
Willow (*Salix* sp.)	13	2.5	1–4
Silverling (*Baccharis halimifolia*)	12	4.1	2–8
Buttonbush (*Cephalanthus occidentalis*)	10	2.6	1–3
Napier grass (*Pennisetum purpureum*)	5	1.8	1–2
Ironweed (*Vernonia altissima*)	3	2.3	1–3
Thorny-amaranth (*Amaranthus spinosus*)	2	2.0	—
Waxmyrtle (*Myrica cerifera*)	2	3.0	—
Panicum (*Panicum* sp.)	2	4.0	—
Shining-sumac (*Rhus copallinum*)	1	2.0	—
Black-titi (*Cyrilla racemiflora*)	1	5.0	—
Red maple (*Acer rubrum*)	1	20.0	—
Goldenrod (*Solidago* sp.)	1	2.0	—
Coastal saline areas			
Irregularly flooded salt marshes			
Hightide bush (*Iva frutescens*)	11	3.0	2–4
Silverling (*Baccharis halimifolia*)	1	4.0	—
False willow (*Baccharis angustifolia*)	1	3.0	—
Mangrove swamps			
Black-mangrove (*Avicennia nitida*)	6	6.0	3–8
Red-mangrove (*Rhizophora mangle*)	2	4.0	3–5
Buttonwood (*Conocarpus erecta*)	2	12.0	9–15
Darling-plum (*Reynosia septentrionalis*)	1	4.0	—
Buttonwood and saffron-plum (*Conocarpus erecta* and *Bumelia angustifolia*)	1	6.0	—

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[1] Habitat types from Shaw and Fredine, 1956.
[2] Corn not cultivated at least 2 weeks before nests were found.

TABLE 1 (*cont.*)

Supporting plant	Number of nests	Height of nests (feet)	
		Average	Range
Upland field areas			
Cornfields[2]			
Corn (*Zea mays*)	16	4.0	3–5
Waterhemp (*Acnida cuspidata*)	1	5.0	—
Sugarcane fields			
Sugarcane (*Saccharum* sp.)	4	1.0	1
Fireweed (*Erechtites hieracifolia*)	2	1.5	1–2
Dog-fennel (*Eupatorium* sp.)	1	2.0	—
Thorny-amaranth (*Amaranthus spinosa*)	1	3.0	—
Uncultivated fields			
Silverling (*Baccharis halimifolia*)	6	4.6	2–6
Thorny-amaranth (*Amaranthus spinosa*)	4	1.5	1–3
Saltmarsh fleabane (*Pluchea camphorata*)	2	2.0	2
Shining-sumac (*Rhus copallinum*)	1	4.0	—
Ragweed (*Ambrosia rugelii*)	1	4.0	—

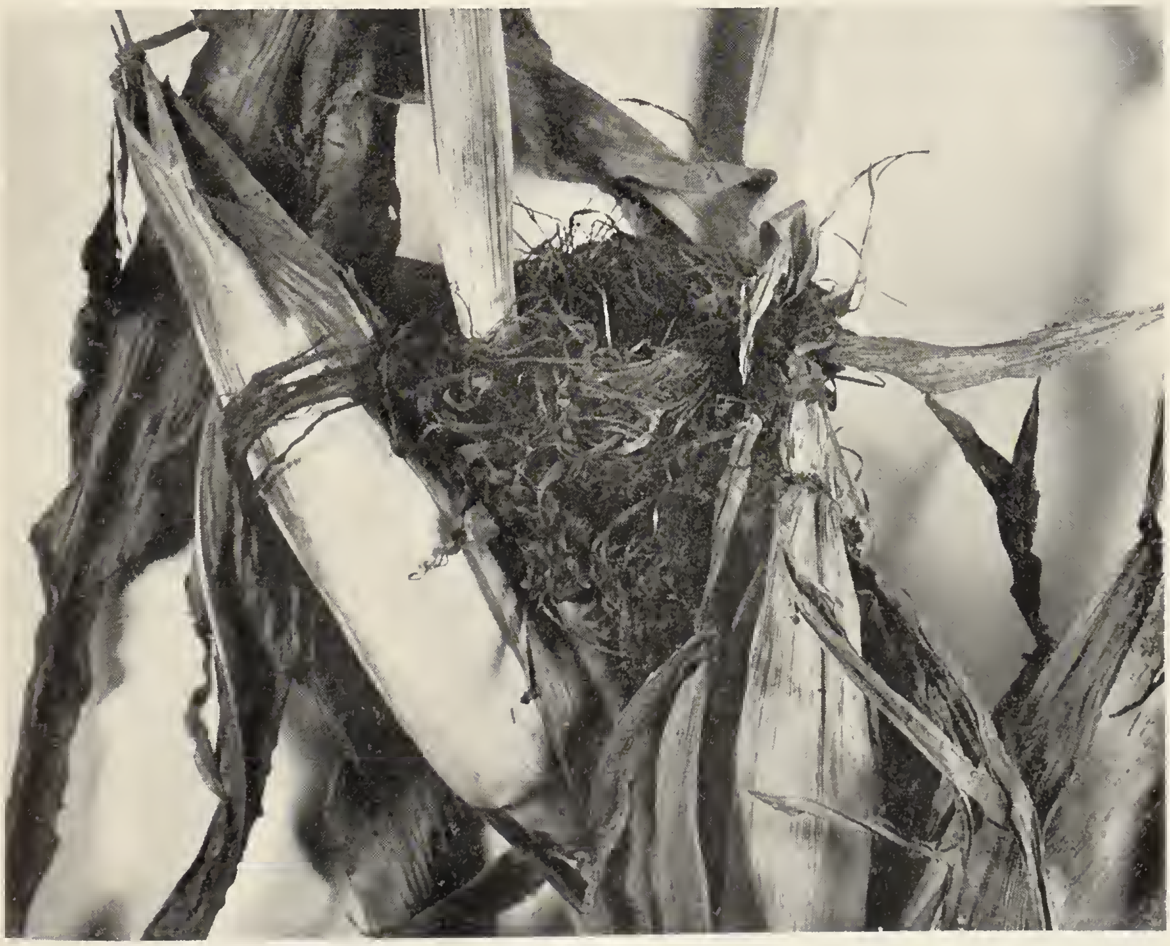

FIG. 2. Redwing nest in sweet corn. Nest is supported by two adjacent stalks. (Photo by Allen R. Stickley, Jr.)

With the multiformity in nesting vegetation there was also a diversity in the height of nests which ranged from one to 20 feet (Table 1). The nest at the 20-foot height was in a red maple (*Acer rubrum*); another nest was 15 feet from ground level in a sweet bay (*Magnolia virginiana*). Both of these nests were located in areas of dense breeding populations. Two other high nests were also found in buttonwood (*Conocarpus erecta*).

SUMMARY

During the breeding season of 1966, as an adjunct to a taxonomic study of Red-winged Blackbirds in Florida, 177 Redwing nests were found. The general habitat types were noted, and the plant species harboring nests were listed.

Redwing nests were found in 30 genera of plants. Buttonbush was the primary choice; it was used to support 50 of the 177 nests. Silverling and willow were the next most often used plants. Nests also were found in other shrubs and trees, in assorted herbs and grasses, and in fields of sweet corn and sugarcane. The great degree of nesting adaptability of the Red-winged Blackbird is attested by the diversity of nesting site selections in several habitats.

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GENERAL NOTES

Additions to the list of birds recorded from Colombia.—The following forms, identified recently in collections made in Colombia by M. A. Carriker, Jr., for the Smithsonian Institution, appear to be first records of occurrence in that Republic.

Coccyzus americanus occidentalis Ridgway.—The eastern race of the Yellow-billed Cuckoo (*C. a. americanus*) is well known as a winter migrant to South America where it is found widely from Colombia and Venezuela to Argentina and Uruguay. The western subspecies *occidentalis* with a total population far less than that of the typical form correspondingly is little known away from its breeding grounds. In the collections made by Carriker I have identified two males, taken at Villa Artiaga, northwestern Antioquia, 27 April 1950, and at Simití, near the Río Magdalena in southern Bolívar, 30 March 1947. From the dates, they may have been in northward migration, and so do not afford wholly definite data on the winter home.

The western race of this species differs from nominate *americanus* in the slightly grayer brown of the entire dorsal surface. The crown especially is grayer. While the western birds as a whole average slightly larger than those of the east, size alone is not a valid criterion for identification as there is broad overlap between the two.

Otus ingens venezolanus Phelps and Phelps, Jr.—A male of the Rufescent Screech Owl taken 12 April 1942, at 6,000 feet (1,830 meters) elevation, above the Indian village of Hiroca on the western slope of Sierra de Perijá, agrees in its color characters with the type of this race, described from a similar elevation on the eastern side of this mountain range in Venezuela. The bird has been known only from a few specimens from Venezuelan Perijá and from Cerro El Teteo, Burgua, Táchira, to the south. The male from above Hiroca has the following measurements: wing 197, tail 103.7 mm.

Chordeiles acutipennis aequatorialis Chapman.—Three males, well-marked examples of this light-colored race of the Lesser Nighthawk, were collected at Unguía in northern Chocó on 9, 12, and 17 March 1950. All were shot during night hunting with head lamps in search of goatsuckers. Carriker noted that the nighthawks were not in breeding condition. The race, described from western Ecuador, is here recorded at a point far distant to the north. Whether it is resident or a wanderer in the northern Chocó is not certain.

Podager nacunda nacunda (Vieillot).—A male Nacunda Nighthawk taken at Camperucho, Magdalena, 10 July 1945, with the wing 239 mm in length, agrees in size with the larger southern race. It represents a migrant away from its breeding grounds far to the south. Two others, male and female, collected at the same time are the smaller northern form *P. n. minor.* The three were shot at night, with the aid of a hunting light. While this is the first report, the typical race should be found as a migrant from the south with some regularity.

The two forms of this species differ in size and slightly in color. Nominate *nacunda*, which breeds from Paraguay and southern Brazil to central Argentina, averages darker, grayer, and less buff on the upper surface. Measurements are as follows: males, wing 236–242, tail 104.3–119.4 mm; females, wing 229–235, tail 101.4–104.5 mm. The subspecies *P. n. minor* is somewhat paler, more buffy above, and is smaller: males, wing 223–230, tail 89.7–101.0 mm; females, wing 204–212, tail 96.6–98.5 mm.

Anthracothorax prevostii viridicordatus Cory.—This race of the Green-breasted Mango, described from the Río Auraré, southeast of Altagracia in northern Zulia, Venezuela, was fairly common in the valley in the Serranía de Macuire at Nazaret, Guajira, northeastern Colombia. There Carriker and I collected three males on 27, 28, and 29 April

1941, and I saw one other on 1 May. They were found feeding at flowers. From 15 to 27 March 1945, Carriker encountered them again near El Conejo in western Guajira, where he took three adult and two immature males, and two females. The race is found locally in northern Venezuela from Zulia through Carabobo and the Distrito Federal to Sucre.

Aulacorhynchus prasinus cognatus (Nelson).—A male and two females of this race of the Emerald Toucanet in the American Museum of Natural History were collected by Harold E. Anthony and D. S. Ball, 30 March and 4 April 1915 at the head of the Río Cutí, Chocó, on the eastern slope of Cerro Tacarcuna. The presence of these blue-throated birds there is not remarkable since they are common on the Panamanian side of the boundary on this mountain. The distinct gray-throated *A. p. griseigularis* is found in the western Andes in Antioquia on the opposite side of the great valley of the Río Atrato.

Veniliornis dignus baezi Chapman.—In 1952 Carriker collected a male of this race of the Yellow-vented Woodpecker at Belén, 21 March, and a female at La Candela 16 May, in the Department of Huila. These two, compared with our series of *V. d. dignus*, are distinguished clearly by heavier dark barring of the breast, the bars being broader and also deeper blackish olive. The race *baezi*, named from northern Ecuador from an area drained by a tributary of the Río Napo, has been known previously only from the Andes in central Ecuador.

Conirostrum leucogenys cyanochrous (Todd), White-eared Conebill.—Four specimens of this honeycreeper taken by Carriker 7 kilometers east of the Río Sardinata, near Petrólea, Norte de Santander, represent this race, described from the Sierra de Mérida, and recorded elsewhere along the eastern base of the Sierra de Perijá in Zulia, Venezuela. Males are distinguishd from typical *C. l. leucogenys* by the lesser extent of the white patch over the auricular region. Females appear darker than those of the typical race, but males while dark are equalled in this by some individuals of the nominate subspecies.

It should be noted that the race *C. l. panamensis*, named by Griscom from Darién, Panamá, with a range extending into northwestern Colombia, is not separable in the more extensive material now available. This name is to be listed as a synonym of *C. l. leucogenys*.—Alexander Wetmore, *Smithsonian Institution, Washington, D.C. 20560, 25 July 1967.*

Copulatory behavior of the Red-necked Grebe on open water.—All species of grebes usually copulate on a nest platform or similar object (Palmer, 1962. Handbook of North American birds. Vol. 1:62–112), but to my knowledge no descriptions of copulation on open water have been reported. It was hypothesized by McAllister and Storer (1963. *Wilson Bull.*, 75:166–173) that copulation on open water is possible only in species with an intromittent organ i.e., the Anatidae.

An apparent copulation on open water by a pair of Red-necked Grebes was observed on 1 May 1965 at Spenard Lake, Anchorage, Alaska. One pair of birds were present on a small bay, approximately 30 yards from the nearest shore. One bird (presumably the male) had more brightly colored plumage than the other. The male was seen to emerge from a dive with a piece of vegetation in its bill. The plant material was then dropped and picked up several times. Suddenly the male seemed to become alert, picked up the weed, and began swimming toward the female, who was approximately thirty feet away. The two came together with necks arched, until their bills appeared to touch. Several times the male turned to the side and then back and again presented the plant material to the female. This activity lasted 15 to 20 seconds. The female then assumed an inviting posture with the neck extended and the fore part of the body lowered in the water so that the basal portion of the neck was nearly submerged, while the cloacal region was quite high. The male swam to the female and placed the plant on her back, near the cloaca. The plant immediately slid into the water but was replaced several times by the male. The female then began to move very slowly forward while maintaining the inviting posture. The male followed, without the weed, and gently nudged the cloacal region of the female with his breast. The male then, with crest up, wings closed, and neck stretched forward, hopped onto the female's back, while the female continued to move forward. Mounting resulted in the female being pushed quite low in the water, with only her head and a small portion of her back above the water. Vigorous paddling with the feet, as indicated by forward movement, probably prevented the female from becoming completely submerged. Mounting lasted three to five seconds and was followed immediately by calling and a bill-touching display. The birds then became quite passive and moved away in a normal swimming attitude. At no time during the above activities was there any sign of aggression.

The bill-touching display has also been described by Johnstone (1953. *Canadian Field-Nat.*, 67:181).—James E. Hemming, *Department of Zoology, University of Montana, Missoula, Montana, 2 August 1966.*

Turkey Vultures found to feed on coconut.—While in Jamaica (23 December 1966 to 3 January 1967), I studied the feeding habits of the Turkey Vulture (*Cathartes aura*) in and around Hector's River, Portland Parish. During that period, over 100 specific instances of the vultures feeding on coconut (*Cocus nucifera*) were recorded.

Because the feeding habits noted above are not normal for the Turkey Vulture, additional evidence was obtained by crop analysis. During a six day period, ten Turkey Vultures were captured using a Bal-chatri trap. Six of the ten regurgitated on being handled and the remaining four were induced to regurgitate by massaging their crops. By visual estimate, the regurgitated material consisted of 90 per cent coconut and 10 per cent rat (*Rattus norvegicus*), a partially digested grasshopper, and some leaves. Meat was used to attract the birds to the trap but none was consumed in this phase of the study. Dead hamsters, white rats, mice, and guinea pigs served as the meat supply.

Bent (1937. Life histories of North American birds of prey, Part I. Dover Publications Reprint, p. 20) mentions that "the birds (Turkey Vultures) have been known to feed on grasshoppers; and they readily eat fish." He summarizes Green's 1927 comments (op. cit., p. 20) as follows: "James Green reports a remarkable observation of finding a flock of 62 vultures, hard pressed for food, feeding on pumpkins." The texture of rotten coconut is similar to that of pumpkin.

Coconut is extremely abundant around the small coastal town of Hector's River. Several small coconut cutting huts supply the vultures with this material through discards. These opened coconuts are found in piles 6 to 8 feet high just outside the huts. The vultures stand on these piles as they feed on the rotting coconuts.

The vultures were given preference tests at the trap location involving a choice between meat, fish, and coconut. The first choice was unanimously meat. After the meat had been eaten or if one bird was occupying the meat successfully, the second choice was the fish. The coconut was touched only in two of the thirteen attempted preference tests. The tests were conducted over an eight day period with gatherings of five to ten vultures at the food site during each test. Coconut, it appears, ranks low on this scale of preference. It does, however, form the bulk of the vultures' diet, because Jamaica has very few native mammals and dead farm animals or fish are usually picked up by human inhabitants before the cautious vultures approach.—Roger C. Crafts, Jr., *Department of Biology, Earlham College, Richmond, Indiana, 16 June 1967.*

The egg tooth of some charadriiform birds.—In their useful reviews, Clark (1961. *Wilson Bull.*, 73:268–278) and Parkes and Clark (1964. *Wilson Bull.*, 76:147–154) have emphasized the need for additional information on the occurrence and structure of egg teeth in some families of birds, particularly the Scolopacidae, and for data on the loss of the egg tooth. Most of the following data were gathered at Churchill, Manitoba, in the summers of 1964, 1965, 1966, and 1967. My research at Churchill was sponsored by the Frank M. Chapman Memorial Fund, The University of Michigan, the National Science Foundation, and the San Diego Society of Natural History.

Charadriidae.—A small deciduous egg tooth occurs on the culmen near the tip of the upper mandible in *Charadrius semipalmatus* and *Pluvialis dominica.* This structure adheres to the culmen until the soft tissues of the bill have dried, at which time it is simply sloughed off. Often the egg tooth is lost by the time the chicks are dry; almost invariably it disappears before the chicks leave the nest. Birds that retain the egg tooth after leaving the nest dislodge it as soon as they begin feeding.

An egg tooth on the tip of the lower mandible has been reported in *Vanellus vanellus* (see Clark, 1961:271). I have found no trace of a similar structure in *C. semipalmatus* chicks that I have removed from the egg or in pipping chicks of *P. dominica.*

Scolopacidae.—Parkes and Clark (1964:150) recorded several apparent variations in the occurrence of egg teeth in this family. Yet, chicks of all the species that I have examined (*Numenius phaeopus*, *Limosa haemastica*, *Totanus flavipes*, *Tringa solitaria*, *Gallinago gallinago*, *Limnodromus griseus*, *Philohela minor*, *Erolia alpina*, *Erolia minutilla*, *Ereunetes pusillus*, *Micropalama himantopus*) are so similar in possessing an egg tooth on both the upper and lower mandibles (Fig. 1) that I suspect the two egg-toothed condition is characteristic of the Scolopacidae. The upper egg tooth caps the entire tip of the rhamphotheca and extends ventrally to the tomium; the cutting surface is a thickened projection from the culmen that points anterodorsally or anteriorly. The egg tooth of the lower mandible consists of a thin, apparently calcareous, sheet that covers the entire tip of the bill. In some individuals this sheet is slightly elevated and thickened at the tip of the bill (e.g., Fig. 1). I do not have sufficient data to determine the extent of inter- or intraspecific variation in this structure.

As in the plovers, sandpiper egg teeth are lost as soon as the bill dries. The thin lower egg tooth is usually sloughed off within a few hours of hatching. Most chicks retain the thicker upper egg tooth for eight to twelve hours after hatching, but I have seen Short-billed Dowitcher (*Limnodromus griseus*) chicks four hours old, whose down was still wet, that had already lost both egg teeth. Six American Woodcock chicks (*Philohela minor*) that I hatched in an incubator lost their egg teeth within 12 to 18 hours of hatching. Wetherbee and Bartlett (1962. *Auk*, 79:117) reported that the woodcock chicks they studied did not lose the egg teeth until two or three days after hatching.

The significance of the double egg tooth in the Scolopacidae deserves further study. In the few species that I have watched hatching, the lower tooth plays no obvious role in rupturing the egg shell or membrane. Rather, its sole function appears to be to protect the delicate tip of the lower mandible. To term this structure an egg tooth may therefore be a misnomer. Since the tip of the upper egg tooth projects anteriorly in

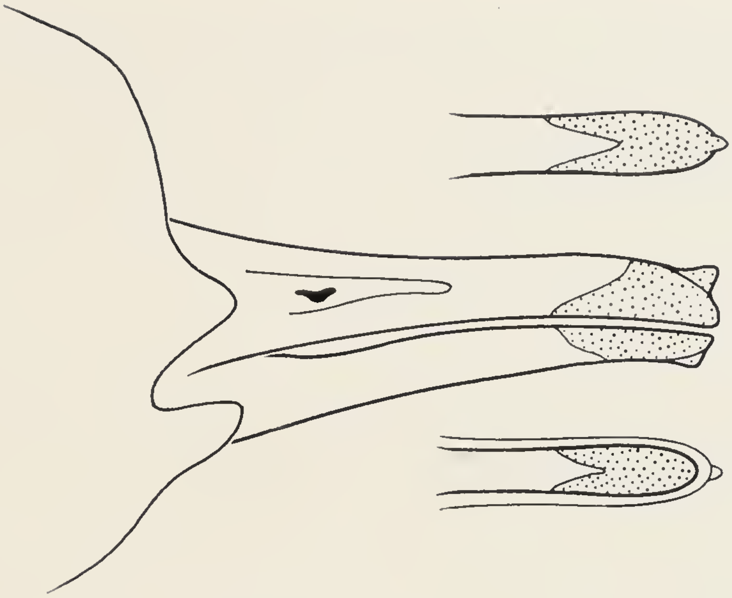

FIG. 1. Egg teeth of *Tringa solitaria.* Drawing made from a chick removed from a pipped egg.

sandpipers, one would expect that many pipping movements are short jabs directed anteriorly. Because the lower and upper mandibles in scolopacids are nearly of equal length, the tips of both must be subjected to constant jarring during the hatching process. Possible damage to the bill tip could be reduced by a protective cap; this may explain the presence of a lower egg tooth in this family, as well as the encompassing of the entire tip of the upper mandible by the base of the upper egg tooth. An egg tooth on the lower mandible also occurs in the Sterninae (Clark, 1961:272) and Phalaropodidae; in these groups the lower and upper mandibles are also relatively straight and of approximately equal length. In gulls, jaegers, and plovers, which lack a lower egg tooth, the tip of the lower mandible may be protected by the overhanging tip of the premaxilla. In these groups the single egg tooth does not extend to the tip of the bill.

Recurvirostridae.—Pipping chicks of *Himantopus himantopus* that I have recently examined have a well-developed egg tooth on both the upper and lower mandibles. Although the tips of these teeth project anteriorly, neither they nor their bases extend as far forward as the tip of the bill. Parkes and Clark (1964) reported the probable occurrence of two egg teeth in *Recurvirostra.*

Phalaropodidae.—Höhn (1967. *Auk,* 84:234) reported that young *Steganopus tricolor* have an egg tooth at the tip of the bill. Two *Lobipes lobatus* chicks that I removed from pipped eggs had egg teeth on both mandibles. The upper egg tooth was like those found in the Scolopacidae. However, the lower egg tooth was much smaller than those of most sandpipers and consisted of a thin, transparent coating that was thickest at the tip of the bill. This egg tooth was lost almost immediately after the chicks hatched.

Stercorariidae.—A pipping chick of *Stercorarius parasiticus* had a typical deciduous egg tooth on the culmen near the tip of the premaxilla; there was no trace of an egg tooth on the lower mandible.

Laridae.—Chicks of *Larus philadelphia* possess a deciduous egg tooth on the culmen only. One chick had lost the egg tooth within 12 hours of hatching; some chicks retain it as much as 24 hours, and perhaps longer.

Study skins of chicks with the egg tooth still attached are needed for many species. Unfortunately, as with the live chicks, the egg teeth rapidly disappear from prepared specimens. Field workers can minimize this loss by briefly dipping the tip of the bill in Duco cement. I have found that specimens preserved in alcohol or formalin will retain the egg teeth until they are subjected to prolonged exposure to air.

I wish to thank Kenneth C. Parkes for commenting on the manuscript and Anne Acevedo for the drawing.—Joseph R. Jehl, Jr., *Natural History Museum, Balboa Park, San Diego, California 92112, 1 August 1967.*

Willet nesting on Long Island, New York.—On 4 June 1966 the writer, together with Frank Bader and John Zarudsky, discovered a Willet's (*Catoptrophorus semipalmatus*) nest on a salt marsh island in the vicinity of Jones Beach State Park, Nassau Co., Long Island, New York. This island is approximately 1.4 miles ENE of the Jones Beach water tower and is due north of the east outlet of Zach's Bay.

The first nest found was situated in a tuft of beach grass (*Ammophila arenaria*) and contained four eggs, one of which was taken for preservation at the American Museum of Natural History. When examined the egg was apparently in an advanced stage of incubation.

On 12 June the three of us, plus Robert Johnson, visited another island about 2.5 miles east of the island on which we found the first Willet's nest. This island also supports a Common Tern (*Sterna hirundo*) colony of 250–300 pairs. While exploring along the edge of the tern colony, a second Willet's nest was discovered, hidden in a clump of beach grass and seaside goldenrod (*Solidago sempervirens*). This nest contained two eggs which felt cold to the touch and were slightly discolored. Possibly the nest had been deserted after heavy rains during the previous week.

On 30 June, the four of us returned to this second island. While scanning the marsh for nestling terns, we came upon an incubating Willet. The bird flushed, exposing a nest with four eggs, one of which was pipped. This nest was located about 80–100 yards east of the second nest.

These three nests represent the only known instances of Willets breeding in New York State, and the only known nesting records in recent years between Nova Scotia and southern New Jersey. John Bull (1964. Birds of the New York area. Harper and Row, New York, p. 199) states that the Willet "has increased considerably in recent years" and cites many June and July records which he labels "stragglers," as "no proof of summering is known." Bull also mentions that the Willet formerly bred on the coast of Massachusetts and very rarely in southern Connecticut. Griscom and Snyder (1955. The birds of Massachusetts. Peabody Museum, Salem, p. 97) state that it last bred there in 1877.

I am indebted to Frank Bader, John Zarudsky, and Robert Johnson for assistance in observations and for providing boat transportation; and to John Bull of the American Museum of Natural History for assistance in the preparation of this note.—Thomas H. Davis, *8613-85 Street, Woodhaven, New York 11421, 30 June 1967.*

The varied diet of the Gull-billed Tern includes a shrub-inhabiting lizard.—On 13 May 1964 we collected two Gull-billed Terns (*Gelochelidon nilotica*) near the new Pinellas Bayway, 2 miles south of Gulfport, Pinellas County, Florida, one of which had an entire green anole (*Anolis carolinensis*) in its gullet. An analysis of the stomach contents of these two birds and of four others collected at the same locality in 1966 is reported here.

Of the two birds collected in 1964 the gullet and stomach of one, SAR 226, male, contained the following green anole matter: one complete and undigested, two intact and partially digested, nine right lower jaws, and one entire tail. The remains of one beetle, and fragments of a crustacean which could not be identified were present also. The stomach of the other, GEW 2423, female, contained an undigested fragment of a green anole tail, three right lower jaws, and the remains of one medium-sized grasshopper.

For the four birds collected on 21 June 1966 the identifiable stomach contents were as follows: SAR 605, male: nine left lower jaws of the anole and two medium-sized grasshoppers; SAR 606, female: two fiddler crabs (*Uca* sp.) and two medium-sized grasshoppers; SAR 607, male: four right lower jaws of the anole and two medium-sized grasshoppers; and SAR 608, female: five fiddler crabs and seven medium-sized grasshoppers.

The birds collected in 1964 were shot over a brushy field which had been disturbed by excavation. The area was predominated by wax myrtle (*Myrica cerifera*) and salt bush (*Baccharis halimifolia*) and included three artificial freshwater ponds containing stands of cat-tail (*Typha* sp.) and one brackish pond. Mangrove (*Avicenna*, *Laguncularia*, and *Rhizophora*) grew in the brackish pond and along the edge of nearby Boca Ciega Bay. In 1964 Gull-billed Terns frequently were seen flying over the shrubs, and approximately three pairs were breeding on a sand fill 1.6 miles away. In 1966 six to ten pairs were presumed breeding 2.2 miles from the brushy field. In 1967, on 22 June, Gary D. Schnell noted about four pairs breeding on the same sand fill, where he saw a large downy chick with a bit of lizard tail protruding from its bill and an adult carrying a frog or toad. In the five years Gull-billed Terns have bred on the sand fills of the Pinellas Bayway (1963–1967) the shrubby field described above has been the closest non-suburban habitat suitable for green anoles.

Nearly all of many sources which mention the food habits of Gull-billed Terns report them feeding on insects, and some authors state that they take no other food. However, so many reports exist of Gull-billed Terns taking other prey that the species should be considered opportunistic in its feeding habits rather than primarily insectivorous. In addition to insects Gull-billed Terns have been reported feeding on earthworms, spiders, various crustaceans, fish, frogs and toads, lizards, small mammals, and the eggs and young of other birds (D. A. Bannerman, 1962. The birds of the British Isles, vol. XI. Oliver and Boyd, London; A. Blanchet, 1925. *Revue Francaise d'Ornithologie*, 9:298–299; P. V. Jensen, 1946. *Dansk. Ornith. Tidsskrift*, 40:95). Some authors state that Gull-billed Terns never dive, but they have been recorded doing so (A. Wetmore, 1926. Observations on the birds of Argentina, Paraguay, Uruguay, and Chile, *U.S. Natl. Mus. Bull.*, 133:136; R. Meinertzhagen, 1954. Birds of Arabia. Oliver and Boyd, London). With future observations of diving it would be interesting to note whether or not the Gull-billed Terns are associated with a feeding flock of typical diving terns.

The most interesting aspect of this record of Gull-billed Terns eating green anoles is that the birds were foraging in a brushy habitat, where the lizards apparently were picked from shrubs. Other reports commenting on inland foraging by this tern indicate that it feeds only over open grassland or agricultural fields, and none recorded the species taking food from brushy areas.—Sievert A. Rohwer, *Museum of Natural History, University of Kansas, Lawrence, Kansas* and Glen E. Woolfenden, *Department of Zoology, University of South Florida, Tampa, Florida, 12 October 1967.*

Phoebe dividing clutch between two nests.—In the course of a study of aspects of the breeding ecology of the Eastern Phoebe (*Sayornis phoebe*) in the area around New Haven, Connecticut, a series of about 50 nests are visited at frequent intervals by myself or an assistant. The nests studied are all under bridges where roads cross streams. In May 1967 a pair of phoebes, in their second nesting attempt, built two nests simultaneously under one of these bridges, and laid three eggs of a clutch in one nest and the other two eggs of the same clutch in the second nest, only just over two feet away but out of sight.

The first nest built at the bridge in 1967 (nest A) was near the south end of the bridge. One egg was laid between 27 and 29 April, but the whole nest had disappeared by 1 May, probably having been removed by humans. In the next ten days building occurred at two sites near the north end of the bridge (Fig. 1). The bridge is supported by 11 transverse girders of H-shaped cross-section and three sets of longitudinal spacing girders (parallel with the stream). The junctions of the transverse girders with the center longitudinal one form a series of corners on each side; the nests were built in two of these corners. Nest B was on the north side of the fourth girder from the north end, on a site which had not been used by phoebes in recent years, but the site of nest C—on the north side of the fifth girder—was occupied in 1966 and some nest material was still present at the time when building started there in 1967. On 11 May nests B and C both had deep cups and fresh green moss on the outside, but nest B was the more substantial.

At 0820 on 13 May nests B and C each contained one egg, and at 1025 on 15 May each contained two eggs. Phoebes nearly always lay one egg each day except early in the season, so that this female was evidently following a normal laying schedule but laying more-or-less alternately in the two nests. On 17 May nest B contained three warm eggs and nest C still had two cold ones. No more eggs were laid, and the clutch thus consisted of five eggs, by far the commonest number for members of this population. On several subsequent visits to the bridge (by A. Harkabus) the eggs in nest B only were found to be warm, and no development occurred in the two eggs in nest C. However, at 1630 on 27 May I found the eggs in nest C very warm and those in nest B slightly above air temperature. Some fishermen were in the area, and may have disturbed the incubating bird a short time previously. A few minutes later I flushed the bird from nest B, but when I remained at the north end of the bridge in order to watch the bird, she approached from the south, fluttering slowly along under the bridge inspecting each of the identical corners; on reaching the nearest nest (C) she settled down on it. Since both nests were on the north sides of transverse girders, a bird approaching from the south could see them only by looking up and back just after passing below them; thus the bird was not within sight of nest B at any time during the course of her approach to nest C. This pattern was repeated twice when I flushed the bird, but when I moved to the south end of the bridge the bird approached from the north and settled on the north nest (B). Although I was not able to keep the bird in view continuously from the time she left one nest until she returned to the other, there was not the slightest hint of the presence of a second female; in fact only one individual was seen on this occasion. Furthermore, at all later visits to the bridge only the eggs in nest B were being incubated. These observations, together with the normal clutch size and laying schedule, as well as the strong territoriality of the species, justify the assumption that only a single pair of birds was involved, even though the individuals were not marked.

Two of the eggs in nest B hatched on 4 June, but the third egg failed to hatch. The

FIGURE 1.

two chicks fledged successfully, leaving the nest between 20 and 22 June, but nest C disappeared between 10 and 14 June. At about the time that the chicks left nest B some new building occurred at the south end of the bridge, and again some material was placed on each of two adjacent girders. Phoebes in this population often start building a new nest, and occasionally even start a new clutch, before the chicks of the previous brood have fledged, but in the present case building was soon discontinued and the final clutch of four eggs was laid in nest B, starting on 24 June.

The events at this bridge provide a dramatic example of the problems sometimes faced by birds nesting in repetitive man-made structures, which have previously been discussed by a number of ornithologists (see, for instance, F. H. Herrick, 1935. "Wild Birds at Home," and J. C. Welty, 1962. "The Life of Birds"). The confusion in the present case apparently resulted from the availability of two separate approach routes (from the two ends of the bridge), each leading to arrival at a different nest from which the other was invisible. One may deduce that during the building period the bird occasionally approached from the south, reached the nest remnant left from the previous year (C), mistook it for the new nest (B) and added material to it. During the laying and incubation periods the nest reached evidently depended on the direction of approach, but towards the end this was probably always from the north when the bird was undisturbed.—N. PHILIP ASHMOLE, *Department of Biology and Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520, 6 July 1967.*

A leucistic Pine Grosbeak.—On 8 November 1965 a large pale finch, alive but weak, was found by a roadside in Ipswich, Essex County, Massachusetts and taken to Mr. and Mrs. Francis Wade of that town. They brought it to me for identification, and this *Pinicola enucleator eschatosus* is now No. 8913 in the Peabody Museum collection. It

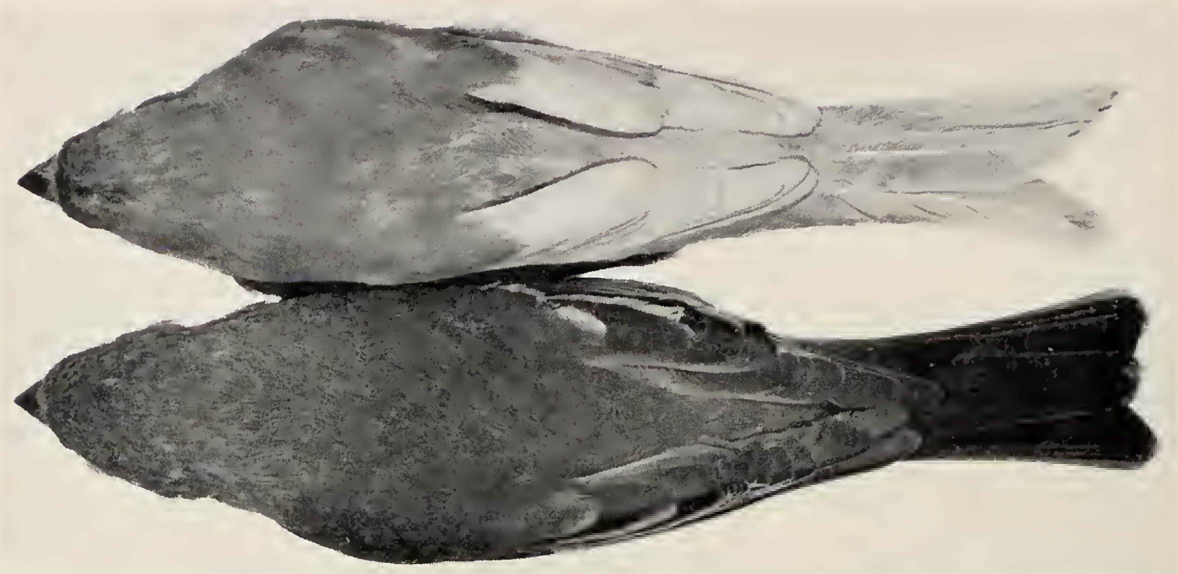

FIG. 1. Leucistic Pine Grosbeak (top) with normal immature male (Peabody Museum No. 8428).

was kept alive under observation for two weeks before being taken for a specimen, and the worn rectrices are the result of its being caged.

In Ridgway's terminology (1912. Color Standards and Color Nomenclature), the bird may be described as follows:

Forehead, auriculars, tinge on hindneck: pale Raw Sienna.

Mantle: pale Wood Brown (near warm Smoke Gray of Villalobos) shading to Yellow Ocher of rump and upper tail coverts.

Wings: in folded wing, general color of primaries and secondaries Pale Olive-Buff (the palest color on the bird). Open wing shows outer edges of vanes this color, inner vanes more nearly pale and grayish Avellaneous.

Tail: folded, the upper side is the general tone of remiges with slight tinge of yellowish. The two central rectrices are nearest a warm Olive-Buff, the others are pale Buffy Brown on the inner and *pale* Olive-Buff (tinged pale Raw Sienna) on the outer vanes. The under sides are pale Fawn, tips palest.

Underparts: throat and breast nearest very pale Avellaneous, sides Avellaneous to pale Cinnamon-Drab, abdomen pale Tilleul Buff.

Bill: culmen Buffy Brown, as are edges of mandible, which is otherwise Pale Pinkish Buff. Legs: Dull Rose color in life.

This appears to be an example of leucism as defined by J. M. Harrison (1964. *In* Thompson, Ed. A new dictionary of birds). Leucism is described as a paleness or varying degrees of dilution of normal pigmentations, and is considered "closely allied" to albinism.

Mr. C. Chandler Ross (in litt.) says that in his research on albinism in birds he did not find a single case of abnormal plumage in the Pine Grosbeak.—DOROTHY E. SNYDER, *Peabody Museum of Salem, Salem, Massachusetts, 10 July 1967.*

The double-scratch in the genus *Passerculus*.—Harrison (1967. *Wilson Bull.*, 79:22–27) recently reviewed the double-scratch in the Holarctic buntings of the subfamily Emberizinae. He recorded the double-scratch in the following nine genera: *Spizella*, *Melospiza*, *Passerella*, *Zonotrichia*, *Amphispiza*, *Arremonops*, *Junco*, *Pipilo*, and *Chlorura*; and suspected it in another seven: *Passerculus*, *Ammodramus*, *Passerherbulus*, *Ammospiza*, *Pooecetes*, *Chondestes*, and *Aimophila*. During the summer of 1964, I made observations of the Savannah Sparrow (*Passerculus sandwichensis*) on Kent Island, New Brunswick, Canada. Savannah Sparrows were noted double-scratching on several occasions. This behavior consisted primarily of a rapid backward kicking of both feet exposing the superficial layer of the substrate. These observations show that the double-scratch positively, though rarely, occurs in the genus *Passerculus*. Harrison has also indicated that the double-scratch is mainly associated with hopping locomotion and is sometimes lost in birds that walk. The Savannah Sparrow is not entirely restricted to a single mode of locomotion since it was often seen both walking and hopping. This probably accounts for the rareness of the double-scratch in this species.

These observations were obtained while working under a National Science Foundation Undergraduate Research Participation grant (G-22902).—Robert E. Gobeil, *Department of Biology, Eastern Michigan University, Ypsilanti, Michigan, 20 June 1967.*

CORRECTION: ON THE INCUBATION PERIOD OF THE SPOTTED SANDPIPER

In calculating the incubation period of the Spotted Sandpiper (*Actitis macularia*) the standard definition (i.e., the time from the laying to the hatching of the last egg) was not used (*Wilson Bull.*, 80:104–5, 1968). In recalculating the incubation period using the standard definition, I find the incubation period to be between 19 and 21 days. This is within the range of 19 to 23 days reported for this species and for its Eurasian relative *Actitis hypoleucos* by other authors (Nelson, *Bird-Banding*, 1:1–13, 1930; Mousley, *Auk*, 54:445–451, 1937; Miller and Miller, *Auk*, 65:558–567, 1948; Preston, *Wilson Bull.*, 63: 43–44, 1951; Witherby et al., *Handbook of British Birds*, Vol. 4, 1940).—Joanna Burger, *Department of Biology, State University College, Buffalo, New York.*

ORNITHOLOGICAL LITERATURE

A Comparative Life-history Study of Four Species of Woodpeckers. By Louise de Kiriline Lawrence. Ornithological Monographs No. 5, American Ornithologists' Union, 1967: 156 pp., 33 graphs and line drawings, 15 tables. $3.75 ($3.00 to members of the AOU).

To study life histories of woodpeckers requires special dedication. Because each pair needs a large area for its support, nests tend to be widely scattered and not easy to find in numbers. The nest holes are often high in dying or dead trees, difficult or dangerous to climb. Even if they can be reached, special procedures are necessary to reveal the contents of the deep, poorly lighted cavities. Despite these obstacles, the woodpeckers, highly specialized anatomically yet remarkably versatile in foraging habits, exert a peculiar fascination on those who become intimately acquainted with them. Among the dedicated students of woodpeckers are Thomas R. Howell, Lawrence Kilham, William E. Ritter, Althea R. Sherman, and James T. Tanner in America; Dieter Blume and Heinz Sielmann in Europe. To this list must now be added the authoress of the present monograph.

This work presents detailed accounts of the general behavior and breeding of four species: Yellow-bellied Sapsucker (*Sphyrapicus varius*), Yellow-shafted Flicker (*Colaptes auratus*), Hairy Woodpecker (*Dendrocopos villosus*), and Downy Woodpecker (*D. pubescens*). All four were studied in the mature, second-growth, mixed forest surrounding Mrs. Lawrence's home at Pimisi Bay in central Ontario, Canada, where in a single day 40 to 50 individuals might visit the feeding station situated amid their territories. Intensive observations of these woodpeckers covered seven of the 25 years during which they were banded and their activities recorded. The banded woodpeckers included 13 sapsuckers, 77 Hairies, and 60 Downies. Some 800 hours of concentrated observation, sometimes continued from dawn to dusk, went into this study.

The Hairy Woodpeckers were resident in the study area throughout the year. Although at first all the Downies were migratory, after the feeding station had been in operation for 14 years some stayed through the winter. The sapsuckers and flickers always migrated. Whether stationary or migratory, all the pairs under observation remained mated for life. This matrimonial fidelity seemed to result not so much from personal attachment of the partners as from faithfulness to the territory; the pair-bond was renewed at the outset of each breeding season. A distinction is made between the "territory" and the "territorial range." The former, a space from about 40 to 100 feet in diameter encircling the potential or actual nest tree, is defended not only against other woodpeckers of the same species but against all intruders which might interfere with the privacy of the resident pair or the rearing of their family. The "range," which includes the "territory," is the much larger area over which the pair forage. From five to eight acres in extent in the sapsucker and the two species of *Dendrocopos*, it has flexible boundaries that are not consistently defended, and it is shared with woodpeckers of other species. Contrary to published statements, Mrs. Lawrence found that the paired male and female of the Hairy Woodpecker normally occupied the same territory throughout the year.

Although the female Downy usually chooses the nest site, in the other three species the male commonly does so; and in all four species he takes the major share in excavation, incubating, feeding the young, and cleaning the nest. He alone stays with the eggs and nestlings during the night, as is usual in the woodpecker family with the exception of a few tropical American species in which the mated pair sleep in the same hole at all times. The nestlings' meals are much more widely spaced in the flicker, which feeds by regurgitation, than in the other three species, which feed directly from the bill. Incubation periods of these three species ranged from 11 to 13 days, which agrees closely with other determinations for the smaller woodpeckers in both the temperate zone and the tropics. Nestling periods were 20 to 22 days in the Downy and from 25 to 30 days in the three larger species. Parents continued to give some food to the fledglings for one to two weeks after nest-leaving in the sapsucker, slightly longer in the Hairy, and up to three weeks in the Downy. This is much shorter than the period of parental care in certain tropical woodpeckers, which may continue for two months after nest-leaving, as in the small Golden-naped Woodpecker (*Tripsurus chrysauchen*) of southern Central America.

These are only a few of the highlights in a report in which a wealth of detailed information and thoughtful interpretation is presented in a clear, forceful style pleasant to read.—Alexander F. Skutch.

Mechanisms of Animal Behavior. By Peter Marler and William J. Hamilton III. John Wiley and Sons, Inc., New York, 1966: 6½ × 9¼ in., xi + 771 pp., many figs. $14.95.

The last decade has seen a tremendous growth of interest in the field of animal behavior. One direct consequence of this has been the addition of courses in behavior to the zoology curricula of numerous colleges and universities. The development of such courses, however, has been hampered by a lack of suitable texts to supplement lecture material. With the appearance of Marler and Hamilton's book, "Mechanisms of Animal Behavior," this deficiency has been at least partially overcome.

The book is an outgrowth of lectures given in Peter Marler's animal behavior course at the University of California, Berkeley. It covers an extremely broad spectrum of topics which, for convenience, can be grouped into four major sections. The first stresses the interplay of exogenous and endogenous factors in controlling various behaviors. This theme, which recurs throughout the book, is well illustrated in chapters discussing the control of locomotor activities, feeding and drinking behavior, circadian rhythms, and reproductive cycles.

This is followed by a group of chapters concerned with external stimuli and stimulus filtering. The basic principles of ethology laid forth by Lorenz in "Der Kumpan in der Umwelt des Vogels" (1935. *J. Ornithol.* 83:137–213; 289–413) and Tinbergen in "The Study of Instinct" (1951) are presented here along with numerous examples of the use of chemical, visual, and auditory cues in inter- and intraspecific communication. Throughout this discussion, appropriate emphasis is placed upon the adaptive function or selective advantage of different behavior patterns. In addition, considerable space is devoted to problems of sensory physiology and psychological studies of visual and auditory preception. This integrated approach allows valuable correlations to be made between the capabilities and limitations of various sensory receptors on the one hand, and the types of stimuli effective in different communication systems on the other.

The next four chapters discuss experimental studies of animal orientation and navigation. This section, contributed by W. J. Hamilton III, provides a fairly complete, up-to-date review of such topics as gravity detection in invertebrates, echolocation by bats, and celestial, topographic, and possible magnetic orientation by birds.

The ontogeny of behavior is the subject of the final section of the book. Marler goes into considerable detail in these chapters describing the behavior of embryos as well as the role of early experience upon the development of both sensory mechanisms and motor patterns. And interwoven throughout this discussion is the now-familiar theme of the integration of intrinsic and extrinsic factors in controlling animal behavior.

As indicated by this quick résumé, the subject material covered in Mechanisms of Animal Behavior is extremely broad. There are, in this author's opinion, only two serious omissions (both of which are acknowledged by Marler and Hamilton). First, there is little discussion of the evolution of behavior and the use of comparative behavioral data in studies of phylogeny and systematics. And second, certain important aspects of behavioral ecology receive no mention. Specifically, I would have expected coverage of J. H. Crook's pioneering studies on the adaptability of avian social systems to different habitat-types, as well as some discussion of Wynne-Edwards' controversial hypotheses of the possible functioning of social behavior in population regulation. But these omissions notwithstanding, this book is without doubt the most comprehensive behavior text compiled to date.

Within each chapter, the authors have selected numerous important studies which they discuss in considerable detail, and it is through elaboration on these examples that an understanding of general behavioral concepts emerges. In many instances the experimental techniques employed in these studies are presented, and the original graphs and tables of data are reproduced frequently in their entirety. No attempts are made to impose specific viewpoints upon the reader; on controversial or unsolved topics, data supporting various opinions are presented with a minimum of editorial comment. As a result, the student is constantly encouraged to evaluate critically both the experimental design and the results of various studies, and to formulate his own opinions concerning the optimal course for future work in areas of his particular interest.

This method of presentation, which deviates radically from that found in many texts, is excellent for advanced students. It conveys a feeling for the experimental approach to zoological problems as well as providing the necessary broad overview of work which has been, and currently is being, performed in the field of animal behavior. This latter function is performed so well, in fact, that Mechanisms of Animal Behavior is an extremely valuable reference source. The extensive chapter bibliographies alone make this book worth its seemingly exorbitant price.

But the listing of repetitive examples also makes reading somewhat dull and encyclopedic for students whose primary interest does not lie in the area of animal behavior. Since general discussions are infrequent, it is easy to become overburdened with trivial facts and to lose sight of the concepts under consideration. In addition, the text assumes a basic background knowledge of neurophysiology and evolutionary theory. Latin names are often used without adequate "translation" into the vernacular, and ethological and psychological jargon is occasionally employed without sufficient definitions or a glossary being provided.

Although these points do not represent serious detractions, they do cause a decrease in both interest and comprehension among untrained readers. When students in Cornell's course in Neurobiology and Animal Behavior were asked to comment upon this book (which had been adopted as the basic text), the predominant criticism was the overemphasis placed upon specific facts and examples and the de-emphasis upon general behavioral concepts. (One student referred to the book as "Marler's Believe It or Not.")

In large part, however, this criticism merely reflects the recent emergence of animal behavior as an experimental science. We are only now beginning to amass sufficient comparative data to allow formulation of hypotheses concerning general trends in the evolution of behavior. Studies providing experimental confirmation of the adaptive significance of particular behavior patterns are still rare. And the gap between neurophysiological and ethological analyses of behavior remains discouragingly wide.

In summary, Mechanisms of Animal Behavior provides comprehensive coverage of a wide spectrum of topics, making it an extremely useful reference source. For advanced students interested in behavior, it can also serve as an excellent, stimulating text. But for introductory behavior courses aimed at the sophomore or junior levels, the ideal textbook has yet to be written.—STEPHEN T. EMLEN.

THE SPECIES OF BIRDS OF SOUTH AMERICA AND THEIR DISTRIBUTION. By Rudolphe Meyer de Schauensee. The Academy of Natural Sciences of Philadelphia. Distributed by Livingston Publishing Company, Narberth, Pennsylvania, 1966: 6½ × 9¼ in., xvii + 577 pp. $10.00.

The better one is acquainted with the vast avifauna of South America, the more appreciative is he of the tremendous task accomplished by the author and his collaborator in bringing forth this much-needed publication.

Here is a tool needed not only by the museum ornithologist working with neotropical birds, but equally of use to the zoological park curator, the aviculturist, the live bird importer, and the ever-increasing number of persons who pursue the avocation of neotropical bird study.

The museum ornithologist is continually faced with the query from the public as to the availability of a handbook covering all of the birds of South America, the inquirers not realizing that such a "handbook" would have to embrace a formidable array of more than 2,900 species.

Rudolphe Meyer de Schauensee, with the able assistance of Eugene Eisenmann, has come closest to giving us that kind of book. The author lists a total of 22 orders, 95 families, 917 genera, and 2,906 species. The treatment of species, although restricted primarily to the continent proper, does include those species of the peripheral islands with certain exceptions.

By limiting the treatment to the species level and indicating polymorphic species by means of an asterisk, the author presents a believable, but nonetheless impressive, picture of this immense avifauna.

If the reviewer must find fault with this meticulous and exhaustive work, the target would be in the area of common names. It is anticipated that any ten ornithologists, selected at random, will have ten separate views of this controversial subject. The author wisely turned the matter of common names over to the person most experienced in that field. Eugene Eisenmann cut his teeth on the subject of common names of neotropical birds when he published his 1955 work entitled, "The Species of Middle American Birds." Eisenmann handles the common name problem in this present volume most ably and although most of the errors have been picked up in the four published pages of "corrigenda," a few flaws still remain unreported. With "nit picking" not intended, the following minutiae are noted. Considerable emphasis is placed on the use or non-use of the hyphen, yet on page 142 one finds both Screech-Owl and Screech Owl. On page 157 the reader has the choice of Lancebill and Lance-bill. Crane-Hawk (p. 60) and Forest-Falcon (p. 61) are hyphenated, but Bat Falcon (p. 64) is not. Quail-Dove (p. 119) seems to require the hyphen, but Pheasant Cuckoo (p. 139) for reasons obscure to this reviewer, does not. Then on page 157 and obviously a typographer's error, one finds both Metaltail and Metailtail. In some instances distributional directions (p. 216) say "westward" when the author obviously meant "eastward." Somewhere between the printing of the title page and the bindery the title is changed from ". . . *And* Their Distribution" to ". . . *With* Their Distribution." These small errors and inconsistencies in no way detract from the overall excellence of this book, and anyone working with neotropical birds cannot afford to be without it.—KENNETH E. STAGER.

THE BIRDS OF COCOS ISLAND. By Paul Slud. Bulletin of the American Museum of Natural History, Volume 134, pages 261–296, 1967: 7¾ × 10⅝ in., 4 pls. (photos), 1 map. $2.00.

Slud's avifaunal survey of Cocos Island has a two-fold function: to provide a checklist of the birds found on and near the island, and to present an annotated list based largely on his sojourn there for two months in 1963. Cocos Island is part of the volcanic ridge that extends from Costa Rica to the Galápagos Islands. The nearest land mass to this small island (roughly 2 × 5 miles) is about 325 miles to the northeast. In three introductory pages Slud discusses the physiography and climate of Cocos, mentions the previous ornithological work done there, and lists the species of birds that have been recorded from Cocos and surrounding waters. Its sheer-cliffed coast line and dense vegetation are vignetted in four excellent photographs. The remainder of the paper discusses each species.

Of the 77 birds recorded for Cocos and environs, Slud recorded no less than 30 for the first time. Eighteen others were seen by others, but not by Slud. He mentions an additional seven species of doubtful occurrence. One of these, a booby, he saw but could not identify. Six were included by others in writings on their visits to the island or were obviously mislabeled specimens.

Slud's account of the Cocos Island Flycatcher (*Nesotriccus ridgwayi*) show how Rica. As in the larger monograph, his style flows easily. His treatment of the avifauna contributes to the paper's readability, for he prefers an ecological approach to a taxonomic one.

Land birds on islands far from the mainland draw the most attention because of their unexpected occurrence. Until Slud's visit, the endemic race of the Yellow Warbler (*Dendroica petechia*) was the only parulid reported from the island. Slud added nine warblers to the Cocos Island avifauna. Of these the most unexpected included three that inhabit eastern North America: the Prothonotary Warbler (*Protonotaria citrea*), the Prairie Warbler (*Dendroica discolor*), and the Palm Warbler (*D. palmarum*). Slud collected specimens of the latter two species. Other passerines recorded for the first time include the Great Crested Flycatcher (*Myiarchus crinitus*), Bank Swallow (*Riparia riparia*), Wood Thrush (*Hylocichla mustelina*), Red-eyed Vireo (*Vireo olivaceus*), Baltimore Oriole (*Icterus galbula*), and Savannah Sparrow (*Passerculus sandwichensis*). Only twelve species reportedly nest on Cocos, of which four are land birds: three endemic species and a distinct race of the Yellow Warbler. Slud's notes provide an excellent insight into the ecology and behavior of these birds. The Cocos Island Cuckoo (*Coccyzus ferrugineus*) is the least common of the indigenous land birds.

Slud's account of the Cocos Island Flycatcher (*Nesotriccus ridgwayi*) show how natural selection may promote the adaptation of a species to a variety of habitats and niches if it can evolve in an isolated environment—one relatively free of competition and with a number of unfilled niches. Slud encountered the flycatcher everywhere, "from the tide-mark scrub to the mangrove-like tangles behind the beach, up the forested slopes, and along the wooded ridges and ravines. It frequented all vegetational levels, from shrub height to the treetops, and temporarily descended almost to the ground."

Of the four nesting land birds the Cocos Island Finch (*Pinaroloxias inornata*) is the most abundant. Slud provides an excellent account of this bird's versatile feeding behavior. The bird clings, hangs, hops, and creeps in its search for food, using its bill to probe flowers for nectar, to pick or peel off bark for insects, to pry up or turn over fallen leaves, fruit, and sticks, to lever up stones, to pick at fruits and blossoms, to obtain seeds by passing the bill along spikes of grass.

For several reasons future surveys will undoubtedly add to the Cocos Island avifauna: (1) The island visits by ornithologists have been relatively few and usually of short duration; (2) the physiography—steep cliffs along the shore, rugged inland terrain, and dense vegetation—handicap a thorough island-wide search for birds; (3) finally, many of the species found there are so few in number that their occurrence must be accidental. Slud's account includes many species recorded only from observations of a single bird (24 species) or two or three individuals (14 species).

Birds of Cocos Island is an excellent survey of that island's avifauna gleaned from the literature, from the author's visit to the island, and from correspondence with recent visitors to Cocos. A useful contribution to the study of island avifaunas.—D. A. LANCASTER.

ECOLOGY AND FIELD BIOLOGY. By Robert L. Smith. Harper & Row, New York, 1966: 7⅛ × 10¼ in., xiv + 686 pp., many figs. and photos. $12.75.

This book is written as a college text in ecology or field biology at the sophomore or junior level. In a field where half-a-dozen good texts are already in print, Smith's work is noteworthy in that it draws heavily on the literature of wildlife and fisheries biology, including much material from state fish and game agencies. With this orientation, the author hopes that his text will serve as a reference work for amateur naturalists as well as for applied ecologists in forestry, fisheries, wildlife, and sanitary engineering. Smith has been remarkably successful in achieving this goal.

The main body of the book is organized into 27 chapters which give the conceptual background of ecology. The author begins with an excellent discussion of the nature of field biology wherein he traces the evolution of ecology from efforts to quantify natural history. The rest of the text is divided into five parts which begin with a discourse on the ecosystem and the community. Energy flow, material cycling, environmental influences, periodicity in biological clocks, and ecological succession are subjects considered in this basic portion of the book. Subsequent sections include thorough treatments of aquatic and terrestrial habitats, population ecology, natural selection and speciation, and, lastly, three chapters on the behavior of animals.

The balance of the book serves as an instructional guide for the reader or student who wishes a further introduction into the literature of natural history and ecology. These supplementary materials include a list of suggested readings for each chapter of the text, a list of recommended books and guides to identification of flora and fauna by each major group, and a list of journals of interest to field biologists, with a brief description of the special character of each journal. A list of general bibliographies is also presented with annotations. This is followed by five generous appendices which begin with an annotated bibliography of statistical methods and continue with a discussion of a list of environmental measurements followed by plant ecology methods. These appendices serve as an excellent introduction to quantitative methods currently in use in the study of plant communities. Similarly, a fourth appendix summarizes basic techniques for studying animal populations. The last appendix is a description of methods for studying animal behavior which, insofar as I know, is the first compilation of this subject in a text book. The book concludes with an 18-page index.

The format of this text is very attractive. Illustrator Ned Smith has been highly creative in interpreting information from technical publications. Photographs are also used to good effect, and include a high proportion by the author.

Students and naturalists will find that Smith has done a commendable job of assembling literature in rapidly developing fields which have not previously been reviewed in ecological texts. The chapter on periodicity and biological clocks, for example, brings new subject matter into focus. Ornithologists will be especially interested in the chapters dealing with the behavior of animals. Bird behavior inevitably forms the core of much of this material.

In a work of this scope, it would be difficult for the author to avoid errors. While a high degree of readability is one of the merits of this text, some clumsy sentences have escaped the copy editor's notice. For example, on page 380, last sentence of second paragraph: "The cause of this behavior appears to be caused by . . . ." Spot checks of the accuracy of documentation reveal some regrettable lapses. Chapter 10 contains one error, chapter 14, six, and chapter 21, seven errors. Most of these are minor discrepancies; however, in two cases (see page 274—Murphy, 1962, and Kempson, et al., 1963), references cited in the text do not appear in the bibliography. Again these are items which should have been picked up by a careful copy editor.

My last criticism of the book would point to the inadequacies of the index. Nearly two pages of the text are devoted to vole and lemming population biology, yet neither mammal appears in the 18-page index. Clearly, the index should be reworked and bolstered if this book is to serve as an adequate reference in field biology. This feature is not so important in a class text and, perhaps, the author and publishers have chosen to compromise at this point.

Despite these shortcomings, one's overall reaction is high admiration for the deft manner in which the author handles a wide range of complex ecological literature. One is also thoroughly impressed with the prodigious amount of reading and notation which underlies this work. In conclusion, whether one wishes an introduction to ecology or a review of new material in a rapidly growing body of knowledge, Smith's textbook will serve him well and serve him with pleasure.—Daniel Q. Thompson.

PUBLICATION NOTES AND NOTICES

Animal Behavior. By Paul A. Johnsgard. Wm. C. Brown Company, Dubuque, Iowa, 1967: 6 × 9 in., x + 156 pp., 6 figs. Paper covered. $2.25.

This is a succinct review in 13 chapters of the ethological approach to the study of behavior without unduly neglecting the physiological and psychological concepts. Throughout the book the subject of evolution remains the dominating issue, "for the behavior patterns of present-day animals are as much a product of natural selection as is their anatomy." Chapter headings include the following: Ontogeny of Vertebrate Behavior, Social Behavior, Communication, Genetics and Behavior, Ecology and Behavior, Taxonomy and Behavior, Behavioral Evolution and Speciation, and Behavioral Isolating Mechanisms. The book is written essentially for the reader with a background knowledge of general biology and evolutionary theory.

An Introduction to Animal Behavior: Ethology's First Century. By Peter H. Klopfer and Jack P. Hailman. Prentice-Hall, Englewood Cliffs, New Jersey, 1967: 6⅛ × 9½ in., xvi + 297 pp., a few figs. $6.75.

A survey of ethology. From the book's jacket: "Developments in ethology up to the turn of the century are presented first. The next two chapters deal with the approaches of two different schools of thought during the period 1900–50: classical ethology and comparative psychology. Several chapters are then given to discussion of the problems that confront ethology and the disciplines on which ethology relies. The final chapters are a synthesis of the various schools' explanations of animal behavior and are directed to answering the questions of how behavior develops and is controlled in the individual, how behavior changes in a population, and how behavior is maintained in a population.

"In accordance with the authors' aim to provide a comprehensive guide to ethological literature, there are annotated bibliographies and an index of the journals in which the behavior literature appears."

Three of the most recent publications in the series, *Supplements to Behaviour*, that concern birds are listed below. All are still available from the publishers, E. J. Brill, Ltd., Netherlands, and may be purchased directly from them.

The Evolution of Social Organisation and Visual Communication in the Weaver Birds (Ploceinae). By John Hurrell Crook. 1964: viii + 178 pp., 20 pls., 14 figs., 2 diagrams, 10 tables. 30 guilders ($8.40).

Predators and Anti-predator Behaviour of the Black-headed Gull (*Larus ridibundus* L.). By Hans Kruuk. 1964: viii + 129 pp., 18 pls., 23 figs., 30 tables. 36 guilders ($10.08).

Ontogeny of Social Behavior in Burmese Red Junglefowl (*Gallus gallus spadiceus* Bonnaterre). By J. P. Kruijt. 1964: x + 201 pp., 25 figs., 11 tables. 28 guilders ($7.84).

Guide des Oiseaux de la Nouvelle-Calédonie et de ses Dépendances. By Jean Delacour. Illustrated by Lloyd Sanford. Editions Delachaux & Niestlé, Neuchatel, Switzerland, 1966: 5½ × 8¼ in., 172 pp., 4 col. pls., 54 bl. and wh. line drawings. $6.00 (Copies may be purchased from the publisher in Neuchatel, Switzerland, or at 32 rue de Grenelle, 75 Paris VII.)

An invaluable guide to the birds of New Caledonia and the Loyalty Islands. Of the 116 species briefly described and discussed, 18 are illustrated in color and 54 in black and white. New Caledonia's most unique endemic species, the flightless Kagu (*Rhynochetos jubatus*), rates quite appropriately a full color plate and exceptional attention in the text. The author takes every opportunity throughout the book to point up species in dire need of protection and to suggest conservation measures. He also mentions some of the rarities that one should look for especially.

ORNITHOLOGICAL NEWS

The 50th Annual meeting of The Wilson Ornithological Society will be held in Williamsburg, Va. on 1–4 May 1969. Accommodations will be well-booked in Williamsburg at that time of year, and members planning on attending the meeting should make their reservations at least 45 days in advance. A list of motel and other accommodations can be obtained by writing to Secretary Jeff Swinebroad (address on inside front cover) or to the Chairman of the Local Committee on Arrangements, Dr. Mitchell A. Byrd, Department of Biology, College of William and Mary, Williamsburg, Va. The feature of the meeting will be a symposium on present and future research in ornithology arranged and chaired by H. B. Tordoff.

The color plate in this issue of *The Wilson Bulletin* was subsidized by the Oklahoma members of the Wilson Society and many other friends and former students of Dr. George M. Sutton in Oklahoma and nearby states. To these many people and to the organizers of the project, Mrs. Lovie Whitaker and Dr. Robert H. Furman, the Editor and the Society are deeply grateful.

Mr. George R. Mayfield is added to the list of persons who have belonged to the Wilson Society for 50 years.

FROM THE AOU

At its annual meeting in College, Alaska on 18 June 1968 the AOU elected the following officers:

John W. Aldrich, President
Eugene Eisenmann, First Vice-President
Donald S. Farner, Second Vice-President
L. Richard Mewaldt, Secretary
Burt L. Monroe, Jr., Treasurer
Oliver L. Austin, Jr., Editor.

During May through July, Ring-billed Gulls from three Great Lakes colonies were wing-marked with 1.5 inch-diameter "Safeflag" tags. Each colony is represented by a specific color. An attempt is being made to determine the dispersal pattern, migration route, and winter range for each population. Anyone observing such wing-marked gulls is asked to notify Dr. William E. Southern, Department of Biological Sciences, Northern Illinois University 60115. The following information is desired: date, exact location, marker color, and the observer's name. Assistance in this project will be greatly appreciated. Respondents will be provided with information pertaining to colony locations and the date of marking.

WANTED—Live goatsuckers (Caprimulgidae) of each species for research on thermoregulation. For holding and shipping information contact George T. Austin, Dept. of Biological Sciences, Nevada Southern University, Las Vegas 89109.

PROCEEDINGS OF THE FORTY-NINTH ANNUAL MEETING

Jeff Swinebroad, Secretary

The Forty-Ninth Annual Meeting of the Wilson Ornithological Society was held Thursday, 2 May to Sunday, 5 May at the Southern Illinois University, Carbondale, Illinois. The sponsoring organization was the Southern Illinois University. The local chairman was Dr. Harvey I. Fisher. Dr. William George served as acting chairman due to illness of Dr. Fisher. One hundred thirty-five members and guests attended the meeting.

The meeting opened on Thursday night with an informal coffee hour at the Holiday Inn. The Executive Council met that same evening. On Friday morning the Society was welcomed by Dean William McKeefrey (in the absence of President D. W. Morris) and Dr. Paul Morrill. President Aaron Bagg responded, and after the first business meeting the paper session commenced. Saturday, the entire paper sessions were devoted to a symposium on "Regional Bird Books" chaired by Chandler S. Robbins.

A barbecue was held on Friday evening at Little Grassy Lake Outdoor Laboratory, courtesy of the Southern Illinois University.

Dr. William W. H. Gunn was toastmaster for the annual dinner held on Saturday evening. Aaron Bagg presented a presidential address on the historical beginnings of the Wilson Society. A special event of the evening was Dr. Harvey Fisher's film of the Laysan Albatross on Midway Atoll.

Field trips went to local areas on Friday and Saturday mornings and on Sunday to a heron colony near Sikeston, Missouri.

The life and works of the late Robert Ridgway were presented in a special exhibit in the Southern Illinois University Museum.

FIRST BUSINESS SESSION

The first business meeting held 3 May 1968 was presided over by President Aaron M. Bagg. The Secretary, Jeff Swinebroad, summarized the principal actions of the Executive Council meeting from the previous evening as follows:

1. The Council reaffirmed the decision of the 1967 Council to hold the 1969 meeting in Williamsburg, Virginia. Dr. Mitchell Byrd of the College of William and Mary was designated local chairman.
2. The Council empowered the President and Secretary of the Wilson Society to make arrangements for a 1970 meeting in the West with representatives of the Cooper Ornithological Society.
3. The Council, responding to Dr. Thomas Imhof on behalf of the Mobile County Bird Club, tentatively accepted his invitation to hold the 1971 meeting on Dauphin Island, Alabama, on the Gulf Coast.
4. The Council recommended that at the 1969 meeting a symposium be arranged on the current and anticipated research in ornithology, that is, the direction of research from 1969 on. This was deemed particularly suitable as the 1969 meeting will be the 50th stated meeting of the Society, and a look forward as well as back would be appropriate.
5. The Council approved an award of $100.00 for the best paper presented by a predoctoral participant in the 1969 paper sessions.
6. Dr. George A. Hall was selected Editor of the Wilson Bulletin.

7. The Council accepted the reports of the Treasurer, Editor, and the Secretary and the Membership Committee and Library Committee.
8. The Council noted the comments of the chairman of the Student Membership Committee.
9. The Research Grant Committee report was approved. The Council was again able to make two awards this year. The Council recommended that if either of the first two choices was unable to accept the award it be made to the third choice. The recipients are named in the Research Committee Report.
10. The Council by acclamation acknowledged the outstanding contribution of the retiring treasurer, C. Chandler Ross.
11. The Council extended a statement of consideration for the efforts of Dr. William George, who was acting chairman of the local committee in the absence of Dr. Fisher.

The following committee reports were presented by the committee chairman or were filed for inclusion in these proceedings:

Report of the Treasurer for 1967

General Fund

Balance as shown by last report dated 31 December 1966			$9,820.95
RECEIPTS			
Dues			
Active Memberships		$6,645.00	
Sustaining Memberships		690.00	
Subscriptions to *The Wilson Bulletin*		1,906.25	
Sales of back issues of *The Wilson Bulletin*		781.28	
Interest and dividends on savings and investments		2,188.82	
Royalties from microfilming back issues of *The Wilson Bulletin*		40.80	
Society's share of income from Christian J. Goetz Estate		388.88	
Total Receipts		$12,641.03	
DISBURSEMENTS			
The Wilson Bulletin (printing and engraving)	$10,863.11		
Less contributions from authors and publications fund	208.80	$10,654.31	
The Wilson Bulletin (mailing and maintenance of list)		1,552.15	
Editor's expense		142.90	
Secretary's expense		68.77	
Treasurer's expense		531.03	
Canadian discount and transfer fees		16.92	
Annual Meeting expense		227.31	
Committee expense		202.18	
International Council for Bird Protection (1967 dues)		25.00	
Transfer to Research Fund		79.00	
Total Disbursements		$13,499.57	
Excess of Disbursements over Receipts for Year 1967			$ 858.54

GENERAL FUND CASH ACCOUNTS	
Checking Account	$ 1,762.41
Savings Account	7,200.00
Balance in Girard Trust Bank, Philadelphia, Pennsylvania, 31 December 1967	$ 8,962.41

Josselyn Van Tyne Memorial Library Book Fund

Balance as shown by last report dated 31 December 1966	$ 215.35
RECEIPTS	
Sale of duplicates and gifts	42.00
Total Balance and Receipts	$ 257.35
DISBURSEMENTS	
Purchase of Books	138.21
Balance in Girard Trust Bank, Philadelphia, Pennsylvania, 31 December 1967	$ 119.14

Louis Agassiz Fuertes Research Fund

Balance as shown by last report dated 31 December 1966		$ 21.00
RECEIPTS		
Contributions		110.00
Transfer from General Fund		79.00
Total		$ 210.00
DISBURSEMENTS		
Award to D. L. Kalma	$ 100.00	
Award to S. G. Sealy	100.00	
Total Disbursements		200.00
Balance in Girard Trust Bank, Philadelphia, Pennsylvania, 31 December 1967		$ 10.00

Endowment Fund

Balance in Endowment Fund Savings Account as shown by last report 31 December 1966		$ 2,993.63
RECEIPTS		
Life Membership Payments		
Cash	$ 1,137.50	
Patronship Payments		
Cash	350.00	
Legacy from Estate of Christian A. Goetz	16,401.60	
Stock Dividends received (included below)		
20 shares Massachusetts Investors Trust	—	
Total Receipts		17,889.10
		$20,887.73

DISBURSEMENTS

Purchase of securities		
50 shares of International Telephone & Telegraph (Cumulative Preferred 4% Stock)	$ 5,000.00	
$5,000.00 Province of Nova Scotia 6½% Bonds due 1992	4,850.00	
50 shares Long Island Lighting Co. 3¾% Conv. Pfd. Stock	5,150.00	
		15,000.00
Balance in Endowment Fund Savings Account, Girard Trust Bank, Philadelphia, Pennyslvania, 31 December 1967		$ 5,887.73

SECURITIES OWNED (listed at closing prices 31 December 1967)

United States Government Bonds	$ 9,498.88	
Canadian Provincial Bonds	4,600.00	
Corporate Bonds	3,900.00	
Convertible Preferred Stocks	14,567.50	
Common Stocks	15,902.50	
Insurance Stocks	5,145.00	
Investment Trusts	8,140.00	
Total Securities Owned		61,753.88
Total Endowment Fund 31 December 1967		$67,641.61

Respectfully submitted,
C. CHANDLER ROSS, *Treasurer*

Research Grant Committee Report

We received seven applications. Two members of the committee agreed that the best application was that of Leon John Gorski, and the third member of the committee ranked Gorski second. Therefore, we recommend him to you as the winner of the Fuertes grant. Gorski, who is 29, is working on a project entitled "Taxonomy and comparative ecology of sympatric populations of 'Traill's Flycatcher.' " He is working on his Ph.D. at the University of Connecticut; his address is 105 Linwood Street, New Britain, Connecticut 06052.

A close second was James M. Utter, whose project is "A comparison of the ecology of three populations of the mockingbird (*Mimus polyglottos*) differing in geographical location." He is working on the Ph.D. at Rutgers. His address is Department of Biological Sciences, Douglass College, Rutgers, New Brunswick, New Jersey 08903. I do not know whether the Wilson Society ever makes more than one award per year, but I am confident that the committee would agree that Utter would be a worthy condidate for a second award. For the record, the committee's third choice was James Jay Dinsmore, whose project is "The behavior and biology of the Sooty Tern (*Sterna fuscata*)." Dinsmore is working on his doctorate at the University of Florida.

Respectfully submitted,
G. M. SUTTON
VAL NOLAN, JR.
HARRISON B. TORDOFF, *Chairman*

Membership Committee Report

The membership committee consisted of 20 members this year, some of whom were recruited during the year. These committee members helped to secure 48 of our new members. Only four members of the committee were not successful in securing one new member. Board members, not officially a part of this committee secured several new members —Hofslund 7, George Hall 6, others 1, 2, or 3 each.

The procedures followed were similar to past years in that each member of the committee was supplied with names of eight or more prospective members and was asked to write letters of invitation to them. One offered to write extra letters and took 29 names. Others took 18 to 20 names. In this way 240 people were contacted.

Sources of names of prospects were three: (1) a few came from a membership list of the A.O.U., (2) a number were from the registration list for last year's annual meeting, (3) many were of nominees submitted by our members when they paid their annual dues. The third source was the most productive. Sending nomination blanks with annual dues notices was a splendid idea, our members' cooperation supplying us with about 125 names and addresses. All of these were given out to my co-workers. I know that 96 were invited to join and that we added at least 25 new members from among them.

Partly due to this fine list of prospects and partly due to the incentive for Oklahomans to join W.O.S. in order to receive this year's Bulletins dedicated to Dr. George Sutton (17 new members in his state), our additions to the membership list for 1967–68 total 152. Last year the total was 131, the year before 123.

The Treasurer, Chandler Ross, reported on 15 April that 99 members have dropped, 29 resigned and five have died this year. For 1966–67 the loss was 110; for the year before, 127.

A supply of brochures and application-for-membership cards has been brought to this meeting and will be available at the registration desk.

Considering the fact that the Treasurer was hospitalized much of December and January, undergoing surgery twice, and the membership chairman underwent a cholecystectomy in mid-January and was out of circulation for a time, we can report a fairly successful year for the membership committee.

Respectfully submitted,

Hazel Bradley Lory

Library Committee Report

Again, during the year just past, no formal meeting of the committee was called. Affairs of the Josselyn Van Tyne Memorial Library went along for the most part uneventfully.

The most notable change was the replacement of Norman Ford by Sheldon L. Miller. As new Technical Aide in the Bird Division of the Museum of Zoology, the latter has also taken over the handling of all our immediate Library business, and has been busy learning the procedures.

During the year 45 separate gifts were received from 37 donors. Among these were 11 books, 83 journals, 3,518 reprints, 4 translations, 1 pamphlet, 1 dissertation, and 1 monograph.

Another increment of Mrs. Van Tyne's gift of the late Josselyn Van Tyne's library made up 3,300 of the reprints.

Thirty-eight out-of-town loans were made to 22 individuals, involving 118 items.

Of the 117 journals received, 84 were by exchange for *The Wilson Bulletin.*

In general, the foregoing figures show a moderate drop from those of recent years, but it is hoped that this is not significant (perhaps the late date of last year's meeting was a factor in distorting the records). All members having need of books from the library, whether for their research or casual reading, are again urged to make free use of its services.

And members are likewise urged to continue adding to the library's collections. Duplicates are sold to augment the New Book Fund. This, due to stepped-up purchases of items for which a need has been expressed, has dropped to its lowest level in recent years. Any cash donations are of course always welcome.

Respectfully submitted,
WILLIAM A. LUNK, *Chairman*

Student Membership Committee Report

This committee did not function as such in 1967.

Conservation Committee Report

A complete report will appear in a future issue of the *Bulletin.*

Constitutional Amendment

The amendment proposes to change the reading of Article II; Section 3 of the Constitution from:

> "Any member may become a Patron, exempt from further dues, by making a payment into *the* endowment fund of the Society of five hundred dollars ($500.00) or more."

to:

> "Any member may become a Patron, exempt from further dues, by making a payment into *an* endowment fund of the Society of five hundred dollars ($500.00) or more."

The purpose of this change of wording is to permit a member to become a Patron by paying $500.00 or more into *any special* endowment (set up for some specific purpose, such as the Fuertes Research Grant), rather than having to make such payment into *the general* endowment fund, in order to become a Patron.

This proposed amendment was read at the Society's Business Meeting of 16 June 1967. It also was circulated to each member of the Society through publication in *The Wilson Bulletin* for September 1967.

The amendment was approved by a unanimous vote of the members present.

Temporary Committees

The following committees were appointed by President Bagg.

Auditing	*Resolutions*	*Nominating*
Edward L. Altemus	Burt L. Monroe, Jr.	Maurice G. Brooks
John H. Foster	John Bull	Olin Sewall Pettingill, Jr.
Alan Crawford, Jr.	Douglas James, Chairman	Phillips B. Street, Chairman

SECOND BUSINESS MEETING

The second business meeting was convened 4 May 1968 by President Aaron Bagg.

The proposed new members were elected by unanimous vote of the members present.

The following reports were presented:

Editor's Report

Volume 79 (1967) consisted of 489 pages and included 34 papers, 46 notes, and 22 book reviews, as well as other regular features. There was one color plate.

During the year 38 papers and 76 notes have been received. The total is about the same as in other years, but the trend noted last year towards fewer papers and more notes has continued. Approximately 70 per cent of each category have been accepted for publication.

It is anticipated that approximately the same number of pages will appear in Volume 80, although the number of papers printed will be less. The Arctic symposium papers have been running longer than average, and this year the Membership list will take about 36 pages of our quota. It is planned to have one color plate in each issue of Volume 80.

The only problem of the *Bulletin* is the continuing one of too little space and too large a backlog. The time lag on many papers has now exceeded 18 months, although most are appearing in 12–15 months.

Two of the color plates for Volume 80 have been subsidized by a donor. A third is being subsidized by the interested friends of George Sutton in Oklahoma, under the leadership of Mrs. Lovie Whitaker, and Dr. Robert Furman. We still have on hand two color plates slated for Volume 81 which could use subsidization.

It is again my pleasure to acknowledge my debt, and my appreciation of the efforts of the members of the editorial board, and numerous other ornithologists who have helped in many ways.

Respectfully submitted,
George A. Hall

Auditing Committee Report

On 19 April 1968 we examined the books and ledgers of the Treasurer, C. Chandler Ross. All of his records and reports appear complete in every detail and have been prepared in accordance with the best practices of the Treasurer's function. As previously, we commend Mr. Ross for his attention to the duties of his office.

Chandler Ross retires this year as Treasurer of the Society after five years of devotion, under three presidents, to the task he assumed. We cannot overestimate his value to the Society during this period. His careful and precise execution of his duties and the many improvements he initiated will make it much easier for his successor to follow in his footsteps. Chandler Ross will be missed by everyone.

Respectfully submitted,
Alan Crawford, Jr., *Chairman*
Edward L. Altemus
John H. Foster

Resolutions Committee Report

WHEREAS Southern Illinois University as the host to the 49th annual meeting of the Wilson Ornithological Society has graciously provided excellent facilities that were essential to a most successful meeting, has made possible a significant exhibit of works of the illustrious ornithologist Robert Ridgway, and has arranged an enjoyable social evening gathering.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society—its council, officers, and members—do extend a formal and warm-hearted expression of appreciation to President D. W. Morris and his staff for their efforts on our behalf.

WHEREAS the selection of so delightful a meeting place in a fine natural and historical setting coinciding with the Illinois Sesquicentennial, and the selection of such a superior program as we have enjoyed at this meeting indicates much forethought, planning, and hard work by the officers of the Society.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society and more particularly we members and guests who have benefited from these services do, at this 49th annual meeting of the Society held at Carbondale, Illinois, this 4th day of May, 1968, express our gratitude to all officers of the Society, and more particularly to its President and committee members and to Chandler S. Robbins for arranging an informative symposium on Regional Bird Books.

WHEREAS the success of this 49th annual meeting stems from the dedication, careful planning, hard work, and patience of the local committee on arrangements.

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society assembled in annual meeting at Carbondale, Illinois, this 4th day of May, 1968, does express its grateful appreciation to Chairman Harvey I. Fisher, Acting Chairman William G. George, and all the members of their local committee on arrangements for making possible an exceptionally enjoyable meeting.

BE IT FURTHER RESOLVED that the Wilson Ornithological Society, its officers and members, regret that Chairman Harvey I. Fisher was unable to attend the meeting, and expresses its most sincere wishes for a swift recovery from his illness.

Respectfully submitted,
The Resolutions Committee
DOUGLAS JAMES, *Chairman*
BURT L. MONROE, JR.
JOHN BULL

The foregoing reports were accepted.

Election of Officers

The Nominating Committee of the Wilson Ornithological Society presented the following slate for the coming year: President, H. Lewis Batts, Jr.; First Vice-President, William W. H. Gunn; Second Vice-President, Pershing B. Hofslund; Secretary, Jeff Swinebroad; Treasurer, William A. Klamm; Elective Member of the Council (to serve three years), C. Chandler Ross.

The report of the nominating committee was accepted and it was moved that the secretary be instructed to cast a unanimous ballot for the slate. The motion was approved without dissenting vote.

PAPERS SESSIONS

George A. Hall, West Virginia University. *Breeding Range Expansion of the Brown Creeper in the Middle Atlantic States.*

Herman Henry Shugart, Jr., University of Arkansas. *Avian Succession in Northwestern Arkansas.*

Robert D. Burns, Kenyon College. *Dead Elms and Red-headed Woodpeckers.*

S. C. Kendeigh, University of Illinois. *Energy Responses of Birds to Their Thermal Environment.*

Ronnie J. Haynes, University of Arkansas. *The Effect of 100 ppm DDT on Energy Stores in the Bobwhite.*

William George, Southern Illinois University. *Vestigial Claws and Supernumerary Primaries in the Wing of the Bobwhite.*

Brian W. Cain, Texas A&I University. *Growth and Plumage Development of the Black-bellied Tree Duck* (Dendrocygna autumnalis).

David Osborne, Miami University (Oxford). *The Relationship of the Skin Muscle to Feather Display.*

Richard D. Porter and Stanley N. Wiemeyer, Patuxent Wildlife Research Center. *Successful Reproduction in a Colony of Captive American Sparrow Hawks.*

Frances Hamerstrom, Wisconsin Conservation Department. *A Harrier Population Study.*

Charles T. Collins, Fairleigh Dickinson University. *New Information on the Spot-fronted Swift* (Cypseloides cherriei).

Thomas R. Howell, University of California at Los Angeles. *Ecological Analysis of the Avifauna of the Nicaraguan Pine Savanna.*

Walter P. Nickell, Cranbrook Institute of Science. *Nesting Adaptations of the Red-winged Blackbird to Man-changed Environments.*

Larry C. Holcomb, Creighton University. *Red-winged Blackbird Sex Ratios.*

Harvey I. Fisher, Southern Illinois University. *Egg Laying in Laysan Albatross.*

Symposium: Regional Bird Books

Chairman: Chandler S. Robbins, Migratory Bird Populations
Station, Laurel, Maryland.

Introductory remarks by Chairman

Nathaniel R. Whitney, Jr., South Dakota Ornithologists' Union. *Who Needs a State or Provincial Bird Book?*

Allan R. Phillips, Instituto de Biologia, Universidad Nacional Autonoma de Mexico. *The Introductory Chapters.*

Nathaniel R. Whitney, Jr., South Dakota Ornithologists' Union. *Gathering and Acceptance of Records.*

John Bull, Ameriean Musuem of Natural History. *Taxonomic Problems and How One May Handle Them.*

Lester L. Short, Jr., American Museum of Natural History. (Presented by John Bull.) *Treatment of Hybrids in Regional Bird Books.*

George Miksch Sutton, University of Oklahoma. *Illustrations for a State or Provincial Bird Book.*

Douglas James, University of Arkansas. *Mapping Bird Distribution.*

David B. Peakall and Margaret H. Hundley, Research Affiliate, N.A. Nest Record Card Program, Syracuse, and Laboratory of Ornithology, Cornell University. *Summary and Analysis of Nesting Records.*

Thomas A. Imhof, Birmingham, Alabama. *Numerical Data—Its Importance and Treatment.*

Douglas James, University of Arkansas. *The Treatment of Banding Data.*

Nathaniel R. Whitney, Jr., South Dakota Ornithologists' Union. *Importance of Specific Migration Dates.*

John Bull, American Museum of Natural History. *Birds Introduced or of Questionable Origin.*

Allan R. Phillips, Instituto de Biologia, Universidad Nacional Autonoma de Mexico. *Comments on the Bibliography, Gazetteer, and Index.*

Burt L. Monroe, Jr., University of Louisville. *Comments on Regional Bird Books for Latin America.*

George A. Hall, West Virginia University. *Regional Book of the Future.*

ATTENDANCE

One hundred and thirty-five members and guests were registered. Thirty states, two Canadian provinces, and Mexico were represented.

From **Alabama**: 1—*Birmingham*, Thomas A. Imhof.

From **Arkansas**: 6—*Fayetteville*, Ronnie Haynes, Douglas James, Frances James, Henry Shugart; *Magnolia*, Carolyn Brown, J. Rolan Brown.

From **California**: 1—*Los Angeles*, Thomas R. Howell.

From **Colorado**: 2—*Boulder*, Lesley Julian, Paul Julian.

From **Florida**: 1—*Homestead*, John Ogden.

From **Hawaii**: 1—*Honolulu*, Andrew J. Berger.

From **Illinois**: 36—*Apple River*, Terrence Ingram; *Cambria*, Lee Bush; *Carbondale*, Joseph Beatty, Alice Briant, George Fisher, Harvey Fisher, Mildred Fisher, Herbert Koepp-Baker, John Krull, Larry Lamley, Eugene LeFebvre, Karl Schwab, Herman Smith, Hilda Stein, Philip Tedrick, George Waring; *Champaign*, James Karr, S. Charles Kendeigh, Ronald Labisky, Roland Roth, Jerrold Zar; *Cobden*, William George, Mrs. William George; *Cottage Hills*, Harold E. Broadbooks; *Macomb*, Edwin Franks, Evelyn Franks; *Metamora*, Randy Root; *Momence*, William Lory, Mrs. William Lory, Dorothy Sprinkle; *Murphysboro*, Mrs. Harvey Gardiner; *Tolono*, Bill Anderson; *Urbana*, William Francis, Mrs. William Francis, Jean Greenberg, Robert Greenberg.

From **Indiana**: 2—*Hanover*, J. Dan Webster; *Vincennes*, Edward A. Munyer.

From **Iowa**: 2—*Cedar Rapids*, Myra Willis; *Davenport*, Peter Peterson, Jr.

From **Kansas**: 2—*Lawrence*, Gary Schnell, John Tatschl.

From **Kentucky**: 7—*Anchorage*, Mr. and Mrs. Burt L. Monroe, Sr., Burt L. Monroe, Jr., Rose Monroe; *Louisville*, Leonard Brecher, Anne Stamm, Fredrick Stamm.

From **Louisiana**: 4—*Baton Rouge*, George Lowery, Jr., Mrs. George Lowery, Jr.; *Houma*, Eric J. Bienvenu; *Natchitoches*, Hugh Land.

From **Maryland**: 6—*Ellicott City*, Earl Baysinger; *Laurel*, Chandler S. Robbins, Jeff Swinebroad, Aldeen Van Velzen, Willet Van Velzen, Stanley Wiemeyer.

From **Massachusetts**: 2—*Dover*, Aaron M. Bagg, Mrs. Aaron M. Bagg.

From **Michigan**: 8—*Bloomfield Hills*, Billie Nickell, Walter Nickell; *Kalamazoo*, Ray Adams, H. Lewis Batts, Jr., Barry Myers, Arlo Rain, Jerome Wenger; *Royal Oak*, Sergei Postupalsky.

From **Minnesota**: 4—*Duluth*, P. B. Hofslund; *LaMoille*, Pauline Wershoren; *Minneapolis*, Walter Breckenridge, Mrs. Walter Breckenridge.

From **Missouri**: 3—*Cape Girardeau*, Paul Heye; *St. Louis*, Richard A. Anderson, Mrs. Joel Massie.

From **Nebraska**: 4—*Lincoln*, Roger Sharpe, James Tate, Jean Tate; *Omaha*, Larry Holcomb.

From **New Jersey**: 1—*Madison*, Charles T. Collins.

From **New York**: 8—*Buffalo*, Richard Brownstein, Joanna Berger; *Ithaca*, Margaret Hundley, Eleanor Pettingill, Olin Sewall Pettingill, Jr.; *New York City*, Dean Amadon, Mrs. Dean Amadon, John Bull.

From **Ohio**: 8—*Ashtabula*, Howard E. Blakeslee; *Gambier*, Robert D. Burns; *Lakewood*, Nancy Klamm, William Klamm; *Steubenville*, Clinton S. Banks, Elizabeth Banks; *Toledo*, John McCormick, Luella McCormick.

From **Oklahoma**: 5—*Bartlesville*, Sophia Mery, Emma Messerly, Harold Smith, Marjorie Smith; *Norman*, George M. Sutton.

From **Pennsylvania**: 3—*Chester Springs*, Phillips B. Street; *Philadelphia*, C. Chandler Ross; *Pittsburgh*, Kenneth C. Parkes.
From **South Carolina**: 2—*Chester*, Mrs. B. C. Carter, Mrs. C. Stone, Sr.
From **South Dakota**: 1—*Rapid City*, N. R. Whitney.
From **Tennessee**: 4—*Knoxville*, F. J. Alsop, III, J. C. Howell; *Maryville*, Ralph Zaenglein; *Nashville*, Albert F. Ganier.
From **Texas**: 1—*Kleberg*, Brian V. Cain.
From **Washington**: 1—*Bellingham*, Meribeth Riffey.
From **West Virginia**: 1—*Morgantown*, George A. Hall.
From **Wisconsin**: 4—*Plainfield*, Frances Hamerstrom, Frederick Hamerstrom; *Viroqua*, Margarette Morse; *West Bend*, Marvin E. Vore.
From **Ontario, Canada**: 2—*London*, Anne Dow, Douglas Dow; *Toronto*, William W. H. Gunn.
From **New Brunswick, Canada**: 1—*Sackville*, A. J. Erskine.
From **Mexico**: 1—*Distrito Federal*, Allan R. Phillips.
Address Unknown: 1—James Pringle.

NEW LIFE MEMBER

Mr. Jay M. Sheppard of Long Beach, California has recently become a Life Member of The Wilson Ornithological Society. A graduate of Miami (Ohio) University, Mr. Sheppard is currently a graduate student at California State College, Long Beach. He is engaged in a life history study of the LeConte's Thrasher as a research problem for a master's thesis. Mr. Sheppard is a member of the AOU, the Cooper Society, Inland and Western Bird-Banding Associations and is a charter member of the Ornithological Society of Vietnam. His ornithological interests include making population counts, banding, as well as photography and sound-recording, and he has published several papers in these fields. His biological interests extend to the collection of tiger beetles as well as the study of mammalogy and herpetology.

THE WILSON ORNITHOLOGICAL SOCIETY

OFFICERS, 1968

ADDITIONAL MEMBERS OF THE EXECUTIVE COUNCIL

Elective Members

Past Presidents

Trustees

EDITORIAL STAFF OF *THE WILSON BULLETIN*

Editor

Editorial Advisory Board

Ornithological Literature Editor

CHAIRMEN OF COMMITTEES

MEMBERSHIP ROLL*

Patrons

Bagg, Aaron Moore, Farm St., Dover, Mass. 02023 ... 1948
Batts, H(enry) Lewis, Jr., 2315 Angling Rd., Kalamazoo, Mich. 49001 ... 1946
Booth, Mrs. Robert V. D., 1085 Bank St., Painesville, Ohio 44077 ... 1949
Brecher, Leonard C(harles), 1900 Spring Dr., Louisville, Ky. 40205 ... 1939
Carnes, Mrs. Herbert E., 11801 Sundown Ave., Scottsdale, Ariz. 85251 ... 1944
Chalif, Edward Louis, 37 Barnesdale Rd., Short Hills, N.J. 07078 ... 1947
Desmond, Thomas C(harles), Box 670, Newburgh, N.Y. 12553 ... 1942
Emerson, Guy, 221 W. 57 St., New York, N.Y. 10019 ... 1938
Foster, John H(awley), P.O. Box 204, Wayne, Pa. 19087 ... 1952
Furman, Dr. Robert H(oward), 1300 Bedford Dr., Oklahoma City, Okla. 73116 ... 1955
Goelet, Robert G., 425 Park Ave., New York, N.Y. 10022 ... 1953
Hamilton, Charles W(hiteley), 2639 Fenwood Rd., Houston, Texas 77005 ... 1948
Mills, Herbert H., Arrowhead Farms, Rt. 3, Bridgeton, N.J. 08302 ... 1951
Peterson, Roger Tory, Neck Road, Old Lyme, Conn. 06371 ... 1942
Root, Oscar M(itchell), Brooks School, North Andover, Mass. 01845 ... 1940
Speirs, Mrs. Doris Huestis, "Cobble Hill," Rt. 2, Pickering, Ont., Canada ... 1936
Spofford, Walter R(ichardson) II, Dept. of Anatomy, State Univ. of New York, Syracuse, N.Y. 13210 ... 1942
Stettenheim, Peter, U.S.D.A. Avian Anatomy Project, Dept. of Poultry Science, Michigan State Univ., East Lansing, Mich. 48823 ... 1951
Stokes, Allen W., Dept. of Wildlife Management U.S.A.C., Logan, Utah 84321 ... 1950
Stoner, Mrs. Lillian C., 399 State St., Albany, N.Y. 12210 ... 1945
Street, Phillips B(orden), Rt. 1, Chester Springs, Pa. 19425 ... 1946
Sutton, George Miksch, Dept. of Zoology, Univ. of Oklahoma, Norman, Okla. 73069 ... 1920
Strong, Reuben M. ... Founder, Deceased
Swetland, David W., Daisy Hill, Chagrin Falls, Ohio 44022 ... 1953
Tucker, Mrs. Carll, Penwood, Mt. Kisco, N.Y. 10549 ... 1928
Van Tyne, Josselyn ... Deceased

† Life Member * Sustaining Member Others—Active Members

Abbott, Waldo G., Museum of Natural History, Santa Barbara, Calif. 93101 ... 1963
Able, Kenneth P(aul), Museum of Natural Science, Louisiana State Univ., Baton Rouge, La. 70803 ... 1965
Abraitys, Vincent, Sergeantsville, N.J. 08557 ... 1956
Acton, James Frederick, 3327 W. 4th Ave., Spokane, Wash. 99204 ... 1967
Adams, C(lyde) Bruce, 40 Summit Rd., Riverside, Conn. 06878 ... 1959
Adams, Heman P(urdy), 7 Highland Ave., Maplewood, N.J. 07040 ... 1959
Adams, William Hensley, Jr., 4004 Moss Dr., Annandale, Va. 22003 ... 1951
Adelson, Richard Henry, Remsen's Lane, Rt. 1, Oyster Bay, L. I., N.Y. 11771 ... 1938
Agey, H. Norton, 908 Ave. H, N.E., Winter Haven, Fla. 33880 ... 1960
Ahlquist, Jon Edward, Peabody Museum of Natural History, Yale Univ., New Haven, Conn. 06520 ... 1959
Aiholzer, John R., Jr., 4138 S. 51st St., Milwaukee, Wisc. 53220 ... 1965
Aikens, Mrs. Edna May, 1132 Caddell Lane, Norman, Okla. 73069 ... 1968
Aldrich, John Warren, 6324 Lakeview Dr., Falls Church, Va. 22041 ... 1930
Alexander, Burton J(erome), 2712 Southern Ave., Baltimore, Md. 21214 ... 1966
*Alexander, Donald C(hild), 16 Pleasant St., Nahant, Mass. 01908 ... 1937
Alexander, Gordon, 765 14th St., Boulder, Colo. 80302 ... 1936
Allen, Arthur W(esley), 561 Eastern Blvd., Watertown, N.Y. 13601 ... 1959
Allen, Ted T(ipton), Dept. of Biology, Jacksonville Univ., Jacksonville, Fla. 32211 ... 1958
Allyn, (Paul) Richard, 709 Myers Bldg., Springfield, Ill. 62701 ... 1944
Almon, Lois, 4909 S. Auburn Dr., Mobile, Ala. 36618 ... 1958
†Altemus, Edward Lee, Lafayette Ave., Fort Washington, Pa. 19034 ... 1954
Altsheler, Mrs. Yancey R(oberts), 800 S. 4th St., Apt. 2606, Louisville, Ky. 40203 ... 1954
Amadon, Dean, American Museum of Natural History, Central Park West at 79th

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* Correct to 31 July 1968.

St., New York, N.Y. 10024 1935
*Amason, Carl R(aymond), Rt. 3, Box 180, El Dorado, Ark. 71730 1968
†Ames, Peter L., 6 Washington Lane, Orinda, Calif. 94563 1963
Ammon, Walter L., 2607 Kessler, Midland, Texas 79702 1958
Anaka, William, Box 62, Gorlitz, Saskatchewan, Canada 1957
*Andersen, Elmer L(ee), 2230 W. Hoyt Ave., St. Paul, Minn. 55108 1965
Anderson, Anders H(arold), 3221 E. Kleindale Rd., Tucson, Ariz. 85716 1937
Anderson, Bertin W(alter), Dept. of Zoology, Univ. of South Dakota, Vermillion, S.D. 57069 1966
Anderson, Donald L., Dept. of Biology, Leidy Hall, Univ. of Pennsylvania, Philadelphia, Pa. 19104 1965
Anderson, Eugene N(ewton), Jr., Anthropology Dept., Univ. of California, Riverside, Calif. 92502 1964
Anderson, H(arrison) Cook, 289 Pleasant St., Laconia, N.H. 03246 1968
Anderson, John M., W. Cornwell Rd., Sharon, Conn. 06069 1938
Anderson, Mrs. Paul T., Wolf Trap Hill, Rt. 2, Winter St., Middleborough, Mass. 02346 1961
Anderson, Richard A(rlen), 1147 Greenshaw Dr., St. Louis, Mo. 63137 1963
Anderson, R. K., Conservation Dept., Wisconsin State Univ., Stevens Point, Wisc. 54481 1962
Anderson, Ted R(oger), 625 Meadowridge, Kirkwood, Mo. 63122 1964
Anderson, William L(eno), 279 Natural Resources Bldg., Urbana, Ill. 61801 1965
Andrle, Robert F., Buffalo Museum of Science, Humboldt Park, Buffalo, N.Y. 14211 1966
Anthes, Clarence A(lvin), 707 N. Moreland Blvd., Waukesha, Wisc. 53186 1939
Arbib, Robert S(imeon), Jr., 226 Guion Dr., Mamaroneck, N.Y. 10543 1947
Armington, Sven, Klarbarsvagen 11, Lidingo 3, Sweden 1948
Armistead, Henry T., 39 E. Benezet St., Philadelphia, Pa. 19118 1966
Arner, Dale H., Mississippi State Univ., Dept. of Zoology, State College, Miss. 39762 1964
†Arnold, Elting, 4914 Dorset Ave., Chevy Chase, Md. 20015 1941
Arnold, Keith A(lan), Dept. of Wildlife Sciences, Texas A. & M. Univ., College Station, Texas 77843 1960
Arny, Samuel A., 7608 Hamlet St., Springfield, Va. 22151 1947
Atkeson, Thomas Zephaniah, P.O. Box 1643, Decatur, Ala. 35602 1953
*Atwater, Miss Doris E(velene), 180 Brattle St., Arlington, Mass. 02174 1968
Austin, Mrs. Dorothy Allen, 4811 Old Orchard Trail, Orchard Lake, Mich. 48034 1967
Austin, George T(rout), 5077 Eugene Ave., Las Vegas, Nev. 89108 1966
Austin, Mrs. Harold C., 1116 Mandana Rd., Oakland, Calif. 94610 1950
Austin, Oliver L(uther), Jr., Florida State Museum, Gainesville, Fla. 32601 1930
Avent, Carrie Pillow, Minter City, Miss. 38944 1959
Axtell, Harold H., Buffalo Museum of Science, Humboldt Park, Buffalo, N.Y. 14211 1950

Baepler, Donald H(enry), Nevada Southern Univ., Las Vegas, Nev. 89109 1955
Bailey, Alfred Marshall, Denver Museum of Natural History, City Park, Denver, Colo. 80206 1928
Bailey, Mrs. Harold H(arris), Rockbridge Alum Springs Biological Laboratory, Rt. 2, Goshen, Va. 24439 1963
Bailey, Karl D., 5275 Adams Rd., Bloomfield Hills, Mich. 48013 1963
Bailey, W. Wallace, Director, Wellfleet Bay Wildlife Sanctuary, Box 236, South Wellfleet, Mass. 02663 1959
Baillie, James Little, Royal Ontario Museum, Dept. of Ornithology, 100 Queen's Park, Toronto, Ont., Canada 1939
Baird, James, 69 Hartwell Ave., Littleton, Mass. 01460 1954
Baird, John C(harles), 169 Norfolk Dr., Fredericton, N.B., Canada 1967
Baird, Mrs. Thomas C., 1200 Cobb Blvd., Kankakee, Ill. 60901 1968
†Baker, Bernard W., Rt. 1, Judson Rd., Spring Lake, Mich. 49456 1938
Baker, Paul S(eaman), 113 Copse Way, Williamsburg, Va. 23185 1946
Baker, Rollin Harold, The Museum, Michigan State Univ., East Lansing, Mich. 48823 1938
Baker, William C(alvin), 559 Euclid St., Salem, Ohio 44460 1931
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CONTENTS

SOLITARY SANDPIPER *(Tringa solitaria)* chick, one day old. Painted direct from life 22 June 1968, by Walter J. Breckenridge. The egg, taken when fresh from a nest in central Alberta, was hatched in an incubator in Minnesota.

VOCALIZATIONS OF THE GREEN AND SOLITARY SANDPIPERS*

Lewis W. Oring

Few areas of ornithology have developed as rapidly and along such exciting lines as the study of avian vocalizations. Logically much of this work deals with passeriforms, for it is on members of this group that many of the classical discussions of song variation, development, function, and learning were based. Certain non-passeriform groups, too, are well suited for studies of this type. Within the Scolopacidae, for example, the relative dependence upon vocal as compared to visual communication varies enormously. The Ruff (*Philomachus pugnax*) is silent (Hogan-Warburg, 1966) and the Buff-breasted Sandpiper (*Tryngites subruficollis*) nearly so (Oring, 1964). Though other calidridines are more vocal, as a group their repertoires are simple. Ferdinand (1966) described spectrographically the complex vocalizations of the Great Snipe (*Capella media*). Similar analysis of the Long-billed Curlew (*Numenius americanus*) (Forsythe, 1967), as well as written descriptions of Black-tailed Godwit (*Limosa limosa*) (Lind, 1961), and Greenshank (*Tringa nebularia*) (Nethersole-Thompson, 1951) vocalizations, indicate that tringines too have well developed vocal powers. Indeed, personal observations of the Eurasian Curlew (*N. arquata*) indicate that its aerial advertisement song may be more complex and variable than the songs of many passerines. The intra-familial voice range described above, coupled with relatively simple voice structures, would seem to make the scolopacids excellent subjects for evolutionary studies of avian sounds.

Of approximately 85 scolopacid species, only the Solitary Sandpiper (*Tringa solitaria*) of the Nearctic and Green Sandpiper (*T. ochropus*) of the Palearctic lay their eggs in arboreal nests—most often in old nests of certain passeriform species. Both *solitaria* and *ochropus* are solitary and territorial the year-round. The Wood Sandpiper (*T. glareola*), a close relative of *solitaria* and *ochropus*, is wide-ranging, utilizes a variety of nest-sites including old arboreal nests, is gregarious to some extent all year, and shows relatively little intraspecific aggression. A comparative behavioral study of this threesome was begun in an effort to gain insight into the adaptive significance of behavioral patterns as shown by close relatives occupying similar (*ochropus* vs. *solitaria*) and markedly different (*ochropus* and *solitaria* vs. *glareola*) ecological niches. This report attempts to describe and compare the vocalizations of *T. ochropus* and *T. solitaria*. Stress has been placed upon the evolution of these vocalizations, their adaptive significance, and their integration into the overall be-

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* Dedicated to George Miksch Sutton who not only helped make this study a reality, but suggested it in the first place.

havioral schemes of the two species. Subsequent papers will deal with other aspects of behavior as well as with the phylogeny of *Tringa.*

STUDY AREA AND METHODS

From 5 April to 3 July 1966 and 10 March to 1 July 1967, I studied *T. ochropus* in Halle-Hunneberg National Forest, 10 km east of Vänersborg, Västergötland. Sweden. One brood was reared in captivity from 31 May to 3 July 1966 after which it was observed in the Copenhagen zoo. *T. solitaria* was studied from 4 to 13 May 1968 at Riding Mountain National Park. Wasagaming, Manitoba, Canada and from 15 to 26 May 1968 at Crimson Lake Provincial Park, 12 km NW of Rocky Mountain House, Alberta, Canada. One clutch, transported from Alberta to Minnesota, later hatched. These young were studied from 21 June to 12 July.

The vocalizations of five pairs of both species were tape recorded with a Uher 514 microphone and 4000L tape recorder at the speed of 19 cm/second. Recordings of adults were aided by the use of a ½m fiberglass parabola. Vocalizations were played at normal speed into a Kay Electric Co. Sonograph machine, model 6061A, at H-S and wide band settings. Frequency measurements were made from narrow band sonograms. Vocalizations were played back in the field through a National Panasonic portable radio model RF885L. Sexes were differentiated only during copulation and egg-laying. In a few cases, members of a pair differed in minor morphological features adequate for individual recognition.

DESCRIPTION OF VOCALIZATIONS

I have called those vocalizations which seem dependent upon sex hormones. which are relatively complex in structure and long in duration, and which function in territory establishment and defense, songs. All others have been designated as calls. An attempt to classify the vocalizations of *T. ochropus* and *T. solitaria* has led to the recognition of two song types and five types of calls in both species. Only those adult vocalizations restricted to the reproductive season appear to be highly stereotyped. Three types of calls are arbitrarily recognized for *ochropus* juveniles and six for *solitaria* young. In the juvenile calls of both species frequency continuums exist with modes apparent at the extremes. All of the juvenile calls of *ochropus* are about 1.5 kc higher than those of *solitaria* whereas the reverse is true of adult vocalizations. Though songs and "epigamic" calls were more frequently given by males than females, all adult vocalizations of both species were given by both sexes. No consistent individual variation was noted. Though some variation in frequency and duration of vocalizations can be accounted for by chance, my data indicate that frequency is influenced by volume (and hence syringeal tension)—louder sounds being slightly higher in pitch. A

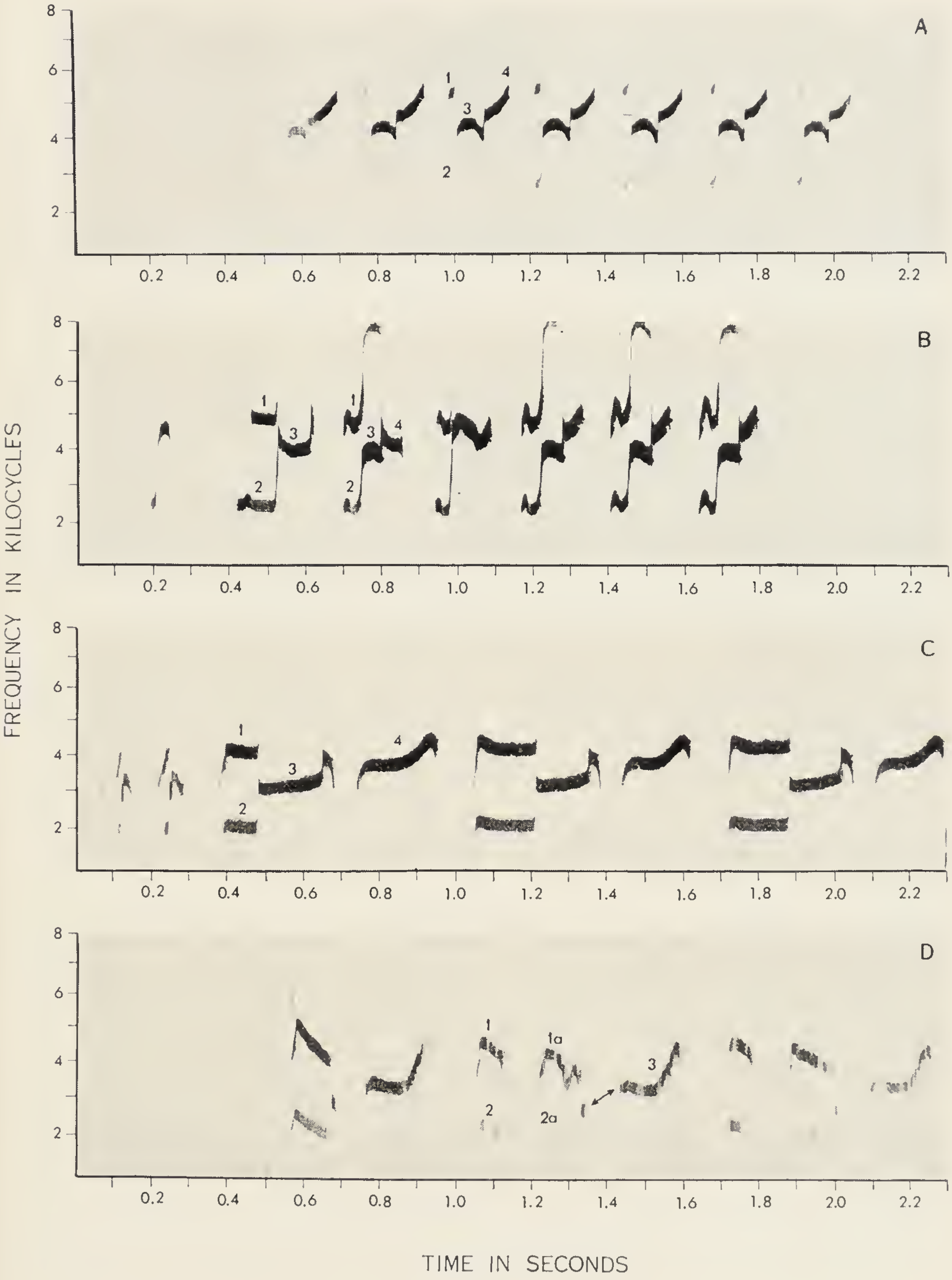

FIG. 1. Spectrograms of *T. solitaria* (A–B) and *T. ochropus* (C–D) songs: A, simple "Type II"; B, first unit is simple "Type I"; second and third are intermediate, and the remainder complex "Type II"; C, "Type I"; and D, "Type II" (first unit aberrant). Numbers above song units pertain to individual subunits referred to in the text. Subunits with like numbers are probably homologous.

TABLE 1
NUMERICAL DESCRIPTION OF ADULT VOCALIZATIONS*

	Tringa solitaria			*T. ochropus*		
	N	x̄	S.D.	N	x̄	S.D.
Song "Type I"						
Duration in seconds	12	0.189	±0.026	44	0.652	±0.076
Interval to preceding song unit in seconds	2	0.140	±0.028	37	0.110	±0.019
Maximum frequency in kc/sec	10	5.51	±0.35	44	4.57	±0.15
Minimum frequency in kc/sec	12	2.38	±0.11	44	1.80	±0.15
Song "Type II"						
Duration in seconds	78	0.159	±0.016	21	0.601	±0.054
Interval to preceding song unit in seconds	76	0.065	±0.009	16	0.121	±0.018
Maximum frequency in kc/sec	78	5.90	±0.30	21	4.89	±0.16
Minimum frequency in kc/sec	78	2.55	±0.41	21	1.80	±0.05
"Contact" call						
Duration in seconds	9	0.045	±0.005	45	0.043	±0.012
Interval to preceding call in seconds	8	0.188	±0.042	35	0.146	±0.042
Average frequency in kc/sec	9	4.70	±0.26	45	3.28	±0.23
"Alarm-attack" call						
Duration in seconds	23	0.050	±0.002	33	0.082	±0.018
Interval to preceding call in seconds	18	0.366	±0.126	23	0.072	±0.041
Average frequency in kc/sec	23	4.77	±0.06	33	3.22	±0.18
"Epigamic" chatter call						
Duration in seconds	26	0.046	±0.021	47	0.078	±0.017
Interval to preceding call in seconds	16	0.088	±0.074	35	0.074	±0.036
Average frequency in kc/sec	26	4.65	±0.23	47	3.18	±0.25
"Epigamic" long whistle call						
Duration in seconds	24	0.083	±0.010	22	0.279	±0.057
Interval to preceding call in seconds	17	0.117	±0.014	21	0.091	±0.019
Maximum frequency in kc/sec	24	5.32	±0.44	22	4.34	±0.24
Minimum frequency in kc/sec	24	3.12	±0.66	22	2.40	±0.27
Average frequency in kc/sec	24	4.81	±0.15			
"Alarm-flee" call						
Duration in seconds	15	0.097	±0.028	30	0.152	±0.051
Interval to preceding call in seconds	10	0.144	±0.061	22	0.093	±0.011
Maximum frequency in kc/sec	15	5.17	±0.24	30	4.50	±0.20
Minimum frequency in kc/sec	15	4.23	±0.12	30	3.08	±0.10

* N = sample size; x̄ = mean; S.D. = standard deviation. Average frequencies were determined subjectively by estimation of the frequency on either side of which lies half of the sound energy.

similar phenomenon occurs in man as volume and laryngeal tension increase. In *Tringa*, higher frequencies seem to be lost when recordings are made over great distances as Marler and Isaac (1960) suggested might be the case in their study of the Chipping Sparrow (*Spizella passerina*). I did not investigate geographical variation.

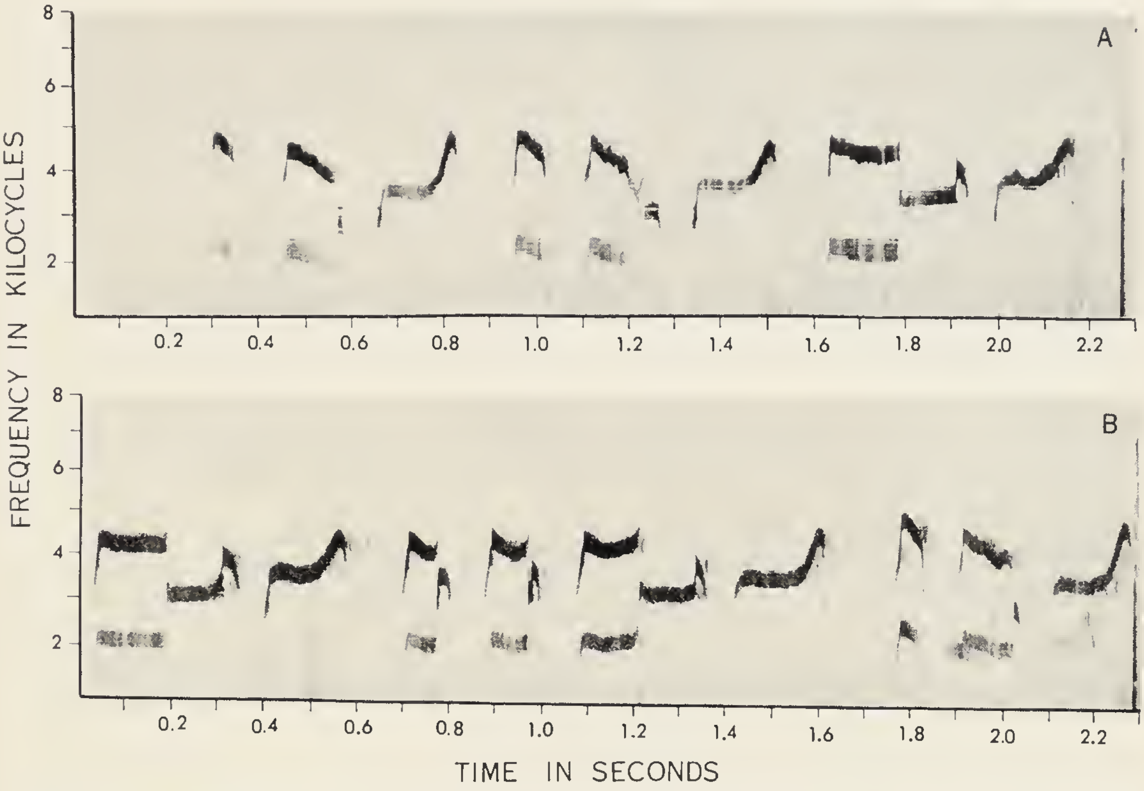

FIG. 2. Spectrograms of *T. ochropus* songs showing change-over: (A) from "Type II" to "Type I"; and (B) "Type I" to "Type II." Units in the middle are aberrant.

T. ochropus: Physical description of songs.—Songs are normally composed of one or both of two basic structural units, hereafter designated "Type I" and "Type II" (Fig. 1 C–D, Table 1). "Type I" units are composed of four main subunits which I refer to as "1" (mean of the duration = 0.160 sec, standard deviation = ±0.018 sec; mean of the average frequency = 4.02 kc/sec, standard deviation = ±0.27 kc/sec), "2" (0.160 ± 0.018 sec, 2.04 ± 0.17 kc/sec), "3" (0.195 ± 0.023 sec, 3.07 ± 0.23 kc/sec), and "4" (0.229 ± 0.050 sec, 3.62 ± 0.28 kc/sec). A harmonic is present above "1" at about 6 kc. Subunits "1" and "2" occur simultaneously and are linked to "3." To the human ear, the combination of "1," "2," and "3" sounds like a clear whistle abruptly lowering in frequency at the midway point. After an almost indiscernible pause (0.065 ± 0.010 sec), subunit "4" ascends as a musical whistle from the point where "3" leaves off.

"Type II" units contain five main subunits which will be called "1" (0.075 ± 0.008 sec, 4.39 ± 0.16 kc/sec), "2" (0.075 ± 0.008 sec, 2.28 ± 0.06 kc/sec), "1a" (0.152 ± 0.015 sec, 4.02 ± 0.18 kc/sec), "2a" (0.152 ± 0.015 sec, 2.10 ± 0.11 kc/sec), and "3" (0.209 ± 0.035 sec, 3.40 ± 0.21 kc/sec). Harmonics are present above subunit "1" at about 6.8 kc and above "1a" at about 6.4 kc. "1" and "2" occur simultaneously as do "1a" and "2a." The two pairs are separated by an interval of 0.077 ± 0.011 sec. "1a" and "2a" are, in turn, separated from "3" by a pause of 0.089 ± 0.021 sec. A "Type II" unit, because of its two pauses, as well as the relative shortness and great frequency range of its subunits, is not as musical as is "Type I."

The two unit types described above are given 1 to 19 times to form a song. The median number of unit repetitions in songs composed of all "Type I" units is 4 (extremes 1–9); in songs composed solely of "Type II" units 6 (extremes 2–19). "Type I" units are occasionally given singly, intermixed with "epigamic" calls. Any one song may be composed of all "Type I" units, all "Type II" units, or a combination of the two. A change-over from "Type I" to "Type II" may occur at any point within a song but it is more likely to occur between songs, hence most songs contain only one of the two types. Of 230 songs recorded during 1967, 69 percent contained only "Type I" components, 25 percent only "Type II," and 6 percent both types.

Songs may be separated by long periods of time or they may be so close together (about 0.1 seconds) that it is nearly impossible to say when one ends and another begins. Up to 67 units in 12 songs have been recorded in a minute; and 148 units in five minutes.

Vocal units are remarkably uniform as regards spectrographic configuration. Of the 148 mentioned above, 145 represented the normal stereotyped structure of "Type II" and three contained an extra preliminary note. Aberrant units sometimes occur at the start of a song (Fig. 1D) but most often are found when a bird changes from one unit type to another in the middle of a song. These usually include characteristics of both normal types (see Fig. 2).

T. ochropus: Biological description of songs.—Songs occur from the time birds arrive on the breeding ground until about when young are fledged. Peak occurrence is from arrival of females until the first egg is laid and, to a lesser degree, during egg-laying and hatching. "Type I" songs may continue until the start of southbound migration and occasionally occur south of the breeding ground during northward migration.

Birds sing "Type I" songs from the ground, elevated singing perches such as rocks or trees, or in the air. When in the air, they may be part of advertisement displays—most often when the bird is taking off or landing—or they may be given during direct flight. When on the ground, singing birds often raise and spread their tails. When both members of a pair are at the nest prior to the laying of eggs, whisper singing (Lister, 1953) is not uncommon. Song "Type II" occurs as part of a complex advertisement and territorial defense display which includes an undulating flight and steep dives. This display is performed over feeding and nesting territories as well as over intervening areas when the two territories are not adjacent most often during early morning and evening. During pair formation and copulation, a similar display of small amplitude is sometimes directed over the female. Occasionally a "Type II" unit is tacked onto a series of "Type I" units during direct flight.

Singing is elicited by the "epigamic" calling or singing of another bird in the vicinity of the territory. The sight of and/or sounds from pipping eggs and newly hatched young also elicit singing. Songs may be given spontaneously. They function in stimulating the female during pair formation and copulation situations, in advertisement and defense of territories, as well as in pair bond maintenance.

Vocalizations preceding and following songs are most often reciprocal song types and "epigamic" calls (see Figure 3 for flow pattern of vocalizations given during sexual and agonistic encounters). In addition to those

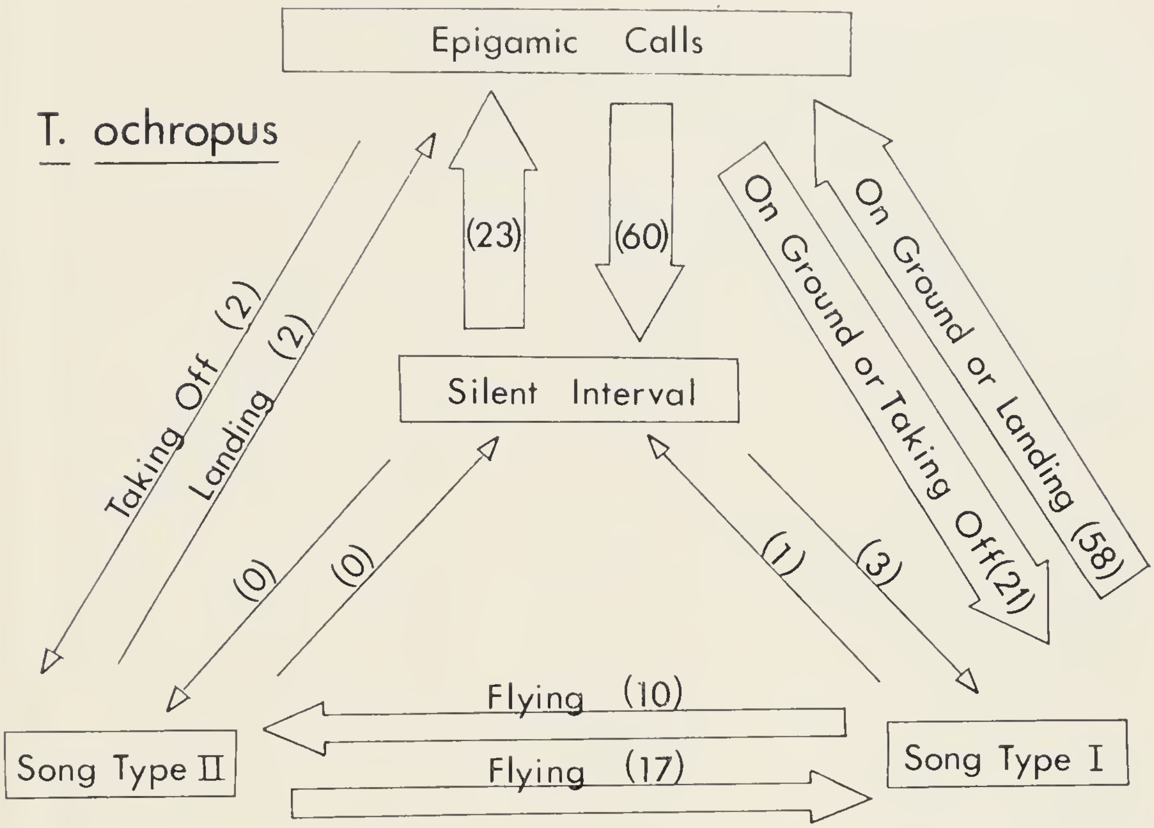

FIG. 3. Flow pattern of *T. ochropus* vocalizations given on the ground and in the air during sexual and agonistic encounters on feeding and nesting territories. Arrow thickness indicates relative frequency of a particular sequence. My sample was biased because recordings were frequently not begun until a bird was already calling or singing. Numbers from "silent interval" to "epigamic calls" to "song Type I" to "song Type II" are thus smaller than normally expected. Song types on this illustration refer to entire songs.

sequences diagramed in Fig. 3, songs are also preceded by "alarm-flee" calls during the pre-incubation period when a bird flies over its nest.

Conspecifics respond to songs as follows: those believed to be unpaired females join in aerial advertisement; mates of displaying males may ignore them or move toward them while uttering "alarm-attack" or "epigamic" calls; and those thought to be unpaired males join in display. The latter eventually leave or are chased. Pairs from nearby territories frequently join in display and chases may follow. When a bird sings in another bird's territory, the host may respond by uttering "alarm-flee" calls from a high perch (sometimes the nest bowl). When far apart, mates may keep track of each other by singing back and forth. Table 2 summarizes the results of song playback experiments.

T. solitaria: Physical description of songs.—These too are composed of one or both of two basic structural units or components again designated "Type I" and "Type II" (Fig. 1 A–B, Table 1). "Type I" units include three main subunits hereafter called "1" (0.094 ± 0.029 sec, 5.12 ± 0.26 kc/sec), "2" (0.094 ± 0.029 sec, 2.64 ± 0.16 kc/sec), and "3" (0.083 ± 0.016 sec, 4.63 ± 0.27 kc/sec). Subunits "1" and "2" occur simultaneously.

TABLE 2

REACTION OF *T. OCHROPUS* ADULTS TO REPEATEDLY PLAYED TAPE RECORDINGS OF "TYPE I" AND "TYPE II" SONGS OF CONSPECIFICS

Date	Classification of subject	Area No.	Activity and location of subject	Reaction
1 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew toward tape recorder, displayed over it more than one minute.
2 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew toward tape recorder, displayed over it less than one minute.
4 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew away uttering "Type I" songs.
5 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew away uttering "alarm-flee" calls.
9 April	Unpaired ♂ ?	1	Feeding within 50 m	Flew toward tape recorder, flew away uttering "alarm-flee" calls, displayed over marsh—all repeated.
10 April (First day ♀'s were in area)	Unpaired ♂ ?	1	Feeding within 50 m	Flew away uttering "alarm-flee" calls; returned to alternately display over recorder, sing above it, and walk to it, tail raised.
12 April	Paired ♀	1	In trees within 50 m	No reaction.
12 April	Paired ♀	1	Feeding within 50 m	No reaction.
12 April	Paired ♂	1	Feeding 500 m away	Flew to mate; both displayed over marsh, then answered each other with "epigamic" calls and "Type I" songs on ground.
20 April	Paired ♀ prior to 1st egg	1	On nest within 50 m	Flew away uttering "alarm-flee" calls; then sang in distance.
20 April	Paired ♂ prior to 1st egg	1	Feeding within 50 m	Flew toward tape recorder, then ran to within 5 m of it, tail partly raised.
17 April	Unpaired ♂ and ♀	2	Pair-formation within 50 m	♂ raised and fanned tail, ♀ raised unfanned tail; pair took off displaying out of sight.
28 May	Paired ♂ and ♀	2	Unsuccessful copulation within 50 m	♀ ignored it, ♂ flew toward tape recorder displaying near it for less than one minute.

In seven of nine cases, they were connected to "3" without a pause; in the remaining cases the pause averaged 0.140 ± 0.028 sec. Subunit "3" is quite variable in spectrographic form but usually is U-shaped—ascending sharply at the end. In one case a constant frequency was maintained. "Type I" units sound like a short, high-pitched whistle abruptly increasing in frequency about the middle.

"Type II" units are composed of four main subunits which will be referred to as "1" (0.031 ± 0.014 sec, 5.32 ± 0.30 kc/sec), "2" (0.031 ± 0.014 sec, 2.69 ± 0.16 kc/sec), "3" (0.065 ± 0.009 sec, 4.21 ± 0.26 kc/sec), and "4" (0.066 ± 0.013 sec, 4.82 ± 0.15 kc/sec). "1" and "2" are N-shaped and occur simultaneously. A fairly strong harmonic occurs above them at about 8 kc. Subunit "3" is continuous with "1" and "2" but at frequencies intermediate between them. Subunit "4" begins at a frequency level intermediate between "1" and "3" and rises sharply. "Type II" units appear to the human ear as high-pitched, short and rapidly ascending whistles.

The two unit types described above are repeated 3 to 12 times to form a song. Any one song may be composed of all "Type I" units, all "Type II" units, or a combination of the two. "Type I" units hardly ever follow a "Type II" unit when they are both part of the same song. The one possible exception recorded is pictured in Figure 1B where song unit composition is I, II, I, II, II, II; but even here, the second and third song units may be considered intermediates. Occasionally, "Type I" units are given singly with "epigamic" calls. Of 28 songs recorded in 1968, two were composed of all "Type I" units, 10 were made up of a combination of the two types, and 16 contained only "Type II" elements. Songs may be separated by long periods of time as is the usual case, or they may be repeated with only about 0.2 second intervals. The greatest number of units recorded in a minute was 24 in two songs.

Vocal units are not nearly so uniform as in *ochropus*. "Type I" units may or may not have a pause in the middle. Subunit "3," while U-shaped in all but one case, is quite variable in configuration. "Type II" varies a great deal with regard to the duration and energy pattern of subunits "1" and "2." Extremes are illustrated in Figure 1 A–B.

T. solitaria: Biological description of songs.—Songs occur from the time of arrival on the breeding ground until at least clutch completion and probably to the start of southbound migration. Migrants in Minnesota during early July are not known to sing. Songs are frequent just prior to egg laying as in *ochropus*.

Birds sing from the ground, from elevated singing perches such as treetops, or in the air—either during direct flight or as part of an irregular shallow arc display. Songs are given at feeding and nesting territories and when birds fly between the two, especially during early morning and evening. When singing on the ground, birds may spread their unraised tails and lift their wings overhead.

Singing is elicited by the singing of a strange bird near the territory or by any of a number of vocalizations of a mate. Songs may be given spontaneously. Songs function in an excitatory capacity in sexual situations, in advertisement and defense of territories, and in pair bond maintenance. Vocalizations preceding and following songs are diagramed in Figure 4.

Conspecifics usually respond to songs by singing after the singer is seen.

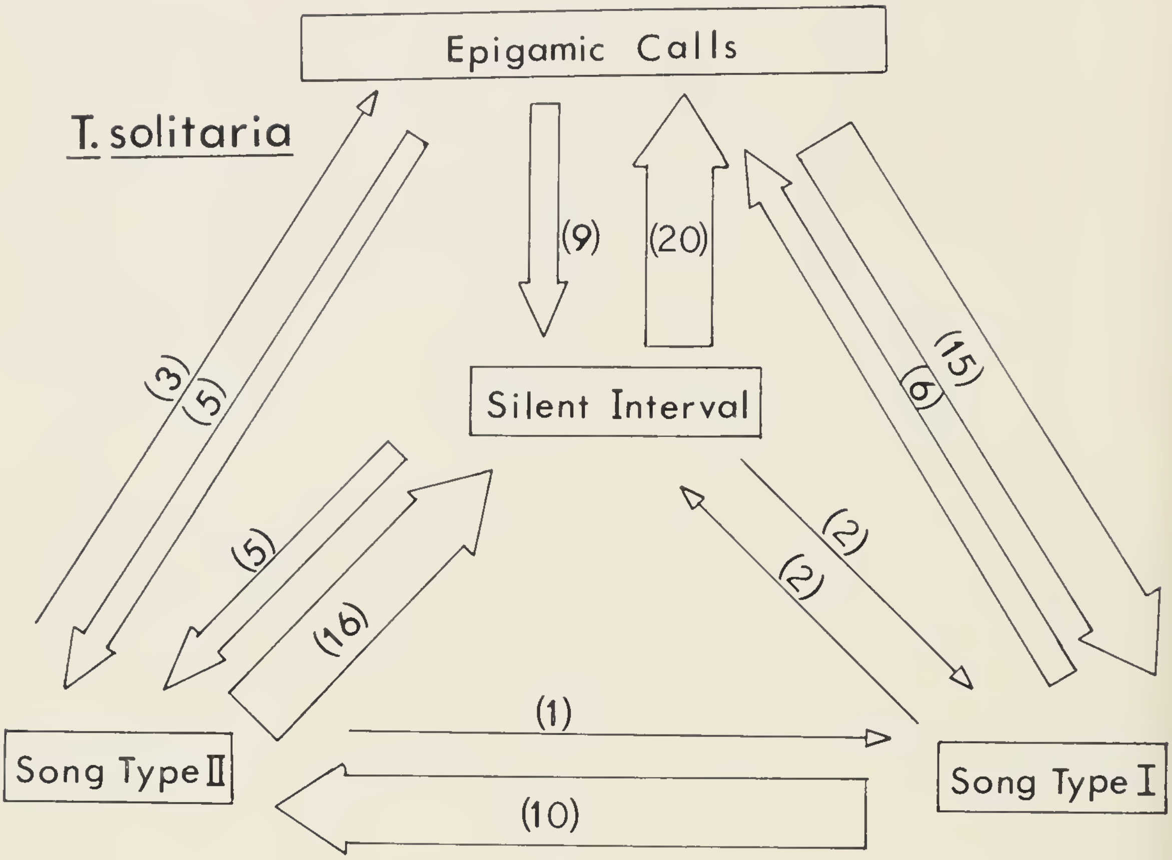

FIG. 4. Flow pattern of *T. solitaria* vocalizations given on the ground during sexual and agonistic encounters at the feeding territory. Thickness of arrows indicates relative frequency of a particular sequence. Song types on this illustration refer to song units rather than to entire songs since songs are not so frequently repeated as in the Green Sandpiper.

Singing intruders are chased from territories just prior to egg laying and perhaps at other times. Members of a pair often maintain contact with each other by singing back and forth. "Type I" and "Type II" songs of *ochropus* were played to *solitaria* at various stages of the breeding season but all results were negative.

T. ochropus: "epigamic" call.—Those vocalizations restricted to the reproductive season but not fitting song criteria of Tinbergen (1939) or Thorpe (1961) have been termed "epigamic" calls. In *ochropus* this includes two structurally different vocalizations which nearly always occur together. They may thus be discussed together when speaking of function but must have separate treatment in discussions of structure. The first of these two types I've designated "epigamic" chatter, the second "epigamic" long whistle.

Chatter is so called because it consists of a noisy, rhythmic series of calls (Fig. 5F, Table 1). These calls, while similar in nature, are always of shorter duration, closer together, and of less frequency range (maximum minus minimum) at the start of the series than at the end. The median number of call repetitions is 4 (extremes 2–10).

In 77 percent of the cases (N = 158), a single long whistle (Fig. 5F, Table 1) followed a series of chatter calls. The name long whistle has been derived from the call's

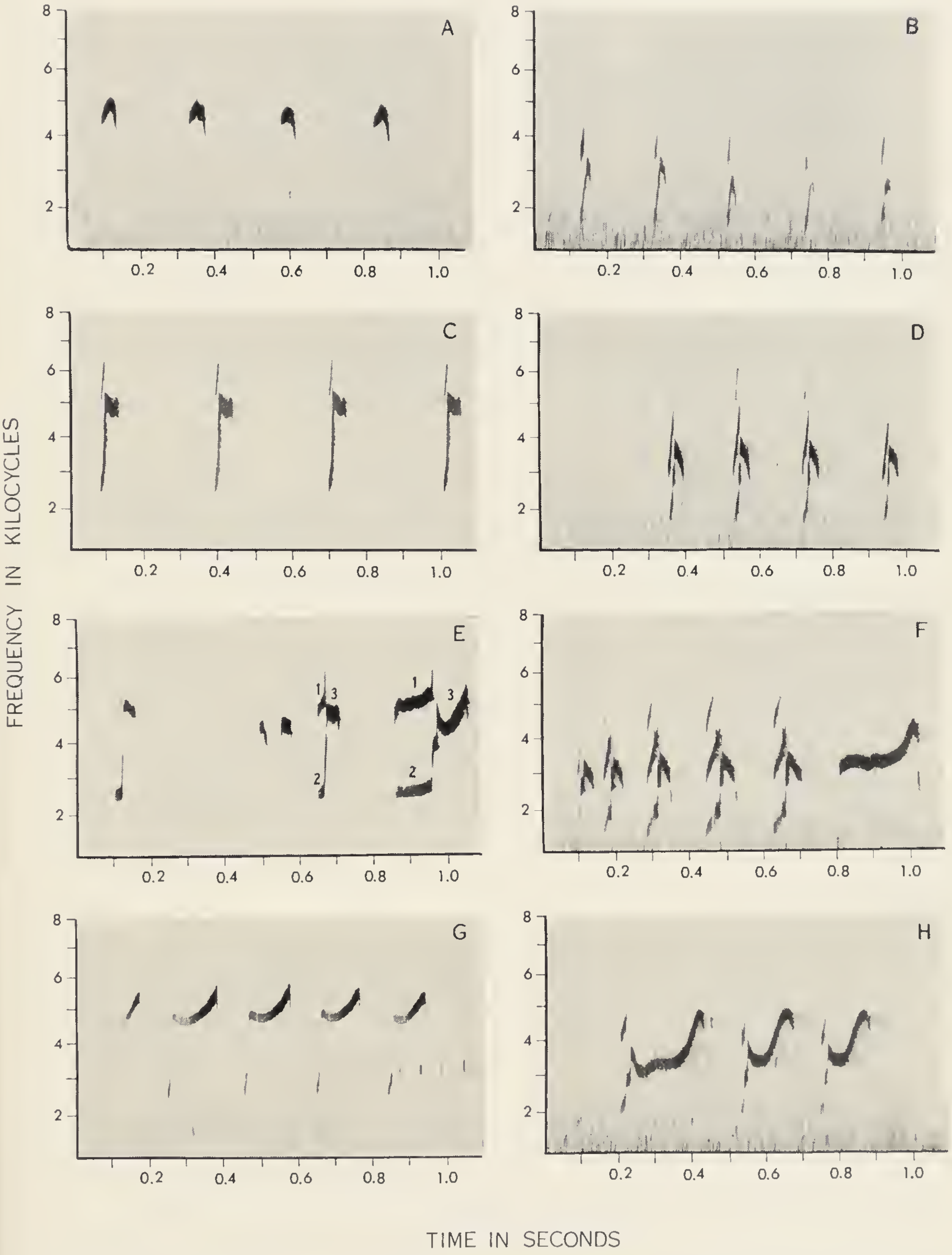

Fig. 5. Spectrograms of *T. solitaria* (left) and *T. ochropus* (right) calls: A–B, "contact"; C–D, "alarm-attack"; E–F, "epigamic"; and G–H, "alarm-flee." Numbers on part E pertain to individual subunits referred to in the text. Subunits with like numbers are probably homologous.

long duration and clear tonal quality. At times, chatter and long whistles are uttered continuously for 15 minutes or more. On rare occasions as many as three long whistles have been repeated in sequence but they nearly always occur singly at the end of chatter.

"Epigamic" calls occur from the time females arrive until the beginning of incubation and briefly when eggs are hatching. Birds call from the ground or elevated perches on the feeding or nesting territory. Calls are elicited by the singing or "epigamic" calling of a mate; or they may be uttered spontaneously. Apparently calls are also elicited by the sight of nest, eggs, or young. These calls function in stimulation of the female during pair formation and copulation situations; and are used by males to entice females to nests. When both members of a pair are at the nest prior to the egg laying period, these calls are often uttered at extremely low volume and are intermingled with whispered "Type I" song. Figure 3 diagrams the relationship between "epigamic" calls and other vocalizations in complex vocal sequences during sexual and agonistic encounters. Conspecifics may, if receptive, move toward a bird giving these calls—sometimes uttering "Type I" songs or "epigamic" calls. When the approach to a calling bird is in the air, it may be accompanied by "alarm-attack" calls.

T. solitaria: "epigamic" call.—As in *ochropus*, there are vocalizations which do not fit the classical definition of song but which are restricted to the breeding season. These calls are highly variable in configuration but seem to have a like function. For comparative purposes, I have retained the terms "chatter" and "long whistle" applied to *ochropus* though they are not descriptively accurate for *solitaria.*

The various short notes, here referred to as chatter, are repeated an average of 4.5 times in a series (see left ⅔ Fig. 5E; Table 1). As many as five series in a row, each separated by only a 0.2 second pause, have been recorded. One or two of the individual call notes include a considerable amount of noise; the others are spread over a narrow frequency range and are produced at very low volume.

Long whistles occur in similar situations to chatter though the two do not occur together in a definite and predictable series as in *ochropus.* Whistles have been recorded in groups of 2, 3, 3, 3, 3, 4, and 4. Characteristically they drop in frequency at the end. Whistles are very closely related to chatter in configuration but have been expanded a good deal in duration (Table 1). Because of this similarity to chatter, they are not illustrated.

The seasonal duration of calls, location of calling birds, eliciting stimuli, function, and reaction of conspecifics seem to be the same as for *ochropus.* Because I left the breeding grounds at the completion of clutches I do not know if these calls are given after that time. The relationship of these calls to other vocalizations within complex vocal sequences is diagramed in Figure 4. The headings song "Type I" and "Type II" refer to individual song units and not to entire songs.

T. ochropus: "alarm-attack" call.—These harsh, rapidly repeated calls are characterized by their short duration, constant between call intervals, and wide frequency range (Fig. 5D, Table 1).

This call type is given in a number of situations: (1) when danger is apparent but not imminent, perhaps to attract the attention of a predator for distraction purposes; (2) when young are threatened, at which time the median number of call repetitions is 4; (3) during short flights on the feeding or nesting territory, especially during approach to the nest when the median number of call repetitions is 10; (4) just prior to leaving for or from the nest when the median number of call repetitions is 4; and (5) during attack in aerial chases. Table 3 summarizes data pertinent to this and other calls of both species.

TABLE 3

SYNOPSIS OF *TRINGA OCHROPUS* AND *T. SOLITARIA* VOCALIZATIONS NOT SPECIFICALLY RELATED TO SEXUAL SITUATIONS

Species and call	Period of occurrence	Place of occurrence	Eliciting stimulus	Function	Reaction by conspecifics	Associated call
T. ochropus "alarm-flee"	At least Mar.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics	Flee	"alarm-attack"
T. ochropus "alarm-attack"	At least Mar.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics; attract predators	Flee, alert, or hide (young)	"alarm-flee"
T. ochropus "contact"	At least Apr.–Sept.	Anywhere	Brood and/or hatching eggs	Intrafamilial contact	Answer with like calls	———
T. solitaria "alarm-flee"	At least Apr.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics	Flee	"alarm-attack"
T. solitaria "alarm-attack"	At least Apr.–Sept.; probably all year	Anywhere	Impending danger	Warn conspecifics; attract predators	Flee, alert, or hide (young)	"alarm-flee"
T. solitaria "contact"	At least May–Sept.	Anywhere	Mate; probably as in *ochropus*	Intrafamilial contact	Answer with like calls	———

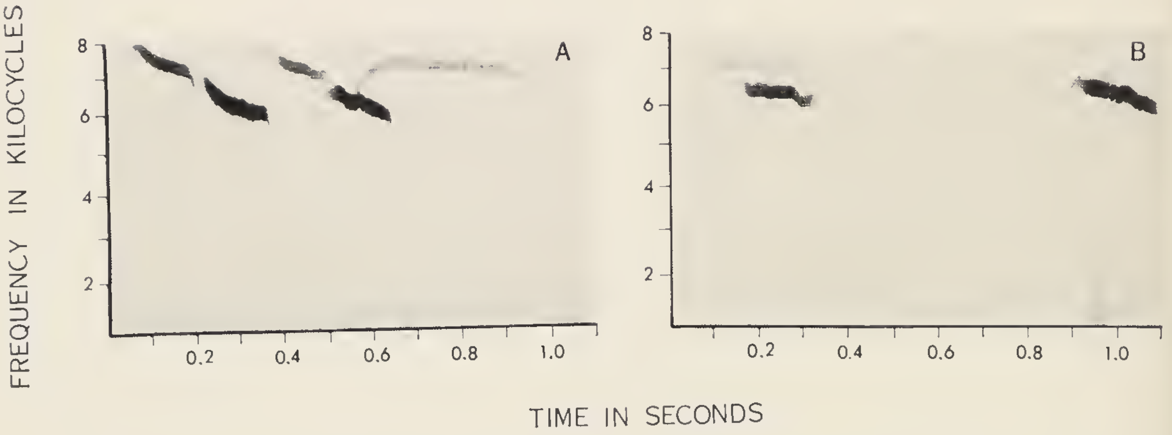

Fig. 6. Spectrograms of the calls of day-old *T. ochropus*: A, "mild distress" (left) and "content" (right); B, "content" (above) and intermediate between "mild distress" and "content" (below and right).

T. solitaria: "alarm-attack" call.—These calls appear as short, harsh, metallic tones (Fig. 5C, Table 1). Like comparable calls of *ochropus*, they are characterized by a certain amount of noise. "Alarm-attack" calls occur in the same situations as in *ochropus*. When an intruder is near the young, the median number of repetitions is 6 (extremes 1–80).

T. ochropus: "contact" call.—These are low volume calls with a relatively small musical element and a relatively great amount of noise. They are the shortest of all *ochropus* vocalizations in duration; and individual calls are nearly twice as far apart as in the "alarm-attack" or "epigamic" chatter (see Fig. 5B, D, and F for a comparison of the three types; Table 1). The median number of call repetitions before and after hatching is 3 (extremes 2–15).

These calls occur in the following situations: (1) between members of a pair while they are feeding separately or are otherwise separated by fairly short distances; (2) between members of a pair while at their nest, mixed at extremely low intensity with whisper "epigamic" calls; (3) during the entire pipping and hatching periods by the sitting adult at various intensities, mostly very low, until the young are dry—at which time the intensity increases and the calls are uttered from the ground—seemingly to induce young to jump; and (4) as follow calls on the ground until the young are fledged. When an adult calls its brood over a great distance, volume and the number of call repetitions increase; but intervals between calls remain the same. This and other calls are summarized in Table 3.

T. solitaria: "contact" call.—As in *ochropus*, these are low volume calls. Their configuration is that of an inverted V; and they have no significant element of noise (Fig. 5A, Table 1). The median number of call repetitions is 3 (extremes 1–17).

These calls have been noted in the first two situations as listed above for *ochropus* and probably occur in all four. See Table 3 for a comparison to other calls.

T. ochropus: "alarm-flee" call.—These are sharply ascending calls characteristically possessing an element of noise at the start (Fig. 5H, Table 1). "Alarm-flee" calls given from the air are usually single whereas a series of three or four is normal when given from a stationary perch. When several calls are given in series, the first is invariably the longest and has the lowest minimum frequency. The duration of successive calls becomes less and less but the frequency usually remains the same or nearly so after the second call. These calls are loud from start to finish and are shrill to the human ear.

The "alarm-flee" call has been recorded from four situations: (1) in flight any time

TABLE 4

SYNOPSIS OF CALLS OF *TRINGA SOLITARIA* AND *T. OCHROPUS* CHICKS*

Species and call	Age when first recorded	Age when last recorded	Associated behavior	Connotation
T. solitaria "contact"	10 hours	17 days (last day birds were healthy)	Laying, sitting, standing, or feeding	contact
T. solitaria "contact" (intense)	2 days	17 days	walking, running, or feeding	contact; intermediate between content and distress
T. solitaria "content-moving"	5 hours	17 days	walking and/or feeding	satisfaction
T. solitaria "content-still"	6 hours	17 days	sitting or standing	satisfaction
T. solitaria "mild distress"	5 hours	17 days	restlessness, searching for food	hunger or cold
T. solitaria "intense distress"	5 hours	17 days	running and pecking	hunger, cold, or pain
T. ochropus "content"	5 hours	22 days	sitting or standing	satisfaction
T. ochropus "mild distress"	5 hours	35 days (beginning of transition to adult "alarm-flee")	restlessness, searching for food	hunger or cold
T. ochropus "intense distress"	3 days	35 days (beginning of transition to adult "alarm-flee")	running and pecking	hunger, cold, or pain

* Table form adopted from Forsythe (1967).

an adult or its brood is directly threatened with danger, the median number of repetitions being 3 (extremes 1–5); (2) when a bird takes off spontaneously; (3) as a bird flies by or from its nest prior to the start of incubation; and (4) when a strange pair attempts to establish itself in the territory of another pair—whether it be the nesting or feeding territory, the median number of repetitions being 1 (extremes 1–3). In the latter case, the female of the established pair repeatedly utters volleys of "alarm-flee" calls from the nest bowl or a perch above the feeding territory while her mate displays in the air. The latter is the only known situation in which these calls are given by a stationary bird.

T. solitaria: "alarm-flee" call.—As in *ochropus*, these calls rise sharply in frequency after an initial noise element (Fig. 5G, Table 1). There is no predictable pattern to changes in duration and frequency of successive calls of a series.

These calls have been noted whenever danger is impending. They were repeatedly given

TABLE 5

NUMERICAL DESCRIPTION OF CHICK CALLS*

	"contact"			"contact" intense		
T. solitaria	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Duration in seconds	12	0.041	±0.007	29	0.065	±0.009
Interval to preceding call in seconds	10	0.249	±0.055	24	0.250	±0.029
Maximum frequency in kc/sec	12	5.29	±0.20	29	5.83	±0.35
Minimium frequency in kc/sec	12	4.63	±0.14	29	4.50	±0.23

	"content" moving			"content" still		
T. solitaria	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Duration in seconds	12	0.119	±0.013	10	0.201	±0.044
Interval to preceding call in seconds	10	0.216	±0.037	—	—	—
Maximum frequency in kc/sec	12	6.04	±0.24	10	5.20	±0.15
Minimium frequency in kc/sec	12	4.73	±0.35	10	4.38	±0.19

	"mild distress"			"intense distress"		
T. solitaria	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Duration in seconds	22	0.113	±0.012	12	0.143	±0.015
Interval to preceding call in seconds	13	0.099	±0.018	10	0.240	±0.024
Maximum frequency in kc/sec	22	6.33	±0.35	12	5.48	±0.19
Minimium frequency in kc/sec	22	4.60	±0.32	12	4.27	±0.11

	"mild distress"			"content"		
T. ochropus	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Duration in seconds	24	0.192	±0.026	10	0.33	±0.042
Maximum frequency in kc/sec	24	7.33	±0.48	10	7.36	±0.22
Minimium frequency in kc/sec	24	6.18	±0.37	10	6.42	±0.25

* N = sample size; $\bar{x}$ = mean; S.D. = standard deviation.

by birds flushed from complete sets of eggs in contrast to *ochropus*. In this situation, the median number of call repetitions was 2 (extremes 1–5).

Calls of T. ochropus chicks.—Three types of calls were noted: (1) "content," (2) "mild distress," and (3) "intense distress." The first two are illustrated in Figure 6 along with intermediates between "content" and "mild distress." "Intense distress" calls were not tape recorded but basically differed from "mild distress" only by their being louder and more repetitious. A summary of pertinent information is given in Table 4; descriptive statistics are included in Table 5. Table 6 summarizes the reactions of chicks to the vocalizations of adults.

Calls of T. solitaria chicks.—These young produced a number of different vocalizations. It is problematical as to how many should be given different names since a continuum from shortest to longest occurred. Modes were apparent at the two ends of this continuum. For the purposes of this paper I have recognized six types—illustrated in Fig. 7A–F. Numerical descriptions of these calls can be found in Table 5 and a summary of pertinent data sufficient for present purposes can be found in Table 4.

TABLE 6

REACTION OF *TRINGA OCHROPUS* CHICKS TO VOCALIZATIONS OF ADULTS

Location	Age	Vocalization	Source	No. Brood Observations	Reaction
Wild	1 day	"contact" call	Parent	2	Jump from nest, move toward parent; "content" call given; one separated from siblings gave "mild distress"
Wild	1 day	"alarm-attack" call	Parent	2	Crouch silently
Wild	1 day	"alarm-flee" call	Parent	2	Scatter, crouch (perhaps in response to "alarm-attack" calls)
Paper bag near nest	1 day	"contact" call	Parent	1	Move toward parent; utter "mild distress" calls
Captivity	1 day	"alarm-flee" call	Tape	1	Scatter to corners, crouch
Captivity	1 day	"contact" call	Tape	1	Move toward recorder
Captivity	2 days	"alarm-flee" call	Tape	1	Scatter to corners, crouch
Captivity	6 days	"alarm-flee" call	Tape	1	Scatter to corners, crouch
Captivity	11 days	"Type I" song	Tape	1	No reaction
Captivity	est. 13 days (just caught in wild)	"Type I" song	Tape	1	Cock head; give "mild distress" calls

DISCUSSION

In view of the lack of information available on the vocalizations of scolopacids, I have not been able to compare a great many species. Instead, I have described sounds produced by two closely related species occupying somewhat similar arboreal niches in different zoogeographical areas. Subsequent reports will compare these two species to closely related ground-dwelling forms. Emphasis in this and subsequent reports will be placed upon the evolution of sandpiper vocalizations.

Alarm calls of a number of European passerines have been analyzed spectrographically; and a remarkable similarity was found. They possessed in common a long duration and uniform high pitch (Marler. 1959). It was concluded that they were mutually well adapted to meet predation pressures in that these alarm calls would be extremely poor for binaural or phase location. This same spectrographic pattern is found in the downy young "content-still" calls of both *T. ochropus* and *T. solitaria.* In view of the similarity of

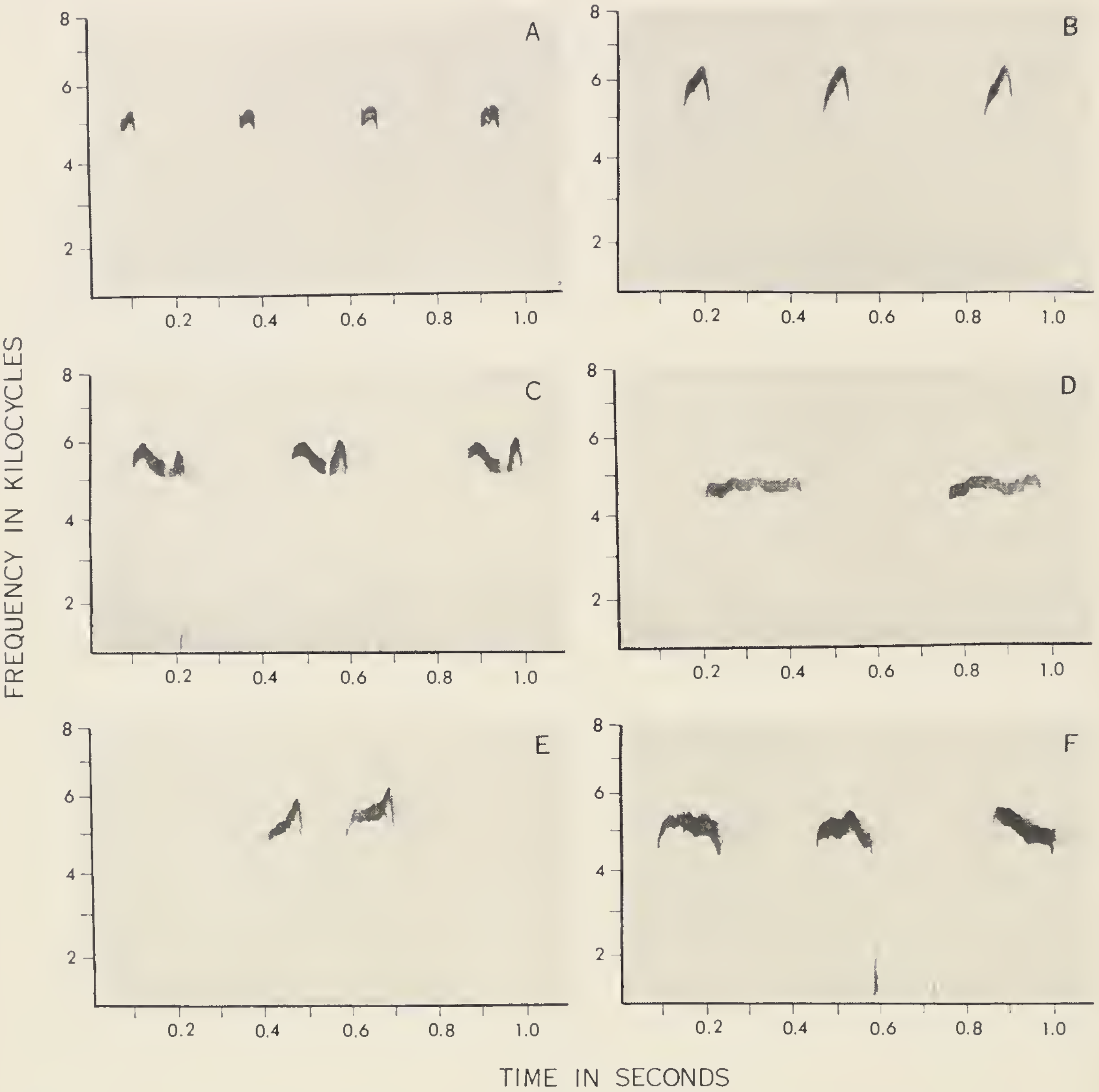

FIG. 7. Spectrograms of the calls of downy *T. solitaria*: A, "contact"; B, "contact" (intense); C, "content-moving"; D, "content-still"; E, "mild distress" (hungry or cold); and F, "intense distress."

ecological situations, including predators, faced by both species (and by the passerines mentioned above) this call similarity is not surprising.

I do not have data to indicate which adult calls, if any, "content-still" calls evolve into during the course of ontogeny. I do know that shortly after *T. ochropus* young fledge, they have no calls as high in frequency as the young "content" call, and that in early fall only "alarm-flee" and "alarm-attack" calls are heard. Distress calls of these species will probably, when careful analysis is complete, be shown to merge with the "alarm-flee" calls of adults.

No short rhythmic calls were noted in *ochropus* chicks. In *solitaria*, the calls I've called "intense contact" in the young are almost identical spectrographically to the "contact" calls of adults. Those of the young birds are however longer, separated by greater intervals, and considerably higher in frequency (Figs. 5A and 7, Tables 1 and 5). How much of this difference is due to syrinx maturation is a point for future investigation. The constant intervals between "intense contact" calls, indicate that they are suited for intra-specific phase location. The fact that they possess a greater frequency range than low intensity "contact" calls (Table 5) further indicates a location function. They may well be intermediate between low intensity "contact" calls, and calls produced in slightly distressful situations. Experiments to test this hypothesis are planned. An intermediate motivational state may also be involved in eliciting "content-moving" calls.

One might argue that "contact," "alarm-attack," and "epigamic" chatter calls of both *solitaria* and *ochropus* adults, are variants of a single call dependent upon changes in the motivational substrate for their identities. Increased structural complexity as well as functional specialization from "contact" to "alarm-attack" to "epigamic" chatter, may be indicative of the phylogeny of this call complex. Certainly their spectrographic forms indicate that they are closely related (Fig. 5A–F). I have preferred, however, to treat them separately in order to emphasize their functional differences. In my opinion, "contact," "alarm-attack," or "epigamic" chatter calls of the two species are homologous and analogous. These three calls, though functioning in different contexts, probably all serve to aid in location of conspecifics. Their structures would seem well adapted for this purpose, for as Marler (in Marler and Hamilton, 1967) pointed out, ". . . low frequencies are best for locating sound by phase differences, and high frequencies are best for intensity difference. The easiest sounds to locate are those that provide cues for all methods, requiring a wide frequency spectrum and sharp discontinuties." In both species, the "contact" call, which is uttered by birds fairly close to each other and which are involved in activities not directly related to the calls, e.g. feeding, possess the poorest location cues. But their shorter duration and smaller frequency range means less sound energy expended and at close range these calls are seemingly adequate for location. "Alarm-attack" and "epigamic" chatter, are more efficient for location purposes according to Marler's criteria. This is not surprising in view of the fact that these calls are functional parts of activities having considerable selective importance.

"Alarm-flee" calls of *solitaria* and *ochropus* are also somewhat similar (both being high pitched and rapidly ascending in frequency) and, I presume, homologous as well as analogous. In both species the calls begin with a noise element not unlike that of "alarm-attack" calls. Whether this structural similarity is indicative of functional and/or evolutionary relationships between the two types is difficult to say. But it is of special interest that all possible gradients between "alarm-attack" and "alarm-flee" calls occur. They were noted once for *solitaria*—when an incubating bird was flushed from its nest but remained near it. While sitting still or moving toward the nest, it gave "alarm-attack" calls: when fleeing it gave "alarm-flee" calls; and when flying short distances to other perches equidistant from the nest it gave intermediate calls. In *ochropus* the same thing occurred when parents circled the fence in which their young were trapped. Calls intermediate between "alarm-attack" and "alarm-flee" thus occur in both species in intermediate motivational situations. Variations of this sort are to be expected in calls not involved in reproductive isolation.

A single "alarm-flee" call such as the first of the series illustrated in Fig. 5 G–H, provides little in the way of location cues. In *ochropus*, one or less often two of these calls is usually given by a flying bird. "Alarm-flee" calls do, however, occur in series—the intervals between them being constant. In particular, this occurs when a stationary female defends a territory from intrusion by a conspecific. In such a case, the addition of location cues afforded by phase differences would seem to be of adaptive significance. In either case—whether given singly or in series—this call seems to convey the message "danger—flee."

In Fig. 5F, as one follows the "epigamic" chatter from left to right, it is noticeable that time intervals as well as call durations increase. This is a regular phenomenon as chatter progresses toward a song (Fig. 1C) or long whistle (Fig. 5F). In Fig. 3. it is shown that chatter normally precedes song "Type I" and that "Type II" is more specialized, occurring primarily in aerial display. I propose that this sequence—from "epigamic" chatter to "Type I" to "Type II"—is a recapitulation of *ochropus* song evolution. All of the elements of "Type I" subunits "1," "2," and "3" including the first harmonic, can be clearly found in epigamic chatter (Fig. 1C). In addition, spectrograms of chatter not reproduced here possess greatly expanded elements. Subunit "4" is strikingly similar to the long whistle (Fig. 5F). The origin of the long whistle and subunit "4" is open to question. They are apparently closely related to each other.

"Type II" units, which are more specialized in structure and function, nevertheless hold clues to their evolutionary origin. If, for example, those subunits labeled "1" and "1a" are rejoined and those labeled "2" and "2a" likewise, they are strikingly similar to units "1" and "2" of the "Type I" song seen in Fig. 1C. And furthermore, if subunit "3" of Fig. 1D is attached to the small energy blotch visible between and to the right of "1a" and "2a," this song suddenly becomes nearly identical with subunits "1," "2," and "3" of song "Type I" (Fig. 1C). What seems to have happened in the course of song evolution is that "1" and "2" have split giving rise to "1" and "1a": and "2" and "2a" respectively; and "3" has broken off from its former connection to "1a" and "2a." It is also possible that "1" and "2" may have arisen secondarily by addition. In either case, a double-pause song highly specialized for aerial displays has evolved. Its characteristics—double pause and increased frequency range—enhance its use as a location cue over great distances.

The songs of *solitaria* have much in common with the basic *ochropus* pattern. As in *ochropus* (Fig. 1C), the three subunits of "Type I" seem to be represented in elements of "epigamic" chatter (Fig. 5E). "Type I" units, and to a lesser extent "Type II" units (Fig. 1A–B), are very much like the "1," "2," and "3" part of "Type I" *ochropus* songs, except that they are shorter in duration and higher in frequency. The series of calls shown in Figure 5E may well be close to repeating the evolutionary history of *solitaria* "Type I" songs. *Solitaria* songs have no intra-unit intervals but inter-unit intervals may be significant aids to location.

In both *ochropus* and *solitaria*, "Type II" units are shorter and have higher maximum frequencies than "Type I" units (less than 5 percent of the time the means of duration and maximum frequency could be expected to overlap). In *solitaria*, the minimum frequency is higher and intervals between songs shorter in "Type II" than in "Type I." In other words, there has been a tendency for the more specialized songs (ones performed at higher intensity) to include more sound energy at higher frequencies per unit of time. The four song types of *solitaria* and *ochropus* all end in clear tones—well suited for conveying species-specific information.

Precise measurements of time spent and energy expended in song production per season are not available. Nevertheless, it is obvious that *ochropus* sings louder and perhaps as much as ten times more often than *solitaria*. Because the two species nest in comparable parts of the boreal forest, lay their eggs most often in old passerine nests, and are solitary year-round, their ecological niches have been presumed nearly identical; but never have dissimilarities been stressed. In southern Sweden, *ochropus* commonly utilizes the nests of three turdid species—the Blackbird (*Turdus merula*), Song Thrush (*T. philomelos*), and Mistle Thrush (*T. viscivorus*). Blackbird and Song Thrush nests are distributed widely throughout the forest wherever stands of immature Norway spruce (*Picea abies*) are located. Though some nest sites were near feeding territories, many were not. Mistle Thrush nests most often were high in Scotch pine (*Pinus sylvestris*), less frequently in Norway spruce. Mature Scotch pines usually are not next to feeding territories as fluctuating water levels periodically kill or damage trees. Thus, nests available for use by *ochropus* are widespread throughout the forest. The closest two used in one year of which I was aware were 400 m apart. On Hunneberg, which includes about 50 sq. km, there were 20–25 breeding pairs. In Alberta, *solitaria* usually uses nests of Rusty Blackbird (*Euphagus carolinus*). Cedar Waxwing (*Bombycilla cedrorum*), and Robin (*Turdus migratorius*). Rusty Blackbirds and Cedar Waxwings breed close to muskeg ponds where *solitaria* feeds. Robin nests are scattered throughout the forest. The nests in which *solitaria* lays its eggs are nearly always close to feeding ponds according to my observations and those of R. Lister and D. Parmelee (pers. comm.). Furthermore, two or more pairs may nest as close as 100 m from each other. Hence the distance over which conspecifics communicate is much less than is normal for *ochropus*. The songs of *ochropus* which are very loud and frequently repeated appear specialized for communication over great distances. The fact that these songs must be effective over long distances may also explain why they are so much lower in frequency than those of *solitaria*, for as I have explained above, there seems to be a tendency for high frequencies to drop out first when recordings are made over great distances. This being the case, I would expect the higher frequencies to be selected against during the evolution of species which communicate vocally over great distances.

T. glareola (Kirchner, 1963) and the Redshank (*Tringa totanus*) (Grosskopf, 1958), both possess at least two song types as do *solitaria* and *ochropus*. In addition. both *glareola* and *totanus* as well as *T. nebularia* (Nethersole-Thompson, 1951) and other closely related but lesser known forms, have calls which are apparently similar in structure and function to those of *solitaria* and *ochropus*. Comparisons between these species are best reserved until spectrographic data are available.

In *ochropus* and *solitaria*, as in the entire *Tringa-Totanus* complex, morphological features differ much less than do vocal ones. Vocalizations are probably much more important in species recognition of territorial males than morphological features as Lanyon (1963) reported for *Myiarchus* flycatchers. Smith (1965) pointed out that when songs are employed for stimulation of the female after pair formation, individuality may be important to achieve synchrony between mates; and this distinctiveness may be visual or vocal. In *ochropus* and *solitaria* a need for individuality is overcome by intense chasing of all intruding males from occupied territories and by the fact that resident females rarely leave their territories.

According to Marler (in Marler and Hamilton, 1967), sympatric species are likely to have songs consistently and distinctly divergent when songs function as reproductive isolating mechanisms—as they certainly do in *Tringa*. One might guess that since *ochropus* and *solitaria* are allopatric, so similar in certain aspects of their ecological niches. and indisputably close phylogenetically, that their songs might be much more similar than they are. Personal observations of *T. glareola* indicate that its song (and aerial display) is much more like that of *solitaria* than that of *ochropus*. Songs of *glareola* may be close to those of parental stock for the entire genus. *Glareola* is sympatric geographically and to some extent ecologically with *ochropus*. Thus, sympatry with a very closely related form has been part of the pressure molding the evolution of *ochropus* songs while it has not been involved in the recent history of *solitaria*. This pressure by a sympatric form may help explain why *ochropus* songs are apparently more stereotyped than those of *solitaria*. On the other hand, evidence from island forms suggests that in the absence of close competitors, variability increases (Marler, 1960)—a situation which may to a lesser extent involve mainland forms facing similar situations such as *solitaria*. In species where song is largely learned, e.g. Chaffinch (*Fringilla coelebs*), the reverse seems to be the case (Thorpe, 1958).

According to Ficken and Ficken (1962), many closely related species of North American warblers have at least two song patterns. One of these, which they call the "accented" song, is highly species-specific; and is used especially in establishing pair bonds and territories. This "accented" song occurs infrequently later in the season when it is replaced by the "unaccented" song—a type which differs little from species to species. An interesting parallel occurs in *ochropus* and *solitaria*. In the former, "Type II" songs occur primarily during pair formation and territorial advertisement; they are very rare in other contexts. "Type I" songs occur frequently both before and after the period of pair formation and territorial advertisement; and though they do occur in these situations, are infrequent during the aerial or highest intensity part of the displays. The two song types of *solitaria* do not fit an "accented"-"unaccented" pattern but rather both occur in a variety of situations. But it is of interest to note that it is the "Type I" pattern of *ochropus* which is most similar to that of *solitaria* (Fig. 1B–C, subunits 1–3). In other words, it is the song which is little involved in pair formation and territorial advertisement that is most similar to that of a very closely related but allopatric species. "Type II" *ochropus* songs, it seems, are roughly equivalent to the "accented" songs of warblers, and "Type I" to the "unaccented."

According to the bird song classification of Hartshorne (1956), the songs of *solitaria* are "discontinuous" (pauses between songs occupying more than 70 percent of the performance time) and "non-versatile" (less than four distinct songs or phrases). This situation is not uncommon among passerines. But according to this same classification, *ochropus* songs are "highly continuous" (pauses between songs occupying less than 50 percent of the performance time) and "non-versatile" (less than four distinct songs or phrases) —a combination which Hartshorne (1956) considered extremely rare. During one minute, e.g., only "Type II" song units occurred and they were repeated 67 times. Excluding all inter-unit and inter-song intervals 40.2 seconds (67 percent) were involved in actual singing. Even when intra-unit intervals are excluded, leaving only the time when sound energy was being produced, this bird was singing 29.2 seconds per minute or 49.7 percent of the total performance time. Hartshorne (1956) also stated that "Indicative of a low level nervous organization—high threshold, great tolerance for monotony—is a lack of clear musical contrasts within the basic song pattern, as well as in its reiteration without ample pauses or variations. The second deficiency is found only in association with the first." This generalization based upon passerines is deficient with regard to *ochropus* for this species possesses clear musical contrasts in its basic song but lacks "ample pauses or variations."

Songs of *ochropus* and *solitaria* function in territorial establishment and defense, pair formation, and in readying the female for reproduction—as in passerines. Also as in passerines, songs are more or less restricted to the reproductive season. Their structural complexity and duration are greater than in many passerines but less than in others. The single major difference seems to be that in passerines, songs are often given without immediate external stimuli whereas in *solitaria* and *ochropus* songs are nearly always given in response to conspecifics. Some singing does occur, however, in the absence of conspecifics during direct flight.

SUMMARY

Tringa ochropus and *T. solitaria* occupy similar ecological niches in the boreal forests of the Palearctic and Nearctic respectively. In both forms, the calls of chicks are high-pitched—about 6 to 7.5 kc in *ochropus* and 4.5 to 6 kc in *solitaria.* Chick content calls of both species are clear, high-pitched monotones. Distress calls are spread over a considerable frequency range and are shorter than content calls. A number of other calls were recorded in *solitaria*; and it is thought that they may represent intermediate motivational situations.

Whereas the juvenile calls of *ochropus* are substantially higher than those of *solitaria*, the reverse is uniformly true for all adult vocalizations. All adult vocalizations are given by both sexes. Adults of both species utter a number of short duration, frequently repeated calls here named "contact," "alarm-attack" and "epigamic" chatter. These calls are all well adapted for locatability. In *ochropus*, all three possess a considerable noise element but most energy is centered about 3.2 kc. Noise is absent in *solitaria* contact calls but present in "alarm-attack" and "epigamic" chatter. These calls center about 4.8 kc.

Both species possess "alarm-flee" calls which are usually given by flying birds, especially when taking off. These calls ascend rapidly—from 3.1 to 4.4 kc in *ochropus* and 4.3 to 5.1 kc in *solitaria.* They possess noise elements similar to those of "alarm-attack" calls; and intermediates occur in intermediate motivational situations.

Long whistles are vocalizations present only during the breeding season in both species—at about 3.2 kc in *ochropus* and 4.8 kc in *solitaria.* The species-specific information which they are well adapted to convey is apparently enhanced by the location cues of chatter which accompanies them. This combination of long whistles and chatter occurs during pair formation, copulation, and other situations about the nest.

Both species have songs composed of one or both of two basic structural units—"Type I" and "Type II." "Type I" units are less specialized. In both species they show close relationships to "epigamic" chatter. The more specialized units, "Type II," arose by

addition and shift of energy in *solitaria* and by fragmentation in *ochropus*. The songs of *ochropus* are composed of 1 to 19 units each of which is about 0.6 seconds long, is separated from preceding and following units by about 0.1 seconds, and is located from about 1.8 to 4.6 kc. Three to 12 units compose the songs of *solitaria*, the units being about 0.2 seconds long; each separated from preceding and following units by about 0.15 seconds. They are located from about 2.5 to 6 kc. In both species "Type II" units are of shorter duration and higher frequency than "Type I." The structures of "Type II" units are better adapted for location over long distances while retaining clear tonal components for the conveyance of species specific information. The fact that *ochropus* songs are louder, longer, lower, and more frequently repeated than those of *solitaria*, may be related to the much greater territory size of *ochropus*. Selection may therefore have favored vocal characteristics capable of being transmitted and received over great distances.

The songs of *ochropus* are similar to the "accented" and "unaccented" songs of some warblers in that "Type II" songs are restricted to pair formation and territorial advertisement and "Type I" songs occur at other times. In addition, "Type I" songs are the ones showing relationships to *solitaria*. The songs of *solitaria* do not fit an "accented-unaccented" pattern.

Songs of *solitaria* are "discontinuous" and "nonversatile." Those of *ochropus* are "highly continuous" and "nonversatile"—a situation apparently rare or nonexistent in passerines. As many as 67 units/minute with 29.2 seconds of actual sound energy production have been recorded.

Adults of *solitaria* did not respond to playbacks of *ochropus* songs while *ochropus* responded to playbacks of conspecific songs by approaching, singing, and often performing aerial displays. Chicks of *ochropus* responded to "alarm-flee" calls by scattering to corners of a box and crouching; to "contact" calls by moving toward the sound source.

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OBSERVATIONS ON BEHAVIOR OF SANDHILL CRANES

J. M. Harvey, B. C. Lieff, C. D. MacInnes, and J. P. Prevett

The Sandhill Crane (*Grus canadensis*) nests on the low, wet coastal tundra near the mouth of the McConnell River (60° 50′ N, 94° 25′ W), on the western shore of Hudson Bay. During studies of geese and jaegers we have made many casual observations of cranes. Although adult cranes are conspicuous due to their large size and loud calls, the nests and young are very difficult to locate. Since the young are also mobile, it is difficult to make any estimate of nesting density. However, in 1966, we located eight crane nests within four square kilometers of a surveyed study area. This is probably the maximum density of nests in the region.

PREDATION

The most unexpected aspect of crane biology was the species' role as a predator of other birds. There is a large Blue Goose (*Chen caerulescens*) colony at the mouth of the McConnell River. Cranes frequently fed in the colony, but until 1967 we had not observed them eating goose eggs. In fact, the only reference of predatory activity by Sandhill Cranes was by T. S. Roberts (*in* Walkinshaw, 1949. The Sandhill Cranes. Cranbrook Institute of Sci. Bull. 29, Bloomfield Hills, Mich.) who included "small mammals and at times young birds and eggs" in the diet of the species.

On 12 June 1967, Prevett observed a single crane eating the eggs from a Blue Goose nest. The adult geese watched from about twenty meters distance but made no attempt to defend the nest. Within five minutes the crane left the nest, moving to a nearby pool where it spent 20 minutes bathing and preening egg remains from its face. Both adult geese returned to the nest. The female alternately settled on the nest and stood up to peck the contents. The nest contained only the fragments of four eggs.

On 18 June Harvey saw a crane attack an unprotected nest after the adult geese had left the area due to his approach. The crane showed little concern for the observer. It pulled some grass and down from the goose nest, then broke an egg with a hard jab of its bill. It ate the eggs one by one, drinking the contents and scattering the shell fragments of each before attacking the next. Upon finishing the first nest, it immediately approached a second. Before it could break an egg, however, an adult Blue Goose landed beside the nest, and stood over the eggs with its head held low, in a threat position. The crane jumped back a meter. The goose then extended its wings, with the wrists high and the tips of the primaries touching the ground, thus presenting the typical high intensity threat display of the Blue Goose. The crane responded with a similar display, and was immediately attacked. The goose may have struck the crane in the upper breast. The crane jumped back, then walked slowly away, leaving the goose near its nest.

On 6 July Prevett saw two adult cranes pecking at the contents of a goose nest located in a clump of dwarf birch (*Betula glandulosa*). Approaching the nest, he found a very young crane, probably not more than two days old, in the birch beside the nest. The down of its face and throat was covered with sticky egg contents. There was one unbroken egg beside the nest. A wet gosling, with the yolk sac incompletely resorbed, lay in the nest. The yolk sac was broken, the skin was torn on the thigh and breast, and the nearby shell was bloody. The adult cranes had probably opened a pipped egg, and removed the embryo. They may have been dismembering the embryo for the young when Prevett approached. In any case, the young crane had been eating the contents of the yolk sac. No adult geese were seen in the vicinity.

In view of Harvey's observation, it seems unlikely that cranes succeed in obtaining many goose eggs when the geese are not disturbed, although we have observed great individual variation in the intensity with which geese defend their nests. However, when a human moved through the colony, gulls (*Larus* spp.) and jaegers (*Stercorarius* spp.) frequently attacked nests vacated by geese fleeing from the observer. Probably at least two of the incidents described involved a crane taking a similar approach. In fact, the first two encounters occurred less than one kilometer from each other, in an area where a single adult crane was frequently seen. The same individual was possibly involved each time.

Cooch (1958. The breeding biology and management of the Blue Goose (*Chen caerulescens*). Unpubl. Ph.D. thesis. Cornell University, Ithaca, N.Y.) did not list the Sandhill Crane as a predator of goose nests. However, he described (Cooch, 1953. A preliminary study of Blue and Lesser Snow Geese on Southampton Island. M.S. thesis (Unpubl.), Cornell University.) the aerial mobbing of cranes by several hundred Blue Geese whenever cranes flew over the goose colony at Boas River, on Southampton Island. MacInnes made similar observations at Boas River, but never in seven years of study at the McConnell River. On Southampton Island cranes were rare. Only three sightings were made during the five weeks of goose incubation in June and July 1961. In each case, the cranes were followed by large numbers of geese as they flew over the goose colony. At the McConnell River, on the other hand, cranes were abundant, and up to a hundred flights over the goose colony were observed each day. The McConnell River geese apparently ignored the cranes.

Cranes were also effective predators on other birds. On 29 July 1967, Lieff watched, from a blind, while three adult cranes ate several Willow

Ptarmigan (*Lagopus lagopus*) chicks in a four hour period. When first seen, the cranes were walking stiffly and rapidly through low willows (*Salix* spp.) and dwarf birch on an island in the McConnell River delta. Occasionally, a crane would stop to probe the vegetation with its bill. A pair of adult ptarmigan were alternately attacking the cranes, or trying to distract them by feigning injury. Neither action was more than momentarily successful, and one or more cranes were invariably left undisturbed. The cranes caught and ate six small ptarmigan chicks in five minutes. In each case, the ptarmigan attacked the crane vigorously, without success. The crane retreated from the immediate area with the struggling chick in its bill. The crane held the chick in the bill until it hung limp, swallowed it whole, and returned to hunt for more.

The ptarmigan continued to harass the cranes for eight minutes after the last chick was eaten, although the male was absent for three minutes of this time. The cranes then sat down and rested. The pair of ptarmigan walked away, apparently without any chicks.

The cranes rested for 15 minutes. then moved slowly down the island, feeding on vegetation. Ten minutes later, one of the cranes was observed holding a starling-sized ptarmigan chick in its bill. A pair of ptarmigan tried vigorously to distract the crane, while it put the chick on the ground and stabbed it to death. For 15 minutes, the other two cranes pursued the successful one, accompanied by the adult ptarmigan. Each time the crane put the chick down, it was immediately forced to pick it up and retreat by the other cranes or the adult ptarmigan. The chick was eventually dismembered and eaten.

Fifteen minutes after the chick was eaten, another crane of the trio caught a similar chick. In this case, the crane which ate the first chick made little attempt to steal the second from its captor. The second large chick was eaten 10 minutes after capture. The three cranes then rested for 30 minutes. Within minutes after they resumed feeding, a third ptarmigan chick was captured. This was eaten after 15 minutes distraction by the adult ptarmigan, although the other cranes paid little attention. The cranes then rested on the edge of the island for 70 minutes. During this period the adult ptarmigan could not be seen, but were apparently hiding in the bushes where the chicks were captured.

When they resumed activity, the cranes flew to another island. Within 10 minutes one crane flapped after a half-grown ptarmigan which ran from cover. The crane caught the chick by one leg, but had difficulty holding it because the chick flapped its wings. A male ptarmigan flew into the face of the crane and the chick escaped by flying. The adult ptarmigan followed the young, but the crane made no attempt to recapture its prey.

Ptarmigan clearly recognized cranes as predators from a distance. On two occasions a brood of ptarmigan was directly in front of the observation tower when cranes flew low over an island about 30 meters away. On one occasion the female ptarmigan gave a warning call and ran between two hummocks, where all the chicks bunched tightly around her. The male sneaked away and hid in the lee of a hummock about 7 meters from the covey. On the second occasion the male hid with the covey behind a hummock. On neither occasion did the cranes change their flight direction. Ptarmigan did not react in this way to flying geese.

We have little other information on the food habits of cranes at the McConnell River. Of two stomachs. one contained only the corms of sedge (*Carex*) or cottongrass while the other contained goose egg remains and a large collared lemming (*Dicrostonyx torquatus*). The lemming was in one piece, but had been crushed before ingestion. Considering the great abundance of lemmings during years of high population, these may constitute an important food supply when available. It is evident from our observations that the cranes are opportunistic feeders, for goose eggs and ptarmigan chicks are available for only short periods during the time that cranes are present at the McConnell River. However, their role as predators, and the importance of vertebrate prey in their diet cannot be assessed from information available. Judged from the apparent skill with which the cranes were observed to catch young ptarmigan. however, it is evident either that predatory activity must be common in the species, or that cranes rapidly learn and perfect new feeding behavior.

CARE OF YOUNG

It appears (Walkinshaw. op. cit., and Novakowski. 1967. Whooping crane population dynamics on the nesting grounds, Wood Buffalo National Park, Northwest Territories, Canada. Canadian Wildlife Service Report Series–Number 1. Queens Printer. Ottawa) that. although cranes usually lay two eggs, they most frequently raise only one young. Lynch (pers. comm.) reported that incubator-hatched Sandhill Cranes are highly aggressive toward their siblings. and frequently the stronger or older individual kills the other within hours of hatching.

We have observed at least four crane broods out of ten with two young at the McConnell River. However, the adult cranes called alarm when a human was more than a kilometer from the young, and frequently staged their distraction displays some distance from the spot where the young were hidden in the vegetation. Thus, the incidence of broods with two young may be higher than indicated.

Two broods observed within four days of hatching indicated how this high incidence of survival of two young may occur. In each case, the observer's attention was drawn by a single adult crane calling loudly. Within a short time, a second crane stood up and called from a spot about 150 meters from the first. When the first adult was approached, it increased the frequency of calls, and walked slowly away, allowing the observer to approach within 20 meters. The second adult joined the first, but, every two or three minutes it would fly back to the place where it was first observed, only to return within a minute or less. It took 15 to 30 minutes to find each crane chick, during which period both adults concentrated on the area near the human. However, in both instances, only one chick was found where the first adult crane was observed. The second chick was discovered in the area where the second adult crane was first disturbed, at least 100 meters from the first chick. When the search for the second chick was in progress, both adults again concentrated their alarm activity near the observer. However, the adult attending the first chick again made frequent visits back to its charge. In both cases it was possible to find the young only because they became cold and began to call. We have frequently observed adults behaving in the manner described, but were unable to find the young. It is therefore impossible to estimate how long this behavior may persist as the young develop.

It was quite clear in both cases that the young were well separated when first disturbed, yet evidently the adults were still able to communicate. If this behavior occurs frequently the Sandhill Crane may often raise two young.

SUMMARY

Sandhill Cranes were observed eating eggs and hatching young of Blue Geese. They also hunted young ptarmigan with skill and success. One crane stomach was found to contain a collared lemming. The two young of a brood were apparently cared for separately, one by each adult, although the adults maintained contact and both defended any threatened young.

ACKNOWLEDGMENTS

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DEPARTMENT OF CONSERVATION, CORNELL UNIVERSITY, ITHACA, NEW YORK (JMH) AND DEPARTMENT OF ZOOLOGY, UNIVERSITY OF WESTERN ONTARIO, LONDON, ONTARIO, 16 MAY 1968.

SEASONAL CHANGES IN BODY WEIGHT AND FAT AND THE RELATION OF FATTY ACID COMPOSITION TO DIET IN THE WILLOW PTARMIGAN[1]

George C. West and Martha S. Meng

Willow Ptarmigan (*Lagopus lagopus*) live throughout the year in the arctic and subarctic of North America and Eurasia. Their presence in large numbers indicates that they are well adapted to their environment which may at times be extremely cold and stormy. Populations of these birds nest in the Alaskan far north and portions of the population migrate south through passes in the Brooks Range to winter in the sheltered valleys which contain large stands of willow and south of the tree line, spruce (Irving et al., 1967*a*). The diet of Willow Ptarmigan consists of over 97 per cent willow buds and twigs during the winter months in the arctic, and of 89 per cent willow in the subarctic, while during the summer the birds shift to green vegetation, usually leaves and berries (West and Meng, 1966; Weeden, in press).

Through a series of investigations, we are trying to understand how the ptarmigan are adapted to their life in the arctic. We have seen that the population segregates into sex and age groups during the course of its migration and on their wintering grounds so that the four categories pursue different winter programs (Irving et al., 1967*a*). Ptarmigan expend approximately the same amount of energy at all seasons and their special seasonal energy demanding activities are distributed throughout the year to maintain a steady level (West, in press). Studies on the feeding habits of the ptarmigan show that they accumulate large quantities of willow in their crops during short winter days while during summer their crops remain uniformly light throughout the long days (Irving et al., 1967*b*).

While processing the birds for their crop contents, we noticed that there was considerable difference in net body weight (whole weight less crop weight) of birds among the four recognizable age-sex categories: adult male, adult female, juvenile male, and juvenile female. It was therefore essential to examine samples of each component of the population to determine if there were seasonal changes in weight and fat. In addition to fats in essential structures, fat in variable reserves represents accumulated provision for energy at rates exceeding dietary intake. Fat accumulation depends upon many environmental factors as well as on the food of the bird and the metabolic state of the bird at the time of fat deposition. We have recently gathered evidence that the fatty acid composition of many of the willows

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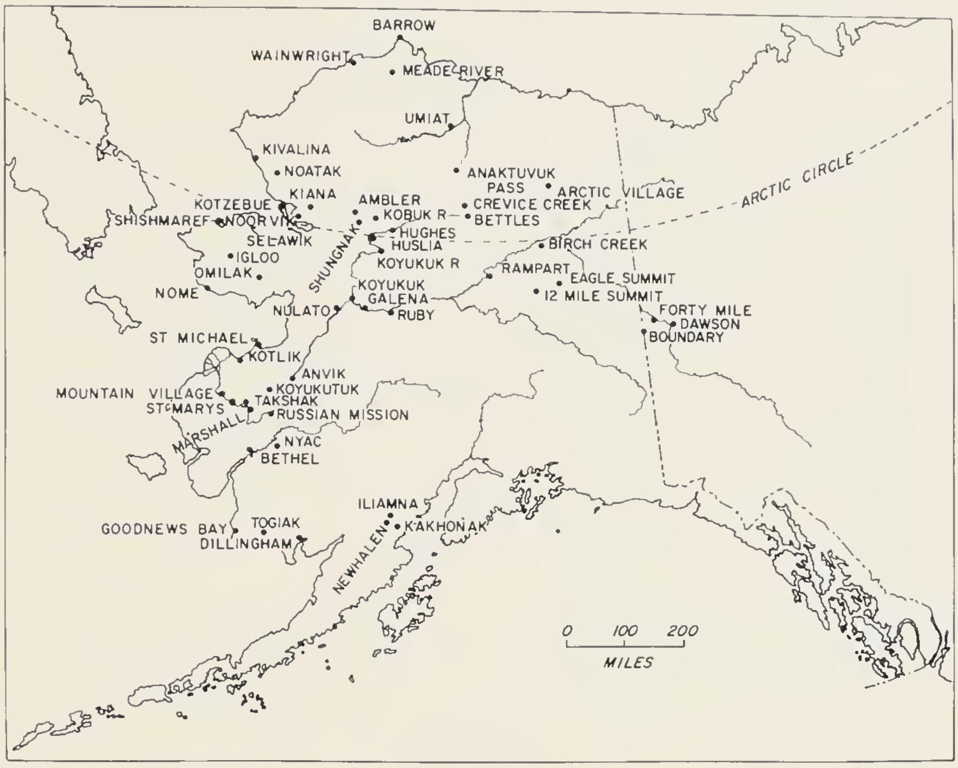

FIG. 1. Map of Alaska and adjacent Yukon Territory showing collecting locations of Willow Ptarmigan.

eaten by the Willow Ptarmigan changes significantly from one season to another (West and Meng, unpublished). We also wanted to see if fatty acids of the diet were incorporated unchanged into the fatty acids in the depot fat of the ptarmigan. This would provide a prime example of a specialist bird incorporating certain fats, in this case willow fats, into its own composition. If ptarmigan proved to be a "willow bird" by virtue of its fat we might then anticipate finding other species of birds with their fat marked by reason of their diet. In this way, we might in the future be able to trace a migratory pathway or at least to tell from where a bird has come by allocating its fatty acid spectrum to the various dietary sources.

METHODS

Willow Ptarmigan were collected by shotgun throughout the year in the Brooks Range of northern Alaska (Fig. 1) specifically at Umiat (69° 24′N., 152° 07′W.), Anaktuvuk (68° 10′N., 151° 46′W.), Crevice Creek (67° 22′N., 152° 04′W.), and Bettles Field (66° 55′N., 151° 28′W.). Individuals collected from these areas are part of a morphologically homogeneous population as determined from wing and tail measurements of over 1200 samples (West et al., 1968). All data on fat and fatty acid composition of ptarmigan were taken from these collections. Additional birds (1400), collected by resident people in villages throughout Alaska, are also included in the net weight analysis. By employing a Duncan's multiple range test it was possible to show that the weights of the ptarmigan collected from the other areas in each of the four age-sex groups were not statistically

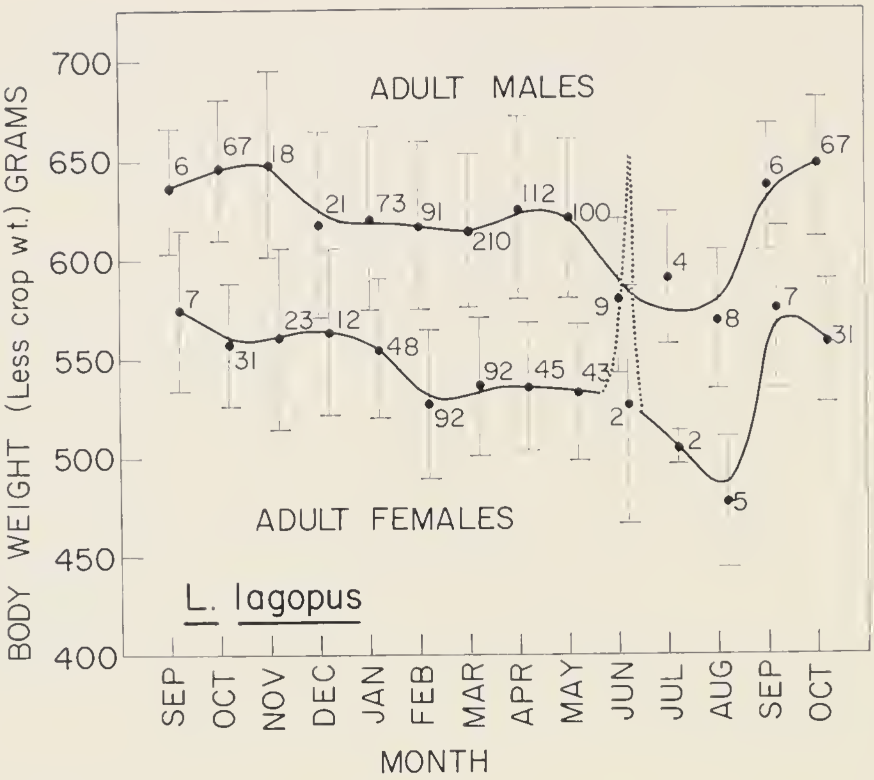

FIG. 2. Seasonal changes in body weight (less crop weight) of adult Willow Ptarmigan. Number beside mean represents sample size; vertical lines indicate one standard deviation. The dotted line for adult females in June indicates the assumed increase in weight due to egg formation (not recorded in the two females shown here collected after egg laying).

different from those collected in the Brooks Range (West et al., MS). The areas of collection are shown in Figure 1.

Birds were frozen in plastic bags immediately after shooting and shipped to the Institute of Arctic Biology for processing. Here they were thawed, weighed, the crop removed and weighed, the bird aged and sexed, and the wing and tail measured. Since weights of crops varied from about 3 grams when empty to 100 to 120 grams when full, the weight of the whole bird minus the crop weight (= net weight) was used in all analyses.

Seventy-nine samples of subcutaneous depot fat taken from the interclavicular area of birds selected at random from collections were analyzed for their fatty acid composition. In addition 82 birds were selected at random from fall, winter, and spring samples for total lipid content and fatty acid composition. The digestive tract, feathers, feet, and manus of the wings were removed prior to grinding and drying. Birds were ground in a large meat grinder and then either dried in air at 80 C or frozen and lypholized. An aliquot of the resultant dry material was extracted using petroleum ether (30–60 C boiling point) in a Soxhlet extractor. Following extraction the lipids were saponified using alcoholic KOH. The depot fat samples were saponified directly. The non-saponified fraction was discarded and the fatty acid salts were converted to free fatty acids with HCl. The fatty acids were converted to their methyl esters by boron trifluoride methanol and chromatographed on DEGS (diethylene glycol succinate) in an F and M hydrogen flame chromatograph. Peaks were identified using standard fatty

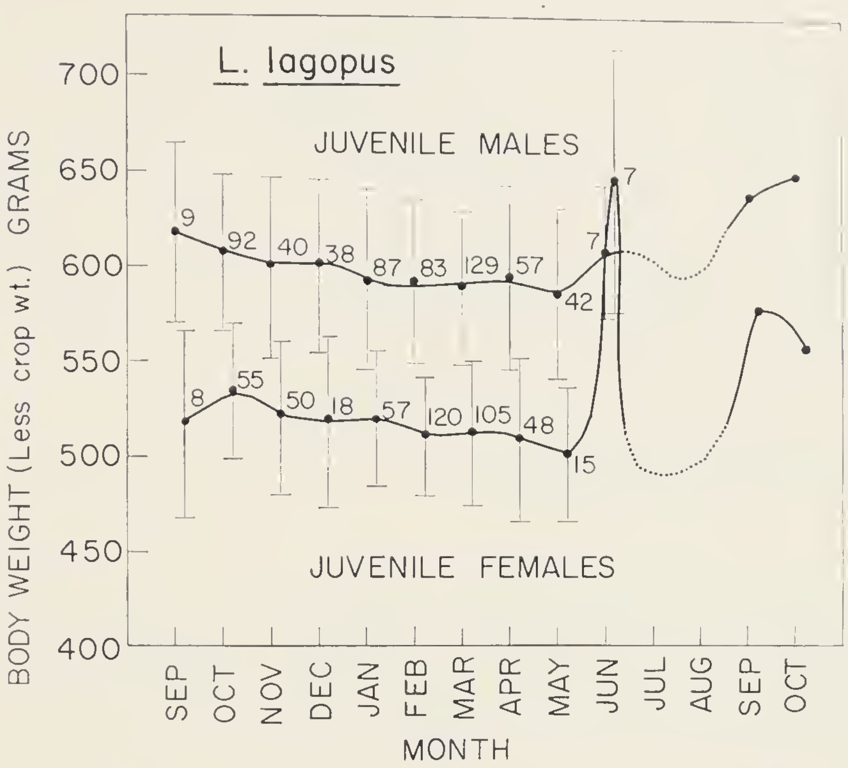

FIG. 3. Seasonal changes in body weight (less crop weight) of juvenile Willow Ptarmigan. Number beside mean represents sample size; vertical lines indicate one standard deviation. Dotted line indicates assumed summer weights. Juveniles in their second September and October are classed as adults. Therefore, the points for these two months are taken from Fig. 2.

acids and by using Ackman's (1963) technique of plotting the logarithm of the relative retention time to stearic acid (C_{18}) against carbon numbers. Peaks were triangulated and areas used to calculate the relative per cent of each acid.

RESULTS

Body Weight.—Adult males were heavier than adult females at all seasons (Fig. 2). Weights were highest during the fall (October and November), declined slightly during the winter and showed a slight peak during April and May. Males showed a decline in body weight in early June while they were undergoing courtship and territorial activities. They reached their lowest weight in August and then climbed rapidly to the maximal weight in October and November. Adult females likewise had a high peak in September, a low in February and a slight rise in April. Their decline began later in the summer than that of the males. The summer low came after egg laying and during the time of care of chicks and reached its lowest point in August. There was an increase of about 100 grams between August and September when the females reached their maximum weight.

First year birds (determined by the presence of the bursa of Fabricius prior to January or by the presence of a darkly pigmented ninth primary

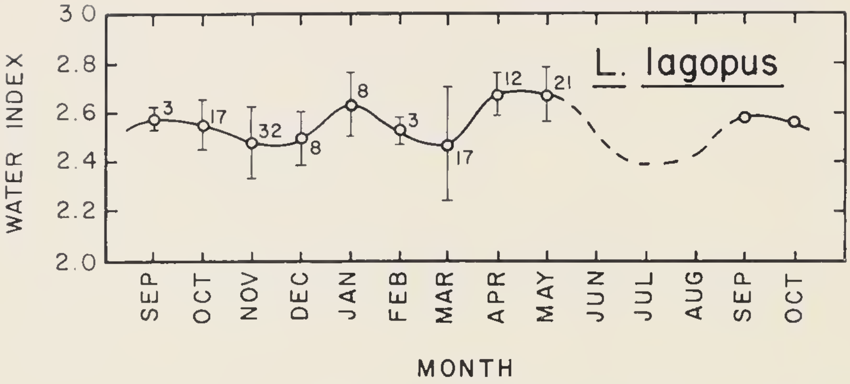

Fig. 4. Seasonal variation in water index (grams water/fat-free dry weight) of Willow Ptarmigan carcasses from the Brooks Range.

feather (West et al., 1968) did not show the same abrupt changes in body weight as did the adults (Fig. 3). Juvenile males however were heavier than the juvenile females at all seasons except briefly during egg laying when weights of collected females were higher than those of males at any season. Weights were highest for juvenile males in September and declined gradually until May. We have no records for the middle of the summer. Juvenile females had their highest weights in October and declined during summer. Females, which breed in their first year, while forming and laying eggs had

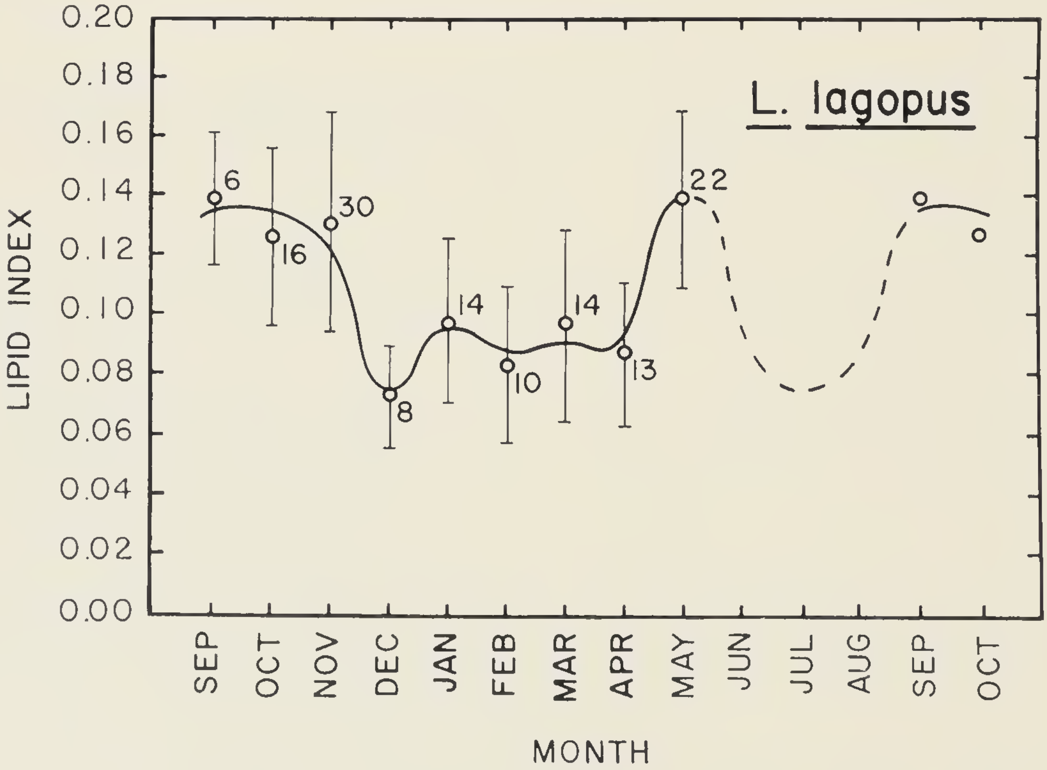

Fig. 5. Seasonal variation in fat index (total ether extractable lipid, grams/fat-free dry weight) of Willow Ptarmigan carcasses from the Brooks Range.

TABLE 1

	Fat-free dry weight (g)		Wing length (mm)*	
	n	Mean ± SD	n	Mean ± SD
Adult Male	20	108.56 ± 10.34	416	205.6 ± 4.7
Adult Female	16	95.24 ± 10.25	165	192.0 ± 4.1
Juvenile Male	19	96.35 ± 8.45	329	201.8 ± 5.2
Juvenile Female	23	87.73 ± 10.35	225	190.1 ± 5.1

* West et al., 1968.

weights almost 150 grams higher than those collected in May before egg formation had taken place.

Body Water and Fat.—There was no statistically significant difference in the proportion of water in the carcasses of different age and sex categories ($p > 0.10$). Body water, calculated as the water index (weight of water/fat-free dry weight of carcass) fluctuated throughout the year being significantly higher in January and April–May than in November and March respectively ($p < 0.01$) (Fig. 4).

Body fat was determined as the lipid index (weight of fat/fat-free dry weight). The fat-free dry weights of carcasses varied significantly among the four age-sex categories (Table 1) but did not vary with time of year from September through May. No values were obtained on summer birds. Lipid indices were therefore calculated for each bird based on the weight of ether-extracted lipid and the mean fat-free dry weight for its age-sex category.

There were no statistically significant differences in lipid index between ages or sexes in any month ($p > 0.4$), but there were statistically significant differences between months of the year (Fig. 5). The index for December was significantly lower than that for either November ($p < 0.01$) or January ($p < 0.05$) and there was a significant rise from April to May ($p < 0.001$).

Fatty Acid Analysis.—The predominant fatty acids in either the total lipids or depot lipids of Willow Ptarmigan are 16- and 18-carbon acids as shown in the two sample chromatograms (Fig. 6). The most abundant acid in the total lipids is linoleic acid ($C_{18=2}$) (Fig. 7). There are significant amounts of 22-carbon acids. There are a few small seasonal changes in fatty acids that can be noticed in Fig. 7; the amount of stearic acid (C_{18}) and docosenoic acid ($C_{22=1}$) increased significantly from fall to winter. At the same time there was a sharp decrease of oleic ($C_{18=1}$) and linolenic acid ($C_{18=3}$). There appeared to be no significant changes between winter and spring. Unfortunately we did not retain specimens for fat analysis for the summer months.

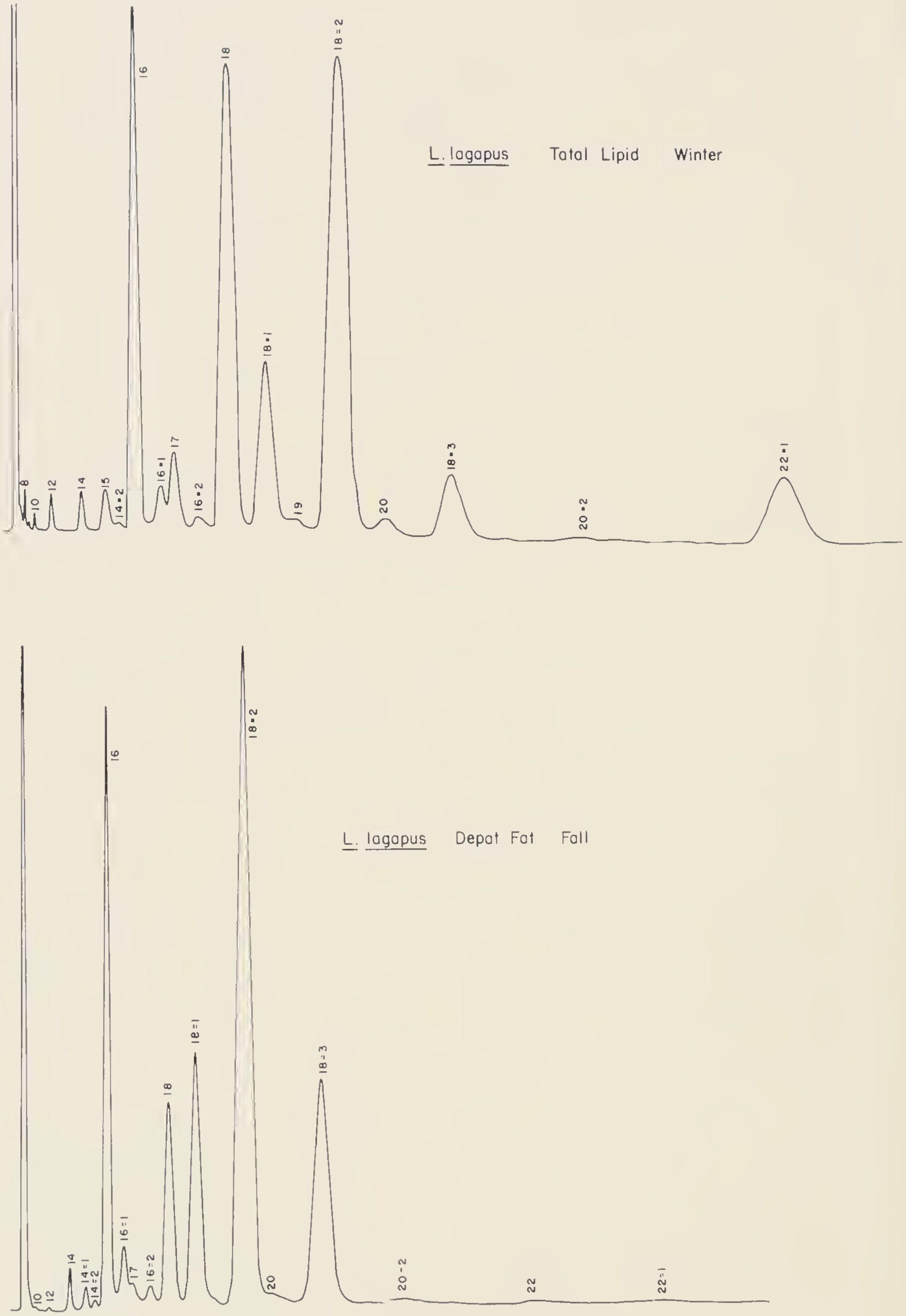

FIG. 6. Sample gas chromatograms of total lipid and depot fat fatty acids of Willow Ptarmigan from the Brooks Range. Each peak represents one fatty acid; the area under the peak indicates relative proportion of acids. Numbers represent length of the fatty acid carbon chain with the number of unsaturated bonds following the =.

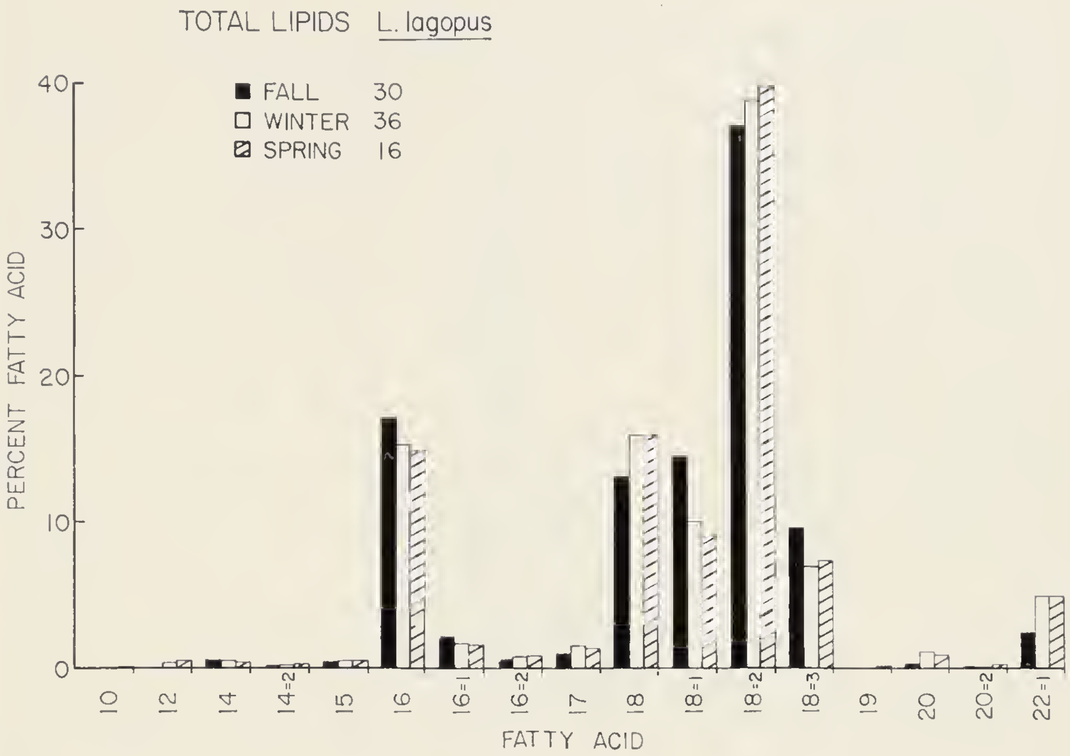

FIG. 7. Seasonal shift in proportion of fatty acids in the total ether extractable lipids of Willow Ptarmigan from the Brooks Range. Numbers on the abscissa indicate the length of the fatty acid carbon chain; the number of unsaturated bonds follows the =.

Depot fat fatty acids presented a picture somewhat similar to that found for total lipid fatty acids with the 16- and 18-carbon fatty acids being predominant (Fig. 8). One exception was that the longer chained fatty acids were not as abundant. The same seasonal shifts occurred in depot lipids as occurred in the total lipids with a decrease in palmitic acid (C_{16}) oleic, and linolenic acid from fall to winter and a concomittant increase in stearic, linoleic, and arachidic (C_{20}) acids. Birds in winter had a higher content of linoleic acid than at any other season. The amount of linoleic acid decreased in spring while the amount of palmitic, oleic, and linolenic acid increased in the spring.

DISCUSSION

Body Weight, Fat, and Water Content.—The marked seasonal changes in net body weight of adult Willow Ptarmigan correspond with observed seasonal changes in activity and energy requirements of the birds and parallel the weights of captive birds (West, in press). The high weight of adults in November and April–May correlate with times of high water and lipid content. The peak in high water and lipid indices in January does not match an increase in weight and is unexplained at present. The spring and fall increases in fat correlate with time of migration of Willow Ptarmigan

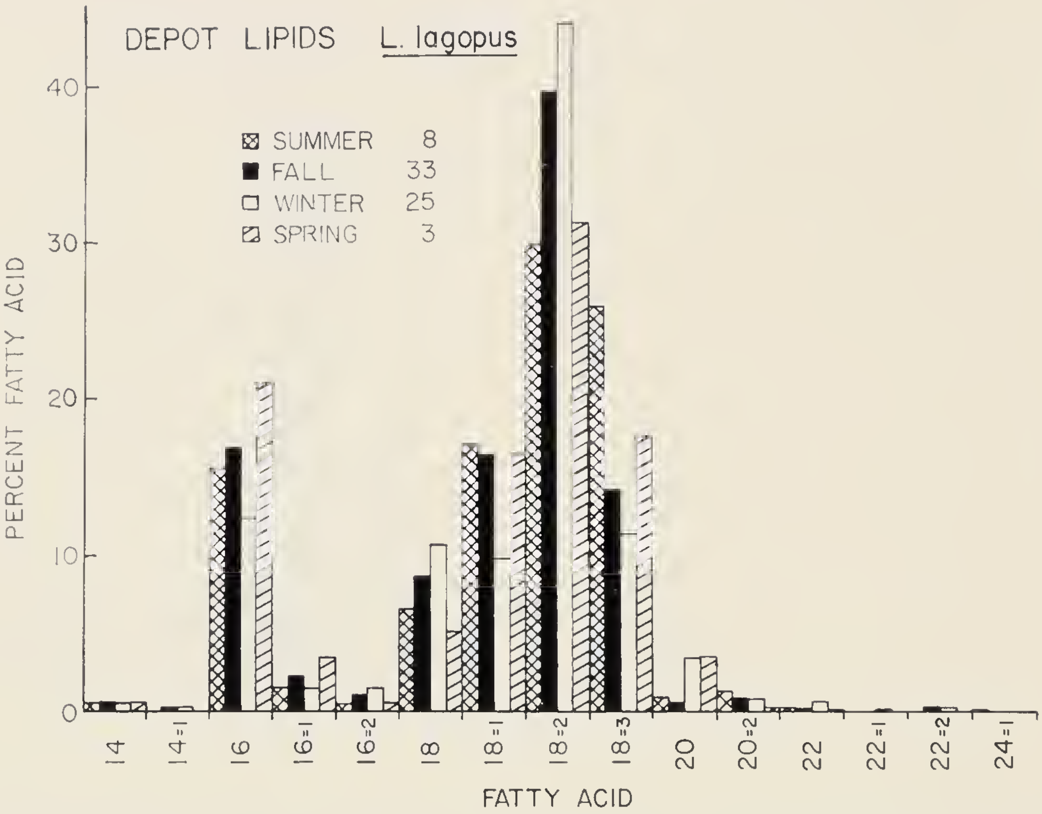

FIG. 8. Seasonal shift in the depot lipids of Willow Ptarmigan from the Brooks Range. Numbers on the abscissa indicate the length of the fatty acid carbon chain; the number of unsaturated bonds follows the =.

in the Brooks Range (Irving et al., 1967*a*). The amount of fat deposited however was slight in comparison with that required for long distance migrants (Odum, 1965; Odum and Connell, 1956). There was a slight depression in weight during the middle of the winter when cold and wind occasionally impede feeding and may have their greatest metabolic effect but in general the fall, winter, and spring body weight level is greatly elevated above that of the summer. First males and then females decreased in body weight during the early summer and increased with great rapidity between August and September. Males decreased in weight between May and June during the time of territory defense and courtship. Females decreased in weight between June and July in the time following egg-laying and during incubation and continued their decline into August perhaps due to the energy demanding stresses of parental care. Molt, which begins in May in males and June in females, continues all summer until early October, except during egg laying (West, in press) and incubation (Weeden, pers. comm.), and places a continuing energy burden for feather synthesis and possibly for thermoregulation on all birds. Although it is not shown in Figure 2, adult females undoubtedly become extremely heavy briefly in

June during egg formation and laying. Our June sample was not taken at the right time to show this for adults but, as with the juvenile females shown in Figure 3, there must have been a sudden (30 per cent) increase in feeding and an increase in body weight contributing to formation of eggs prior to egg laying. This sudden increase in weight has been documented by Irving (1960) for passerines and sandpipers just prior to egg laying, and noted also by Weeden (pers. comm.) for Rock Ptarmigan (*Lagopus mutus*).

Juvenile females become fully grown or equivalent in size to the adult female in their first spring and undergo a complete breeding cycle during their first year as evidenced by the presence of fully formed eggs in the oviducts. Although both juvenile males and juvenile females make migrations comparable to that of adult females they did not show the two pronounced peaks in weight of the adults during spring and fall. Juveniles are evidently still growing in their first winter and the addition of protein results in less weight decline in winter than the adults.

The general pattern of body weight change in Willow Ptarmigan was similar to that of the non-migratory Ruffed Grouse (*Bonasa umbellus*) in that there was a slight decline during late winter, a sharp rise during the spring, and a fall in the summer in birds collected in New York (Bump et al., 1947). However, the Ruffed Grouse did not show a distinct peak in fall. Juvenile Ruffed Grouse showed the same weight pattern as the adults after May and showed a rather steady increase in weight in their first fall, reaching adult weight in spring. In Willow Ptarmigan there is an abrupt increase in weight that occurs only in the bird's second (and subsequent) autumn and there is no evidence of an increase during the first winter.

Koskimies (1958) has shown that total body weight (with crop) of the Finnish Capercaillie (*Tetrao urogallus*) and Blackgame (*Lyrurus tetrix*) increased slightly from September through November then declined in December. Increases were greater for juveniles than for adults. The situation with Willow Ptarmigan varies with age and sex and only adult males achieved a weight maximum in November. The small sample sizes in September in all four categories of Willow Ptarmigan make comparisons difficult, but it appears that adult males lost weight in winter before adult females, perhaps because they remain farther north in a climate that gets colder earlier and where energy requirements may be higher (Irving et al., 1967*a*; West, in press). Adult females which migrate south along with the juvenile females did not lose weight until February when their weights did not abruptly change but continued to fall gradually throughout the winter.

Siivonen (1957) stated that the weight cycle of adult tetraonid females differs from that of males in that the former has two weight peaks per year and the latter only one. Alaskan Willow Ptarmigan appear to be an exception to this rule since both sexes show two weight maxima: males in October–November and April–May; females in September–December and again in early June.

Odum and his associates have assumed that the fat-free dry weight of a single species remains constant throughout the year for birds of similar wing length (Odum and Connell, 1956: Connell, Odum, and Kale, 1960). The fat-free dry weight of Willow Ptarmigan carcasses differs significantly with age and sex, and these categories also differ significantly in wing length (Table 1). Although we could not demonstrate statistically significant seasonal differences in fat-free dry weight, the data show peaks in fall and spring with a low in winter. Samples are lacking for summer but observation by us and by Robert Weeden indicate that summer birds, especially incubating and brooding females, lose a significant amount of body mass in summer. These observations need documentation. We cannot now see why there are significant seasonal changes in water indices of Willow Ptarmigan. The seasonal shifts do not follow the changes in fat precisely (Figs. 4, 5). In fall, the water index falls prior to fat; in spring, the water index rises prior to fat, and in mid-winter, they both rise together. Some animals show increases in water volume which are either due to acclimation to cold or heat (Hart, 1964) but we are not aware of any studies of water content throughout the year in wild birds.

The seasonal change in lipid index may be related to a number of factors such as preparation for migration in fall and spring or preparation for summer breeding and for winter cold stress. However, the changes in fat index which vary from 0.07 in December to 0.14 in September and May, represent a difference of only 6.5 grams of fat. This would amount to a little over 60 kilocalories, or less than one-third of the average daily energy requirement of wild Willow Ptarmigan (West, in press). Obviously ptarmigan are not fat birds at any time of the year unlike many passerines, and the fat deposited in the body does not constitute a substantial energy reserve.

Fatty Acids.—The composition of fatty acids in the diet of Willow Ptarmigan has been compiled from data obtained on all of the plant species which are present in the ptarmigan diet (West and Meng, 1966) (Fig. 9). Fatty acid composition was determined by gas chromatography for each species independently (West and Meng, unpublished) and Figure 9 represents a proportional configuration of the fatty acid composition of the diet. The diet consists largely of 16-, 18-, 20-, 22-, and 24-carbon acids. The predominant acid is linoleic acid ($C_{18\text{-}2}$).

There are marked changes in the diet lipid composition with season. From summer to fall there was an abrupt decrease in palmitic (C_{16}) and linolenic ($C_{18\text{-}3}$) acid and an increase in linoleic ($C_{18\text{-}2}$), arachidic (C_{20}), behenic

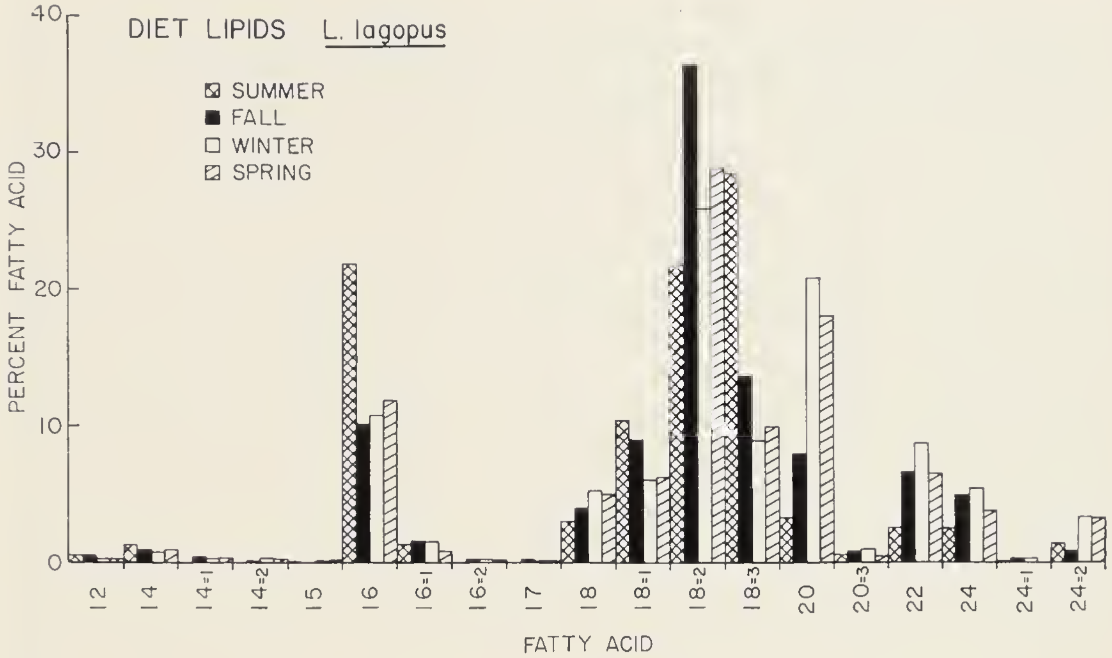

FIG. 9. Seasonal changes in the fatty acids consumed in the diet of Willow Ptarmigan in the Brooks Range. Numbers on the abscissa indicate the length of the fatty acid carbon chain; the number of unsaturated bonds follows the =.

(C_{22}) and lignoceric acid (C_{24}). The abrupt changes in these acids reflect the shift in the ptarmigan diet from the summer one of leaves and berries which are high in palmitic (C_{16}) and linolenic ($C_{18=3}$) acids to the fall one of willow buds and twigs. From fall to winter there were increases in stearic (C_{18}), arachidic (C_{20}), behenic (C_{22}) and tetracosadienoic ($C_{24=2}$) acids. and decreases in oleic ($C_{18=1}$), linoleic ($C_{18=2}$) and linolenic ($C_{18=3}$) acids. The increases in the saturated and long-chain fatty acids are due to the changes that occur in willows from fall to winter (West and Meng, unpublished). The increases in saturation, especially in the arachidic acid (C_{20}) fraction, coincides with an increase in saturated triglycerides in the sheathes of the willow buds. There were small differences in fatty acid composition from winter to spring when the diet shifted slightly to include exposed *Dryas* leaves and other low vegetation (West and Meng, 1966). It will be noticed that the spectrum of fatty acids in the diet ranges from 12–23 carbon chains with the majority located in the 16- and 18-carbon number groups.

When the diet lipids are compared with the total lipids or especially with the depot fat situation (Figs. 7, 8, and 9), it is obvious that the ptarmigan are "willow birds" in that their fatty acid composition resembles that of the major fatty acids in the diet closely even to the point of including in total lipids appreciable amounts of 20 to 22 carbon acids, unusual in vertebrate fats. Linoleic acid ($C_{18=2}$) is the predominant acid in both diet and bird. The abrupt seasonal changes in fatty acid composition of the diet lipids was not present in the total lipid fraction. The changes from fall to winter in increased saturation and chain length are not evident in either the total lipids nor in the depot lipids. One striking feature was the reduction in amounts of acids with a chain length greater than 20 carbons that occurred when diet fatty acids are converted into depot fat fatty acids by the bird. The alterations that occur from diet lipid to depot lipid can occur either through bacterial action in the cecum or through transformation in the liver. It is also possible that there is a differential retention and deposition of certain acids. Therefore, although the general picture of ptarmigan depot lipids is similar to that of their diet, the great changes that occur in diet lipids between seasons is not clearly reflected in the depot fats.

Although a great deal of work has been done on the effects of diet lipids on the lipid composition of laboratory animals (Edwards et al., 1962; Beare and Kates, 1964; Carroll, 1965; Feigenbaum and Fisher, 1959; Machlin et al., 1962) and humans (Imaichi et al., 1965) very little has been done on wild birds with the exception of our recent work on Common Redpolls (*Acanthis flammea*) (West and Meng, 1968) and that of Moss and Lough (1968) on four species of game birds. With redpolls it was possible to show that there were great changes in depot fat composition between spring migrating birds and those during the breeding season and that these differences may have been due to different seed diets in the wild. However, redpolls in captivity did not alter their depot fat fatty acid composition when fed experimental diets that had different fatty acid compositions.

Moss and Lough (1968) investigated the depot fat fatty acid composition of two Red Grouse (*Lagopus lagopus scoticus*) a close relative of the Willow Ptarmigan (*Lagopus lagopus alascensis*) under discussion here. The Red Grouse is sedentary and its diet consists mainly of heather (*Calluna vulgaris*) unlike the migratory and willow-eating Willow Ptarmigan. The major depot fat fatty acids of both birds closely resemble that of their respective diets. Both diets are high in linoleic acid ($C_{18=2}$) as are the depot fats.

Walker (1964) in studying the major fatty acids in some migratory birds, showed that there were definite species differences which could have been related to diet. In all of the species she studied however, oleic acid ($C_{18=1}$) was the predominant component. Even the herbivorous Bobolink (*Dolichonyx oryzivorus*) had conspicuously less linoleic ($C_{18=2}$) than oleic acid ($C_{18=1}$). In the Willow Ptarmigan and Common Redpoll, both herbivores, the predominant acid was linoleic ($C_{18=2}$).

In making the generalization that depot lipids of birds are largely derived from the diet, caution should be exercised since the work with redpolls indicates that with increased fat deposition from different diets a more uniform fatty acid composition of the depot fats results. We still do not know the complete role of the cecal microbiota in synthesizing fatty acids (McBee and West, 1968) and at the present we cannot be certain if all of the essential fatty acids are directly derived from diet or are synthesized in the cecum.

SUMMARY

Body weight less crop weight of adult Willow Ptarmigan from western, northern, and central Alaska are higher in fall and in spring than in winter in periods corresponding to migration of these birds. Summer weights are much lower than winter weights. The decline in weight corresponded to the time of courtship and territory defense in males, and to post-egg-laying incubation and parental care in females. During egg formation and laying, weights of juvenile females and presumably adults, were higher than at any time of year. Juvenile ptarmigan reach a maximum juvenile weight in their first fall and then gradually decline in weight throughout their first winter and spring. Juveniles can no longer be distinguished from adults by known morphology after their second fall and their weights are then included in the adult weights and at that time show a marked increase over summer.

Water index of Willow Ptarmigan carcasses (whole bird less digestive tract, feathers, feet, and wings from the wrist distally) varied from September through May being significantly higher in September, January, and April–May than in those months preceding. Lipid index (ether extractable lipids) of Willow Ptarmigan carcasses varied with the change in body weight being high in fall and spring and lower in winter. However there was a significant increase in January not related to body weight. Although no data are available for summer birds, it is assumed that fat decreases with body weight.

There is a direct correlation of diet fatty acids with those deposited in the bird either as total lipids or as interclavicular depot lipids. The predominant acids are 16- and 18-carbon chains with the most abundant being linoleic acid ($C_{18=2}$). The long chain fatty acids (C_{22}–C_{21}) present in the diet are poorly represented in the total lipids and in only trace amounts in the depot lipids. The marked seasonal shifts in diet fatty acids are not pronounced in the birds' fat. This indicates that although the general pattern of diet and bird fatty acids are similar, small seasonal changes are not evident and certain long chain fatty acids in the diet are either not utilized or converted to other forms by the bird.

ACKNOWLEDGMENTS

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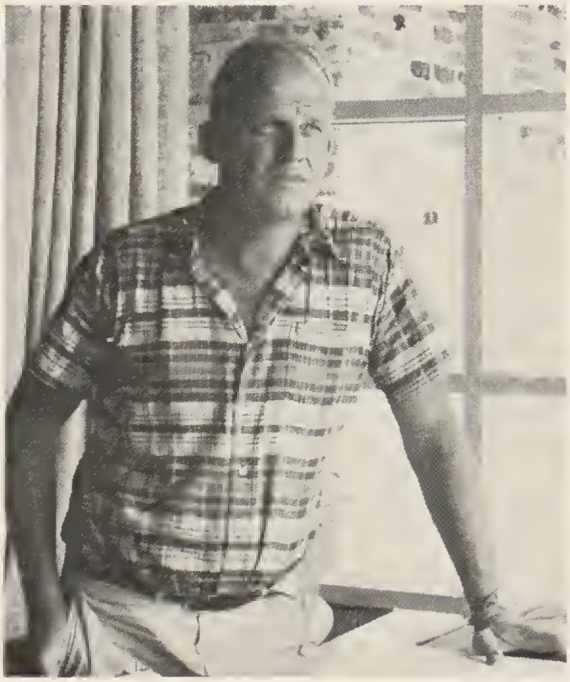
NEW LIFE MEMBER



Mr. John H. Dick of Meggett, South Carolina has recently become a Life Member of The Wilson Ornithological Society. Mr. Dick is well known to most members of the Society as the outstanding bird artist whose paintings and drawings were featured in such books as "Warblers of America," "A Gathering of Shorebirds" and "The Bird Watcher's America." Besides his painting Mr. Dick is engaged in an active program of field work and bird photography. He also maintains a collection of live waterfowl, which was visited by some members of the Society on the occasion of the Charleston meeting in 1963. Mr. Dick attended Brooks Prep School and the Yale Art School, and is a member of the AOU and the Cooper Society.

TERRITORIAL RELATIONSHIPS OF BLUE-WINGED WARBLERS, GOLDEN-WINGED WARBLERS, AND THEIR HYBRIDS

Millicent S. Ficken and Robert W. Ficken

Territorial relationships of congeners are of special interest to ecological and evolutionary theory (e.g., Orians and Willson, 1964; Hamilton, 1962), although such systems in hybridizing forms have been the subject of very few studies. The Blue-winged Warbler (*Vermivora pinus*) and the Golden-winged Warbler (*V. chrysoptera*) have recently come into contact in the northeastern and north central United States and hybridize (Short, 1963); they provide a good opportunity for a study of territorial relationships of two species and their hybrids.

The purpose of this paper is to describe intraspecific territorial relationships, those of two hybrids, of hybrids and a parental species, and interspecific ones. From this study we determine the role of visual and vocal releasers in elicting territorial behavior. Although these have been the subject of numerous experimental studies using both visual (e.g., Noble and Vogt, 1935) and vocal releasers (e.g., Dilger, 1956; Lanyon, 1963; Gill and Lanyon, 1964), few such studies have used observations on natural encounters. Finally, the role of the territorial system in the speciation of this complex is discussed.

METHODS

Territorial behavior was studied in a colony consisting of both species and Brewster's hybrids at Varna (Tompkins Co.), New York in May and June, 1961, May through August of 1962, and May, 1963 and 1966. Additional observations of male Blue-wings, a Brewster's hybrid, and a Lawrence's hybrid were made near Thurmont (Frederick Co.), Maryland in May 1964.

Notes were taken on all agonistic interactions. In addition, territories were roughly mapped by observing the positions of males for at least two days and usually over a period of several weeks.

THE BIRDS

The two species differ primarily in size and color of wing bars, back and breast color, and face pattern. Hybrids show varying degrees of intermediacy. The plumage colors of the birds we studied are indicated in Table 2. Short (1963) showed that many birds that appear "pure" in the field actually show introgression from the other species. However, for the purpose of this study, Blue-wing and Golden-wing refer to birds that looked typical of that species in the field.

The primary song of the Blue-wing is a *bee* followed by a long *buzz*, that of the Golden-wing a *zee* followed by a variable number of short *bee* notes (Ficken and Ficken, 1967). Each individual hybrid that we studied consistently gave the song of one or the other parental species. A secondary song, similar in both species. consists of a trill followed by a *buzz*.

OBSERVATIONS

General aspects of territorial behavior.—Resident male Blue-wings arrived between 6 May and 14 May in the Varna colony in 1962 and 1963. Golden-wing males arrived from 12 May to 23 May and Brewster's hybrid males from 6 May to 12 May. "Pure" males usually obtained conspecific females within a week of their arrival. Both sexes confined all their activities to the territory from the time of arrival until the young were fledged. After this time territorial boundaries broke down.

Territories usually consisted of overgrown fields with many shrubs and small trees (under 20 feet) bordered by taller deciduous trees. Size of territories varied from less than one acre to almost two acres. Small trees within the territory and trees at the edge of the territory were used as singing posts, particularly during incubation. All the nests that we found were situated at the field-woodland edge and this is the typical nest site in both species (Bent, 1953).

Vocalizations concerned with territorial defense.—Unmated males sing primary songs almost uninterruptedly as they forage. Later in the season, particularly in the Blue-wing, and following territorial encounters in both species and hybrids, the secondary song, similar in both species, is given (Ficken and Ficken. 1967). Our observations indicate that since secondary song usually only occurs after an encounter has already started, that it is not important in initiating interspecific encounters. Song is usually absent during encounters and is only resumed after a few minutes, typically when one of the encountering males has left the area. Songs given during and immediately following encounters are usually different from songs of undisturbed birds. In Golden-wings the primary song is shortened or the secondary song is given while Blue-wings usually give only secondary songs (Ficken and Ficken. 1967).

Some interactions consist solely of song exchanges. The following is an example of one such short intraspecific exchange: Blue-wing No. 1 approaches Blue-wing No. 2 to 10 feet in the boundary zone between their territories. Blue-wing No. 2 sings primary song. Blue-wing No. 1 which had been singing primary songs before No. 2's approach. changes to secondary song. No. 1 leaves. Interspecific exchanges also occurred but more rarely. For example, a Blue-wing and a Golden-wing with overlapping territories had the following exchange while in the same tree: Blue-wing, which had been giving primary song, switches to secondary song and Golden-wing shortens primary song. Both move off, in opposite directions. Similar exchanges were noted between a Brewster's hybrid with Blue-wing song and a Brewster's hybrid with Golden-wing song.

Other types of vocalizations are uncommon during territorial encounters. A snapping sound made by contact of the mandibles occurred occasionally during chases and fights. Chip notes were sometimes given in intraspecific Blue-wing encounters. On one occasion a marsh-wren like chatter was given by a Golden-wing during a chase.

Postures and displays associated with territorial defense.—These are similar in the two species and hybrids, and the following is an inventory of such behavior.

Crown raising. Pronounced raising of the crown feathers was occasionally seen in both species immediately following an encounter. This movement was more obvious in the Golden-wing because of the conspicuous crown patch.

Soliciting. We observed three instances of male Golden-wings after repeated encounters (twice with Blue-wings, once with a Brewster's hybrid) turn away from the opponent and perform a display resembling a female soliciting copulation. Male Soliciting incorporates quivering wings, raised tail and erected crown feathers and a lowered breast (illustrated in Ficken and Ficken, 1962). The display was given by the bird that seemed to be losing the encounters and immediately followed a chase by the opponent. We never observed it in Blue-wings but Frank Gill (pers. comm.) reports a similar posture in this species; after an attack by the opponent the Blue-wing raised its tail while the wings were drooped and quivering.

Tail Spreading. This is a prominent feature of all male encounters in both species and hybrids, and the tail often seems maximally spread, exposing much white. It is often performed in flight, particularly by a bird that is being chased. It is also sometimes given by a perched bird immediately after an encounter.

Chases. Chases are of common occurrence during territorial encounters, one bird usually flying at the other bird, which flees while the first bird continues pursuing it.

Supplanting. One bird flies at the other, the other leaves, and the first bird lands in the second's original position.

Flying past. This was only observed in encounters between two Brewster's hybrid males. One bird flew past the other, landing about ten feet away. The second bird then engaged in this behavior, and some encounters of 20 minutes duration consisted mainly of this behavior.

TABLE 1
A COMPARISON OF INTERSPECIFIC AND INTRASPECIFIC ENCOUNTERS

	Both males unmated	One male mated	Both males mated	No. encounters without fights	No. encounters with fights	Duration (S = < 5 min., M = 5–20 min., L = > 20 min.)
Interspecific	0	5	5	4	6	S 4 M 4 L 2
Intraspecific	6	3	1	10	0	S 3 M 4 L 2

Fighting. Fighting involves actual contact of the two birds, rather than the sham fights seen in the American Redstart (*Setophaga ruticilla*) (Ficken, 1962).

Comparison of interspecific and intraspecific encounters.—Territorial encounters were most frequent and intense before nest building; during incubation only occasional chases were seen. The following are extracts from our field notes of intraspecific and interspecific encounters:

17 May 1962. Varna, N.Y. Golden-wing male chases Blue-wing male which had approached to within 30 feet. Both females are in the immediate area. Blue-wing male flies off with tail widely spread. Two minutes later he chases the Golden-wing male. Males separate and stay 75 feet apart for several minutes. Then male Blue-wing chases male Golden-wing. Golden-wing raises crown feathers markedly after being chased. He lands in the same tree as the Blue-wing but faces away from him . . . . Blue-wing male flies after Golden-wing male. They perch briefly 20 feet apart and then they fight. Blue-wing male flies off.

11 May 1962. Varna, N.Y. Two Blue-wings, both unmated, have adjacent territories. One male chases the other. Harsh chips are heard in flight. White in tails of both birds is very prominent during chases. Chases continue for several minutes over the same small area. During the chases one is usually about a foot behind the other. They land 20 feet apart and harsh chips are heard. One male then leaves the encounter area.

Table 1 compares intraspecific (Blue-wing vs. Blue-wing and Golden-wing vs. Golden-wing) and interspecific encounters, excluding interactions consisting solely of song exchanges. Intraspecific encounters occurred more commonly among unmated males; interspecific encounters did not take place unless one male was mated. Fights were observed only in interspecific encounters. Intraspecific encounters were usually confined to a narrow boundary zone between two territories. On the other hand, interspecific encounters took place over a much wider area. The duration of encounters was similar in both situations. The postures and displays during and after encounters were similar in interspecific and intraspecific situations.

TABLE 2
RELATIONS BETWEEN PLUMAGE, SONG, AND TERRITORIAL BEHAVIOR
(BW = Blue-wing, GW = Golden-wing)

No. of cases	Birds	Song	Plumage
			OVERLAPPING TERRITORIES
5	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Golden-wing	GW	White breast, face and throat patch, yellow wing bars
1	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Lawrence's hybrid	BW	Yellow breast, face and throat patch, white wing bars
2	Golden-wing vs.	GW	White breast, face and throat patch, yellow wing bars
	Brewster's hybrid	GW	White breast, no face or throat patch, yellow wing bars
			NON-OVERLAPPING TERRITORIES
10	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Blue-wing	BW	Yellow breast, no face or throat patch, white wing bars
6	Golden-wing vs.	GW	White breast, face and throat patch, yellow wing bars
	Golden-wing	GW	White breast, face and throat patch, yellow wing bars
1	Brewster's hybrid	GW	White breast, no face or throat patch, yellow wing bars
	Brewster's hybrid	BW	White breast, no face or throat patch, white wing bars
1	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Brewster's hybrid	GW	Yellowish breast, no face or throat patch, yellow wing bars

Territorial relationships of birds similar in song and plumage.—Table 2 summarizes the territorial situation as related to the visual and vocal releasers of the birds involved. No birds with similar plumage and song had overlapping territories. Furthermore, although territories were often adjacent to a conspecific, in one case a barrier of unsuitable habitat was between the territories (Fig. 1). In this case when Golden-wing No. 2 arrived, three days after Golden-wing No. 1, he attempted to settle near Golden-wing No. 1 on the same side of the swamp, but after several short encounters he moved across the swamp and shared a territory with Blue-wing No. 3. A similar state existed between the two Blue-wings. Blue-wing No. 5 attempting to settle on part of Blue-wing No. 3's territory, but after two short encounters he also moved across the swampy area. The swamp served as a barrier, minimizing contacts between conspecifics, and except for the initial encounters, none took place subsequently except for an occasional chase.

Unfortunately, we were unable to determine the territorial relationships of two yellow-breasted Brewster's hybrid males with Blue-wing songs which were near Blue-wings. In both cases the Brewster's males were unmated and had encounters with the mated Blue-wings near the females. Other than on these occasions, their territories seemed not to overlap.

Territorial relationships of birds dissimilar in both song and plumage.—In all cases observed where a Blue-wing and a Golden-wing were near each other there was territorial overlap between them which was often extensive (Fig. 1). We have an impression of mutual avoidance of unmated males. The two males were only rarely seen together in the same tree. They were usually some distance away from each other and tended to occupy the same areas at different times as Moynihan (1963) found in different species of honeycreepers.

The only interspecific encounters observed occurred in the presence of newly arrived females. If two mated males were close at other times, no encounters resulted. There were no encounters once nest building commenced. In one case, nests of a Blue-wing and a Golden-wing pair were 75 feet apart and both species were seen frequently in the overlap area.

Territorial relationships of birds similar in plumage but dissimilar in song.—We observed territorial relations to two male Brewster's hybrids, similar in plumage but one singing Golden-wing songs and the other Blue-wing songs (Fig. 1). Male No. 1 initially wandered over a 1.5 acre field and seemed to utilize all of it although he spent more time on the upper slope while singing and foraging. Six days later (12 May) the other Brewster's hybrid arrived at the field and was seen foraging on the upper slope. Several short encounters between the two males were observed. The following day long lasting, more intense encounters were observed. By the end of the day the newer arrival, No. 2, confined his activities to the lower part of No. 1's territory. The boundary between the territories seemed quite rigid. No further encounters were observed except for one short fight when No. 2's female entered the boundary zone followed by her mate. Both males tended to avoid the boundary and never were observed crossing it.

Meyerriecks and Baird (1968) observed that a yellow-breasted Brewster's hybrid with Golden-wing songs had many boundary encounters with a Blue-wing and they maintained non-overlapping territories.

Territorial relationships of birds dissimilar in plumage but similar in song.—A male Lawrence's hybrid had a territory extensively overlapping that of a male Blue-wing (Fig. 1). Both males were mated. On three occasions they were observed within 30 feet of each other in different parts of the overlap area but they simply ignored each other.

We also observed a white-breasted Brewster's hybrid with Golden-wing songs which had extensive territorial overlap with a Golden-wing (Fig. 1). The only encounters which we observed occurred when the hybrid (at the time unmated) approached the female Golden-wing within ten feet on two occasions. Lunk (1938) also observed overlapping territories of a Golden-wing and a Brewster's hybrid.

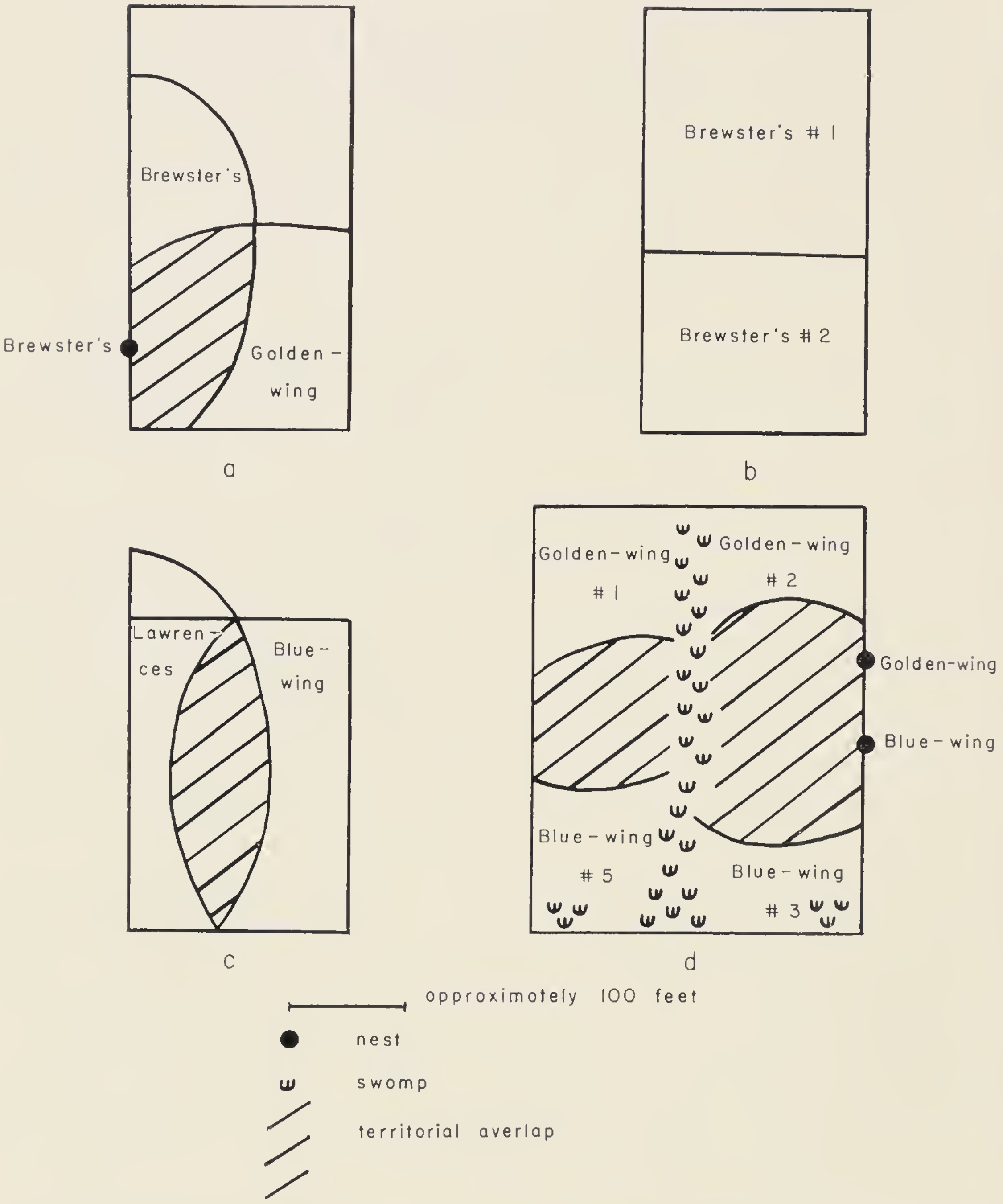


FIG. 1. Territorial relationships. Rectangles represent a field bordered by deciduous trees. a) Overlapping territories of a Brewster's hybrid and a Golden-wing. b) The same field the following year with non-overlapping territories of two Brewster's hybrids. c) Overlapping territories of a Lawrence's hybrid and a Blue-wing. d) Territories of two pairs of Blue-wings and two pairs of Golden-wings, showing overlap interspecifically and non-overlap intraspecifically.

Agonistic interactions with other warbler species.—Agonistic encounter also occurred with other warbler species. These encounters were usually of very short duration and there was no evidence of territorial exclusiveness. In all cases Blue-wings and Golden-wings were the aggressors, e.g., instigated fights and chases. Chestnut-sided Warblers (*Dendroica pensylvanica*) and Yellowthroats (*Geothlypis trichas*) frequently had territories overlapping those of the two *Vermivora* species. Encounters between Blue-wings and Yellowthroats were more common than those of Golden-wings and Yellowthroats. On the other hand, male Golden-wings had intense encounters with male Chestnut-sided Warblers and fighting occurred in three out of six cases observed. On two of these occasions the male Golden-wing gave secondary song following these encounters, a behavior similar to that following intense intraspecific encounters. Encounters were also seen between Golden-wings and a migrant Myrtle Warbler (*D. coronata*) and between Blue-wings and migrant Nashville Warblers (*V. ruficapilla*). In summary, Blue-wings had five out of six encounters with birds of similar color, i.e., birds with yellow breasts. Golden-wings, on the other hand, had seven out of eight encounters with birds similar in color pattern (e.g., with Chestnut-sided and Myrtle Warblers, which are similar to the Golden-wing in having a yellow crown and a white breast).

DISCUSSION

Birds with similar songs and plumages have non-overlapping territories; birds with different songs and different plumages have overlapping territories. We were also fortunate in having birds which differed in only one of these features. The Brewster's hybrids with different songs but similar plumages which had non-overlapping territories point to the importance of visual releasers in species recognition. In the cases of Brewster's hybrids overlapping territories with Golden-wings and Lawrence's hybrid with a Blue-wing, the chief differences between the males involved is in facial pattern. Blue-wings and Brewster's hybrids have a black line through the eye while Golden-wings and Lawrence's hybrids have prominent face and throat patches. Thus, the principal feature involved in species recognition with regard to territorial behavior seems to be facial pattern. Facial pattern is probably of great importance in species and sexual recognition in birds (e.g., Smith, 1966). For example, Noble and Vogt (1935) showed that the face mask of the male Yellowthroat was important in sexual recognition, the male attacking a mount which he had previously responded to sexually after a face mask was pasted on.

Gill and Lanyon (1964) conducted a series of experiments on the visual and vocal basis for species discrimination in Blue-wings. In combination with playback of *V. pinus* primary song, stronger responses were elicited by *V. pinus* mounts than by mounts of *V. peregrina*, *V. chrysoptera*, *Dendroica petechia*, and *D. pensylvanica*, indicating that males were discriminating visually. Weak responses to non-conspecific mounts even in conjunction with a playback of *V. pinus* song indicate, as do our observations, the importance of visual releasers in evoking aggression.

The territorial system of these warblers helps to explain some unusual associations between two males and a female. Some such cases are clearly "helpers" at the nest (Short, 1964) and may be temporary, e.g., occurring just during the parental period. Other associations begin earlier. For example, Campbell (1940) noted a male Lawrence's hybrid with Blue-wing songs accompanying a male Blue-wing and a female Golden-wing on 30 May. It was not known whether one or both males were mated to the female. Also, a male Brewster's hybrid was first associated with a pair of Golden-wings on 30 May. In June he accompanied the Golden-wings and young. Apparently in both cases the aggressive reactions of one male toward the other were weak. This association of two males occurs more commonly between males that have overlapping territories. It is possible that the territorial system could affect pairing relationships and even lead to polygamy in some cases.

The territorial system could increase interspecific sexual activity and hence hybridization in other ways. During intense interspecific encounters females become sexually stimulated and chances for copulation with a non-conspecific are increased. Also, males with overlapping territories sometimes approach a mated non-conspecific female on the same territory (Ficken and Ficken, 1968). Lanyon (1956) points out that territorial exclusiveness of two meadowlark species (*Sturnella magna* and *S. neglecta*) increases reproductive isolation. "Since copulations apparently occur only within the meadowlark territory, the male's defense of his territory constitutes an important check on interspecific matings across territorial boundaries."

SUMMARY

Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids were studied. Behavior involved in territorial defense is described. Males with similar plumages and songs maintain non-overlapping territories while those with dissimilar plumages and dissimilar songs have overlapping territories. Males with dissimilar plumages but similar songs have overlapping territories while those with similar plumages but dissimilar songs maintain non-overlapping territories. It was concluded that plumage is more important than song in species recognition by males as measured by territorial behavior. Face pattern seemed the most important feature in species recognition. Overlapping interspecific territories probably increase the chances of mixed matings.

ACKNOWLEDGMENTS

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HABITAT SELECTION: DIFFERENCES IN STEREOTYPY BETWEEN INSULAR AND CONTINENTAL BIRDS

David H. Sheppard, Peter H. Klopfer, and Hans Oelke

Even a casual visitor to an island must note the reduction in the number of species relative to adjacent continents. The whys and wherefores of this situation are not especially obscure, though it remained for MacArthur and Wilson (1963) to provide a quantitative statement of the causal relation between the diversity of an island's fauna on the one hand and its size, topography and distance from the mainland on the other. Nor have the evolutionary effects of island isolation been ignored, as witnessed by the testimony of biologists from Darwin (1859) to Mayr (1963). Ethologists have examined changes in bird song as related to a reduction in species diversity (see Thorpe, 1963), and ecologists have long been concerned with changes in food seeking or nesting activity coincident upon the absence of competitors (e.g., Crowell, 1962 and Grant, 1966). We have sought to enlarge upon one aspect common to these several themes: is there a reduction in the behavioral stereotypy of island species?

Consider the data of Crowell: on Bermuda, only three species of birds are common. While they appeared to him to behave in much the same way on Bermuda as in their habitats in the eastern United States, on the islands they occupied a greater variety of habitats. Klopfer (1967) found a similar situation for Bananaquits (*Coereba flaveola*) in Puerto Rico and Central America. The unanswered question is whether individual birds on Bermuda (or Puerto Rico) expanded their range of habitats or, alternatively, whether the expansion was of the species habitat, i.e., with each individual as restricted as ever, but with more varieties of individuals. This study reports on analysis of stereotypy in foliage preferences and feeding activity of a few individual Catbirds and Cardinals from Bermuda and the Durham area in the Piedmont of North Carolina.

METHODS

The feeding activity of wild Catbirds (*Dumetella carolinensis*) and Cardinals (*Richmondena cardinalis*) was recorded at 10 second intervals and feeding height and distribution were recorded where the bird was first seen and again where it was last seen. Feeding activity included foraging (searching) movements as well as actual feeding and, thus, the data are not strictly comparable with those of Crowell (1962) who recorded only active pecking. The definition of vegetation layers depended upon the general configuration of the vegetation in any particular habitat. For example, the maximum height of the shrub layer varied between 2.5 and 6.5 meters. The radial position of the bird was recorded as trunk (main stem of tree), intermediate, or terminal (branches reduced to less than 1 cm in diameter).

Foliage preferences were tested in two rooms, each divided into two equal chambers by netting. The chambers in each room were identical except for the foliage. Fluorescent lighting was provided continuously and identical perches consisting of parallel bars were placed in each chamber. Connecting the chambers in each room was a small box, open at each end with a battery of three photocells at each opening. The photocells were connected to counters and the length of time that the bird spent in each chamber was automatically recorded. Food was placed in the center of the box and water was provided in each chamber. The rooms were identical with the first and second rooms used by Klopfer (1965) and previously described.

Before experiments were begun, the birds were trained, in groups of three, to move from one chamber to the other. In addition, before each trial, the bird was permitted a habituation period of 8–24 hours. In actual trials birds were tested singly for at least three days. The chamber into which the bird was first introduced was alternated with each trial.

To test foliage preferences, artificial leaves were offered in the following combinations: large oak-large elm, large oak-small elm, small oak-large elm. The lengths of the artificial leaves were as follows: large oak—24 cm, large elm—14 cm, small oak—14 cm, small elm—8 cm. The leaves were suspended from the perches, walls and ceiling with masking tape. Arrangement of leaves in each chamber was identical.

For each trial, the proportion of time spent by the bird in each chamber was calculated and a discrimination index (H) derived using the graph presented by Klopfer (1965). This graph is a modification of the expression of diversity, $\Sigma P_i (-\log_e P_i)$ (MacArthur and MacArthur, 1961).

RESULTS AND DISCUSSION

Crowell (1962) found that Bermuda Catbirds and Cardinals spent a greater proportion of their time in ground-feeding than did their North American counterparts and this observation is confirmed by results presented here (Table 1). The indices of diversity (H values) obtained by Crowell did not support the hypothesis that island birds, apparently living under conditions of reduced inter-species competition, are less stereotyped in their feeding activity. However, Crowell's mainland comparisons were based on birds scattered widely over the eastern seaboard. In contrast, H values obtained in the present study (Table 1) are slightly higher for Bermuda Catbirds and Cardinals, suggesting that the island birds are slightly less stereotyped with regard to feeding activity.

Analysis of the vertical (layer) and radial distribution of feeding activity

TABLE 1

FEEDING ACTIVITY OF BERMUDA AND MAINLAND CATBIRDS AND CARDINALS

	Bermuda Catbirds		N.C. Catbirds		Bermuda Cardinals		N.C. Cardinals	
Feeding activity	n	H	n	H	n	H	n	H
Ground	289	0.315	266	0.293	607	0.243	164	0.309
Trunk	83	0.150	10	0.046	8	0.046	1	0
Foliage	1,127	0.223	1,267	0.155	230	0.354	753	0.171
Fruit/flower	8	0.046	0	0	2	0.023	0	0
Hawk/hover	17	0.046	21	0.046	3	0.023	10	0.046
Totals	1,524	0.78	1,564	0.54	850	0.69	928	0.53

(Table 2) also produced consistently higher H values for Bermuda birds. The field data suggest that Bermuda Catbirds and Cardinals are less restricted in their feeding activities than North American birds. This can be interpreted to mean that the food niches occupied by these species are larger on the Bermudas than on the mainland, and that while Crowell's treatment of his data, which take foliage density profiles into consideration, may seem more precise than ours, this is not necessarily the case. When the chance of observing birds is less in one layer than another, the method of simply recording the position of the bird, rather than limiting observations to the actual taking of food (as did Crowell), may be more meaningful. Often the position of the bird can be detected in dense foliage, even when actual feeding cannot. In any case, our data are suggestive of greater plasticity in the foraging behavior of Bermuda birds.

As a group, Bermuda Catbirds did appear to be slightly less stereotyped in their artificial foliage preferences than did North Carolina Catbirds

TABLE 2

FEEDING DISTRIBUTION OF BERMUDA AND MAINLAND CATBIRDS AND CARDINALS

	Bermuda Catbirds		N.C. Catbirds		Bermuda Cardinals		N.C. Cardinals	
	n	H	n	H	n	H	n	H
Vertical distribution								
Ground	72	0.322	61	0.309	29	0.365	48	0.328
Shrub	224	0.306	273	0.171	44	0.352	153	0.274
Canopy	73	0.322	5	0.046	19	0.328	29	0.265
Totals	369	0.95	339	0.53	92	1.04	230	0.87
Radial distribution								
Trunk	17	0.169	3	0.046	3	0.150	0	0
Intermediate	118	0.367	28	0.230	33	0.340	64	0.367
Terminal	162	0.333	248	0.104	27	0.363	118	0.280
Totals	297	0.87	279	0.38	63	0.85	182	0.65

TABLE 3
ARTIFICIAL FOLIAGE PREFERENCES OF BERMUDA AND NORTH CAROLINA CATBIRDS

Choice of artificial foliage	Bermuda Catbirds			North Carolina Catbirds		
	No. of birds	% of time in Oak	Mean H	No. of birds	% of time in Oak	Mean H
Large Oak-Large Elm	6	57	0.19	6	61	0.28
Small Oak-Large Elm	6	44	0.09	6	34	0.17
Large Oak-Small Elm	6	69	0.19	8	65	0.21

(Table 3). Mean H values for Bermuda Catbirds are consistently lower (weak preference) for each pair of discriminanda, though none of the differences can be shown to be statistically significant given the smallness of the sample and the need for relying upon relatively weak nonparametric tests.

The data can be further broken down to reveal the relative importance of leaf size and shape as possible cues in habitat selection (Table 4). When offered a choice of large and small leaves, most birds of both groups preferred large leaves. North Carolina Catbirds spent 63 per cent of their total time among large leaves compared with 62 per cent for Bermuda Catbirds. Oak foliage was only slightly preferred to elm; North Carolina birds spent 52 per cent of their total time in oak and Bermuda birds 56 per cent. The slight preference for oak could be related entirely to the larger size of the artificial oak leaves. Mean H values again indicate that Bermuda Catbirds are slightly, but consistently, less stereotyped in their artificial foliage preferences.

Catbirds used in the preference tests showed considerable variation between individuals in the relative importance of leaf shape and size as discriminanda. Nevertheless, individual birds tested with all three pairs of artificial foliage tended consistently to select one particular type of artificial foliage. Of five North Carolina birds tested, three consistently selected large leaves and two consistently chose leaves of a particular shape (one chose oak and one elm). Similarly, of the six Bermuda birds tested, three consistently selected large

TABLE 4
RELATIVE IMPORTANCE OF LEAF SIZE AND SHAPE IN SELECTION OF ARTIFICIAL FOLIAGE BY CATBIRDS

	Number of birds selecting:							
	Large leaves		Small leaves		Oak		Elm	
	n	Mean H	n	Mean H	n	Mean H	n	Mean H
North Carolina Catbirds	11	0.20	3	0.18	10	0.24	10	0.20
Bermuda Catbirds	9	0.17	3	0.04	10	0.21	8	0.09

leaves and two consistently selected leaves of a certain shape (again, one chose oak and one elm). One Bermuda Catbird did not show a consistent preference for either leaf shape or leaf size.

The data presented here lend support, though tenuous, to the hypothesis that niche size and behavioral stereotypy are directly related. Species living on islands or in temperate habitats where numbers of species are reduced and average niche size is, presumably, larger should be less stereotyped in their behavior than species living on continents or in the tropics where niches are presumed smaller. Those aspects of behavior related to food and space (generally the most important niche parameters), in particular, should vary directly with niche size.

It is unlikely that most birds use only one cue in selecting their habitat. In the case of a bird responding to a single cue, all other discriminanda would be irrelevant and, though the bird might be highly stereotyped for the appropriate cue, this would not be detected if irrelevant discriminanda were offered. It is possible that discriminanda used in the present study were completely irrelevant but, since most of the birds exhibited consistent preferences, this does not seem to be the case.

A related problem, less easy to resolve, is whether the artificial foliage choices were of equal relevance to Bermuda and North Carolina birds. If the cues were of less relevance to Bermuda birds, this would account for the slightly lower H values of these birds without necessarily being related to a difference in niche size. Oak and elm are abundant in North Carolina but not on the Bermudas. Thus, one would expect oak and elm leaves to be of less significance to Bermuda birds. The only evidence that can be offered to refute this is, again, the consistency with which both groups of birds selected leaves of a particular size or shape.

The possibility that leaf size and shape are of minor importance as cues should also be considered. For example, the apparent preferences of Catbirds for large leaves could be related to light intensity and preference for leaves of a certain shape could be related to light pattern. Experiments to test these possibilities are continuing.

The idea that niche size and behavioral stereotypy are interrelated is an attractive one and the data presented here do offer some evidence of such a relationship. Perhaps a more detailed approach, such as completely defining the food and space components of each niche and relating these to habitat cues, should be used.

SUMMARY

Indices of diversity indicate that Bermuda Catbirds and Cardinals may be slightly less stereotyped in their feeding activities than North Carolina birds of the same species. Bermuda Catbirds were also slightly less stereotyped in their artificial foliage preferences.

Some support is presented for the hypothesis that Bermuda birds, living under reduced interspecies competition, may occupy larger niches with an associated reduction in behavioral stereotypy.

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ECOLOGICAL FACTORS CONTRIBUTING TO NESTING FAILURE IN A HERON COLONY

Julian L. Dusi and Rosemary T. Dusi

The nesting failure in a heron colony because of predation, interaction between species, and drought, is reported here. The colony, which is one of several studied by the writers, was located about 15 miles southeast of Dothan, Houston County, Alabama. It was a large composite colony for the years 1963 and 1964, during which we observed it. The land manager, I. B. Bodiford, said that it was a thriving colony as long as he could remember. The Little Blue Heron (*Florida caerulea*); the Cattle Egret (*Bubulcus ibis*); and the White Ibis (*Eudocimus albus*), were the major species, and the Snowy Egret (*Leucophoyx thula*); the Common Egret (*Casmerodius albus*); and the Anhinga (*Anhinga anhinga*), were the minor species present.

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PROCEDURE

During the winter, 1964–1965, the 14-acre swamp colony area was subdivided into quadrats 200 feet square. to facilitate nesting success studies to be made. This is illustrated (Fig. 1) to show the areas used by the nesting birds.

After the nesting population arrived, several studies were made. Nests were tagged and nesting success data taken. Young were weighed and banded. Food pellets, regurgitated by the young, were saved for food habits studies. Ectoparasites, in the form of hippoboscid flies, were removed and saved. Behavioral observations were made and predation recorded. Finally, weather and other habitat observations were made and were supplemented by precipitation data supplied by Rufus O. Crosby, U.S. Weather Bureau Airport Station, Dannelly Field, Montgomery, Alabama.

RESULTS AND DISCUSSION

Nesting Activity.—The sequence of nesting and roosting activity for the colony in 1965 is given in Table 1.

Several species were present when the area was initially visited on 17 March but no nests were found until 29 April. After that, nests with young were present until 7 June. when nesting had stopped after a prolonged drought. Nests were again found on 17 July and were present in the colony until 31 July.

Predators affecting the nesting activities were seen in the form of five large gray rat snakes (*Elaphe obsoleta spiloides*). taken from and near

Fig. 1. The 14-acre swamp colony area. Quadrats are outlined and numbered. The area used for nesting during the three years and that portion used in 1965 is shown separated from the rest of the wooded area. The major trees of the nesting area are swamp tupelo (*Nyssa biflora*) and the common baldcypress (*Taxodium distichum*).

Table 1
Species Composition and Activity at the Nesting Colony Area

	Species composition						
Date	L.B.H.	Cat. E.	Com. E.	Sny. E.	Anh.	W.I.	Activity
17 Mar	250	16	2	2	1		Roosting
						42	Feeding
3 April	30	60				45	Roosting
29 April	47						Nests Marked
7 May	190	169				200	Roosting
	51	28					Nests Marked
8 May	16	10					Nests Marked
	22						Young Measured
7 June		17				19	Roosting
23 July	25	950				30	Roosting
24 July		40					Nests Marked
		10					Young Measured
	62	1157	2			97	Roosting
25 July		7					Young Measured
30 July	3	6					Young Measured
	8	59				30	Roosting

Abbreviations: Little Blue Heron (L.B.H.), Cattle Egret (Cat. E.), Common Egret (Com. E.), Snowy Egret (Sny. E.), Anhinga (Anh.), White Ibis (W.I.).

several empty Little Blue Heron nests on 14–16 May. Two more rat snakes were removed on 1 June and an additional one on 25 July. Barred Owl (*Strix varia*) vocalizations were heard in the afternoons through most of the nesting period. Fish Crows (*Corvus ossifragus*) were present in the general area throughout the study period and they nested in a pine grove at the periphery of the swamp.

During the week-end of 14–16 May we re-measured and permanently banded the nestlings in Quadrat 4. Several empty nests were found. In Quadrats 1 and 2 there was little Cattle Egret activity and many nests were empty.

We decided to check the general area for some explanation of the decline in population density, and on 21 May we rented a Cessna 172 at the Dothan Airport and flew over the corner of the state, southeast of Dothan, looking for other possible nesting colonies and counting groups of herons. A number of Cattle Egrets was seen feeding with cattle, no White Ibises were seen, and no other colonies were found. The rest of the day and 22 and 23 May were spent in the colony area, measuring and banding nestlings and checking nests. About 45 nests were active at this time. The lack of rainfall had resulted in the swamp water level being about one foot below normal.

The water level was even lower by the week-end of 30 May to 1 June. The number of active nests was further reduced. Two more large rat snakes were removed from nests and Barred Owl feathers were found in one empty nest.

By 7 June, population density was at a low. Only 17 adult Cattle Egrets and 19 White Ibises came in to roost that night. The remaining nestling Little Blue Herons were all too large to catch and measure. No rain had fallen in several weeks and the swamp was at a low for the season.

No further trips were made to the colony area until 17 July. Several rains had fallen and in order to see whether any renewed nesting activity had occurred, we again flew over the colony area. We saw a large number of white birds in the trees of Quadrats 1 and 2, where the earlier groups had nested. Even though we flew within 50 feet of the birds, they did not fly as most adults usually do, so we assumed that they were young unable to fly. We could not visit the colony area until 23 July. Then we were surprised to find that the birds in the trees were nesting adult Cattle Egrets. At dusk the roosting composition was an estimated 25 Little Blue Herons, 25–30 White Ibises and about 950 Cattle Egrets. The next day we marked 40 Cattle Egret nests in Quadrats 1 and 2 and measured 10 recently hatched young. It had been raining at Dothan that morning but did not rain near the colony area. The roosting population that night was 1,457 Cattle Egrets, 62 Little Blue Herons, 97 White Ibises, and 2 Common Egrets. Seven additional Cattle Egret nestlings were measured and marked on 25 July. A gray rat snake was taken from a nest. Three adjacent nests that were now empty had contained eggs the day before.

Finally, on 30 July, most of the nests were empty or the eggs present were punctured. We measured three Little Blue Heron nestlings and six Cattle Egrets. The evening flight was approximately 30 White Ibises, eight Little Blue Herons, and 59 Cattle Egrets. When we returned the following morning, a large flock of Fish Crows was in the colony area and left when we approached. On examination, all of the remaining nests were empty of nestlings and eggs. This was the final nesting attempt in this colony area in 1965.

Nesting Success.—During this nesting study, 117 Little Blue Heron and 214 Cattle Egret nests were marked and studied. No Common Egret, Snowy Egret, White Ibis or Anhinga nests were seen.

Of the 117 Little Blue Heron nests, 17 or 14.5 per cent contained young that matured and left the nests. An additional 16 nests contained young that hatched but perished. In the 17 successful nests, 73 eggs were laid, 65 of these hatched, and a total of 52 young was produced.

The 214 Cattle Egret nests were all unsuccessful.

Unfortunately, during the two preceding seasons no nests were marked but they were concluded to be highly successful seasons because all of the species nested and in 1963, with partial effort. 30 Little Blue Heron and 283 Cattle Egret nestlings were banded, as well as 4 Common Egrets, and 5 White Ibises. In 1964, 326 Little Blue Herons, 413 Cattle Egrets, 24 Common Egrets, 10 Snowy Egrets, and 82 White Ibises were banded.

Predation Effects.—Predators present were: alligators, gray rat snakes, Barred Owls, Fish Crows, and man.

The alligators were important as predators only when the nestlings fell into the water so that their effect was as scavengers. They did, however, restrict the other predators from moving through the water to the nest trees.

The gray rat snakes travelled from tree to tree, passing over the alligators and reaching the nests. A total of eight gray rat snakes was taken from the nests. It is difficult to assign the amount of nest failure that these snakes caused. In the case of the snake taken 25 July, four nests that contained eggs the day before were empty and it was fairly certain that the rat snake had eaten the eggs. If all eight snakes caused just that amount of predation, 32 nests, or 10.2 per cent of the unsuccessful nests of Little Blue Herons would have been a result of their action. They could have caused much more or less nest failure and there could have been other rat snakes present that we did not find.

The pair of Barred Owls has been present in the swamp for the several years it had been studied by us. We had not considered the potential of the owls as predators until 1 June, when owl feathers were found in nests that had contained young. During their early nestling life, herons would be easy prey and an owl could quickly empty an entire nest. After the young reached the age of two weeks, they could climb well enough that an owl could probably catch only one individual from a nest at any visit. A pair of owls could account for a fairly large number of young during a nesting season. We found the first young of 1965 on 9 May, and they were present until 1 June. Then from 24 July until 30 July, young were again present. This totals at least 31 days when nestlings were present. If each owl of the pair removed only one nestling for each day they were available, it would total 62 nestlings. This may partially explain why the Little Blue Herons of 16 nests hatched young but they were not successful in rearing them and why in the successful nests, 65 nestlings were hatched but only 52 were reared. It might also account for Cattle Egret young that disappeared.

Predation by Fish Crows was high, from all apparent indices, but it was not measured. Almost synonymous with the appearance of eggs in the nests, eggs with punctured shells were found in the water near the nests, or still in the nests. The punctures were large and indicated crow damage. On 31 July, the damage to eggs and nestlings was very evidently crow predation. Large numbers of Fish Crows have been present in the colony vicinity during the several years of our studies. During high heron population levels and periods of adequate nest protection, their predation effect has been minimal but the low population levels of 1965 and poor Cattle Egret nest attention, made it possible for the crows to be important predators.

Man did little predation at this colony. It was near the land manager's house and he kept people from shooting in the colony. Our presence may have had some undesirable effects but it was not predation.

Since nesting success had not been studied in previous years, it is difficult to compare the predation of this year with the others. It may have been at least as great in 1963 and 1964 but went unnoticed because there was such a sizable group of nesting birds. We did not find any snakes in previous years or find owl feathers in the nests. We therefore assume that the snake population had increased in numbers and that they exerted a much higher predation pressure.

Interaction between Little Blue Herons and Cattle Egrets.—There was apparently little interaction between the Little Blue Herons and Cattle Egrets except in nest establishment. The Little Blue Herons arrived first and established their nests first. The Little Blue Herons were incubating before the Cattle Egrets started nesting. The Egrets nested near the Little Blue Herons in the less favorable sites and often within a foot of a heron nest. There was a little strife observed during past seasons but no indication of nest desertion by Little Blue Herons. During the 1965 season, there was little strife observed in the form of threat postures and vocalizations during the first nesting attempt of the egrets. During the second nesting, the egrets swarmed into Quadrats 1 and 2, where a relatively small number of Little Blue Herons was still nesting. The nesting group seen from our reconnaissance flight of 17 July was fairly large (50–100), but the roosting group of 23 July was about 950 and on 24 July was 1,457. The nesting group apparently disturbed the Little Blue Herons somewhat but the added roosting mass caused practically all of the Little Blue Herons in that area to desert. In two instances, we found an egret egg in a heron nest and feel certain that the rapid establishment of some egret nests resulted from the taking over of heron nests, or at least the removal of sticks from heron nests for use in building egret nests.

Precipitation Effects.—Apparently precipitation has different effects on the different species which normally nest in this colony area, but most notably the Cattle Egrets and White Ibises. Bent (1926) stated that the Scarlet Ibis (*Eudocimus ruber*) nests in the rainy season. We believe that this is also the case with the White Ibis. We have not seen this stated in the literature regarding the Cattle Egret but is it a simple deduction, that if Cattle Egrets

TABLE 2
RAINFALL FREQUENCY NECESSARY TO PREVENT DROUGHT IN THE COLONY AREA

	May	June	July	August
Moisture holding capacity per foot of Norfolk Sandy Loam (inches)	1.2	1.2	1.2	1.2
Evapotranspiration rate (In./day)	0.142	0.173	0.154	0.141
Frequency which 1.2 inches of rain must fall to prevent drought (days)	8.4	6.9	7.8	8.5

obtain their food mainly from pasture insects and if pasture grasses wither and die if moisture is insufficient and no longer support the food population of insects, then Cattle Egret nutrition will be insufficient for reproduction physiological activities and the reproduction behavior ceases. Quite frequently the egrets also move from the drought areas to more lush pastures.

The colony area studied is in a belt which has received 56 to 58 inches of rainfall per year, based on 45 years of data from the U.S. Weather Bureau (Anonymous, 1965). The precipitation is not even and it is not unusual to have a two or three week period without rain during the nesting season. The soils surrounding the swamp are Norfolk sandy loam and related coastal plains soils that have a moisture holding capacity of about 1.0 to 1.2 inches per foot (Ward, 1959). Also, according to Ward, the major root occupancy zone of pasture plants is 0 to 8 inches. If we use his evapotranspiration data for the nesting months and then compute the number of days without rain during which a foot of Norfolk sandy loam with 1.2 inches of water holding capacity will supply moisture to pasture grasses, we see how frequently it must rain if pastures are to continue growth and supply Cattle Egrets with food (Table 1). In Figure 2, we have plotted the daily rainfall data for the Dothan weather station for the period 1 April, through 15 August, for the two good nesting years, 1963 and 1964 and the year of nesting failures, 1965. Then we added the evapotranspiration rate line, the computed days when drought conditions were present and finally the two nesting periods for Cattle Egrets in 1965. The Dothan airport weather station was the nearest station where complete records were available and it unfortunately was 23 miles northwest of the colony area. Our weather observations of presence or absence of rain were used to modify the 1965 data.

From Figure 2, it is readily seen that drought conditions existed each of these three years.

In 1963, only five drought days occurred after 10 May, and the Cattle Egrets and White Ibises had a long nesting season. Summerour (1964) observed Cattle Egret nests with young as late as 10 August.

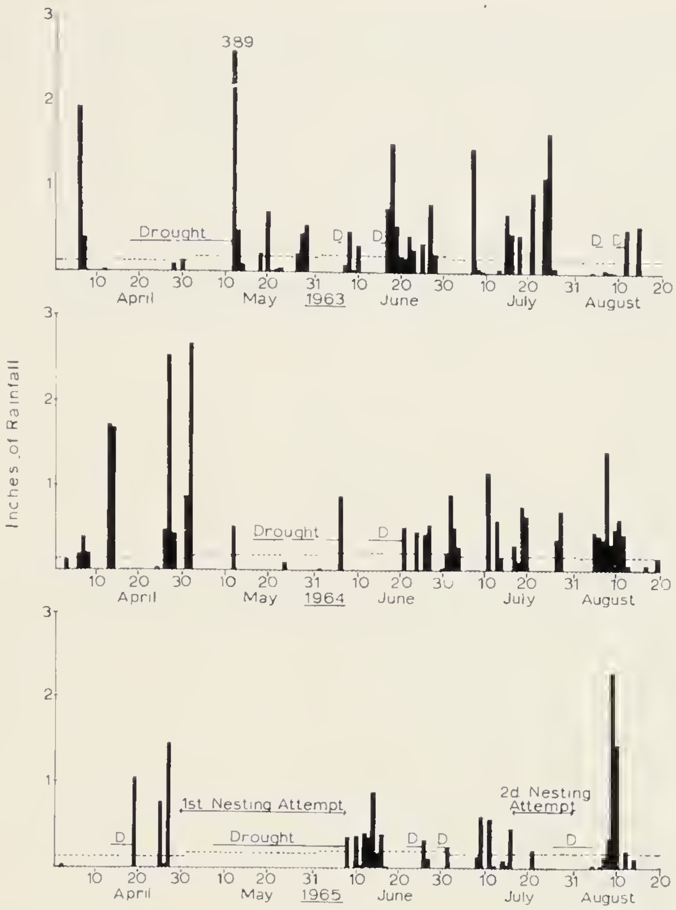

Fig. 2. The rainfall, evapotranspiration, drought periods, and nesting periods for the swamp colony area during the nesting periods of 1963, 1964, and 1965.

In 1964 drought was fairly continuous from 16 May to 19 June. This season it was quite wet until early May, and Little Blue Herons, White Ibises, and Cattle Egrets were nesting in large numbers by the start of the drought. Since most of the clutches were laid by the beginning of the drought period and with the important facilitation effects of the other species nesting in large numbers, the Cattle Egrets apparently retained their active nesting behavior. After 20 June, there was an abundance of rain, pastures regained their lushness and Cattle Egret and White Ibis nesting continued on into August. On 1 August, we counted more than 50 Cattle Egret nests with eggs and 30 nests with small young.

The 1965 season started with so much drought in April and May, that the White Ibises did not nest, even though a group roosted in the area. A much smaller group of Little Blue Herons nested than during the preceding two years. The Cattle Egrets started their first nesting period at the beginning of a long dry period. Actually no rain fell in the immediate colony area from 27 April until 8 June. With little facilitation from other nesting waders, little to eat, and with higher than usual predation pressure, they deserted.

The break in drought, in mid-June and early July, apparently incited nesting activity again and we first saw the nesting group on our 17 July flight. That was the start of another dry period and the slight rain of 20 July, delayed drought conditions only a few days. Very few other herons were nesting. The Little Blue Herons had deserted because of the interspecific strife from so many roosting Cattle Egrets. Therefore, there was no nesting facilitation from other herons or ibises. When the drought conditions again prevailed, nest attention lagged and the Fish Crows took care of what eggs and young remained.

SUMMARY

The nesting failures of the heron colony reported here, resulted from a number of interacting and contributing factors.

The very low nesting success of Little Blue Herons (14.5 per cent) appears to have been the result of a high predation pressure from gray rat snakes, Barred Owls, and Fish Crows. The interspecific pressure of a large number of roosting and nesting Cattle Egrets in mid-July caused a number of Little Blue Herons to desert, contributing further to the low degree of nesting success.

The White Ibises apparently did not nest because of the extensive drought in late April, May, and early June, that then continued in mid-July.

The Cattle Egrets were completely unsuccessful in their two nesting attempts because the long early drought and the late drought reduced the amount of food available. The apparently heavy predation pressure, especially from Fish Crows, and the lack of breeding behavior facilitation, caused by too few other nesting wading birds present in the colony area, resulted in many desertions and completed the factors resulting in complete failure.

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THE MAINTENANCE BEHAVIOR OF THE BLACK-CROWNED NIGHT HERON

George R. Maxwell and Loren S. Putnam

This paper is concerned with a three month study of the maintenance behavior of the Black-crowned Night Heron (*Nycticorax nycticorax*) and includes a description and interpretation of the activities observed. Maintenance behavior, as used in this paper includes movements concerned with locomotion, preening, scratching, care of feet, shaking, stretching, defecation, bill-wiping, sleeping, throat pulsation, yawning, resting, and feeding.

The Black-crowned Night Heron is well suited to this type of study due to its colonial nesting habit. The work by Meyerriecks (1960) reinforced our interest in herons and this paper follows the style established in his monograph, so that these data may be utilized more easily. Specific comparisons of night heron with Green Heron behaviors are made whenever the differences or similarities are striking enough to merit them.

Some work has been done on the food preference of the night heron (see Palmer, 1962 and Teal, 1965), but little on the feeding behavior of immature herons. A detailed description of the behavior leading to the food transfer, as well as the food transfer itself, has not been available.

Field observations were made in Fox's Marsh on North Bass Island, Ottawa County, Ohio, in western Lake Erie during the summer of 1963. Further observations were planned but the colony failed to breed in the marsh the following year. The marsh, about 1500 feet by 500 feet, is located at the south-west corner of the island. In the past it has been connected with the lake, but due to low water and wave action, it is now separated by a gravel bar. In the spring the marsh contains, at the deepest point, three feet of water, but becomes almost dry by August. The primary vegetation includes buttonbush (*Cephalanthus occidentalis*), which supported the night heron nests, water persicaria (*Polygonum lapathifolium*), and cattail (*Typha latifolia*).

The night herons were observed and photographed from an elevated blind located in the center of the marsh, by use of a 15× telescope adapted to a single lens reflex camera. Drawings were made from the photographs. Total observation time in the marsh was 114 hours.

Data for this paper were collected while the senior author was a research assistant at Franz Theodore Stone Laboratory of The Ohio State University, Put-in-Bay, Ohio.

LOCOMOTION

Walking.—Most walking observed occurred on the buttonbush in the nesting area. Some walking is involved when the birds feed in shallow water. The movements are slow and deliberate. The head and neck are lowered and slightly retracted to a crouch position and the foot is raised and placed firmly ahead. After a grasp is achieved the other foot is advanced. We have seldom seen a night heron run. These descriptions are similar to those of the Green Heron (*Butorides virescens*) given by Meyerriecks (1960).

Flight.—The flight of the night heron differs from that of the larger herons in that the crow-sized night heron appears to have a labored flight in contrast to that of the graceful Great Blue Heron (*Ardea herodias*). Some gliding was observed during sustained flights and during flights against moderate winds. On sustained flights the heron has the neck retracted with legs parallel and extended to the rear. Only the toes extend beyond the rectrices. The *quack* call is commonly given while the heron is on the wing, especially at night and in response to a disturbance in the colony.

Some attempts have been made to record wing-flap rates and speed. Blake (1948) gives a wing-flap rate of 2.6 per second. We counted wingbeats during ten one-minute periods and determined an average of 2.8 wingbeats per second for herons leaving the breeding area. In Palmer (1962) the flight speed is given as 18–21 miles per hour. In this study the flight speed of the night heron was measured by motorboat and found to be approximately 20 miles per hour.

Green Herons differ from the night heron in that the night herons seldom glide during a sustained flight, although some gliding has been observed just before landing. The Green Heron is similar to the night heron in that both have a wing-flap rate of 2.8 per second and a speed of around 25 miles per hour (Meyerriecks, 1960).

Takeoff.—Intention movements (see Heinroth, 1911, and Daanje, 1950) indicate that takeoff is imminent. The night herons' most obvious intention movement is head rotation. Just prior to takeoff the night heron looks around. Defecation was found to be an indicator of imminent takeoff. If a preening bout or period of resting is followed by defecation, there is a good chance flight will follow.

From a study of a series of still photographs the takeoff procedure appears to occur in the following manner. The night heron sleeks the feathers and lowers the body rearward in much the manner for defecation. This shifts the body weight and centers it over the legs, giving the bird initial thrust. The head and neck are retracted, the tail spread slightly, and the wings extended upwards as the night heron thrusts itself forward with its legs. The head and neck are extended for the first downstroke, but retracted for

FIG. 1. Preening breast or abdominal feathers.

FIG. 2. Side preening.

the following upstroke. At about thirty feet elevation the feet are brought together and extended rearward as the wing beat rate decreases to the sustained flight rate.

Landing.—The night heron approaches the landing site in either a straight or circular glide path. At about 200 feet from the landing site the glide begins with feet dropped and head fully retracted; the heron then extends its neck and starts flapping the wings approximately 30 feet from the perch. Crest erection was not noted during the approach. The wing flapping frequency increases until the bird is over the perch. The perch is grasped by the feet and the wings continue to beat until equilibrium is established. The head and neck are retracted to the perched position and the wings folded. Meyerriecks (1960) noted that on the landing approach of the Green Heron, when the neck and head are extended, almost invariably the crest is erected.

BODY MAINTENANCE

Preening.—Preening is a common activity of the night herons and occupied approximately 20 per cent of the 7.7 hours devoted to observing preening frequency. Even while caged the night herons were observed keeping their feathers continually tidy (Heinroth, 1929). Table 1 gives the frequency and percentage of time devoted to preening the major body areas. The entire body surface except the head and upper neck can be reached by the bill. Preening methods used by the herons were the same for all individuals, but there appeared to be no uniformity in the preening pattern. The eyes are alternately opened and closed during a preening bout.

The breast and abdominal feathers are reached by lowering the neck to an angle of 90 degrees from the perched position until the top of the head is nearly parallel to

TABLE 1

FREQUENCY AND PERCENTAGE OF TIME DEVOTED TO PREENING IN EACH MAJOR BODY AREA DURING 7.7 HOURS OF OBSERVATION. FIVE BLACK-CROWNED NIGHT HERONS WERE OBSERVED.

Region	Total preening time (minutes)	Percentage of total preening time
Breast	24	26
Underwing and sides	21	23
Neck	18	19
Upperwing	9	10
Primaries	9	10
Back	6	6
Head	3	3
Tail	3	3

the ground (Fig. 1). The heron gently nibbles the feathers with the bill and smooths them with a stroke sweeping from base to tip. Some small feathers come out during the preening bout but no actual pulling of feathers was observed. A bluish color on the bill was noted after preening and was assumed to be from powder-down. There was no return to the powder-down tract when preening other areas, so that any dressing of plumage as suggested by Hindwood (1933) was confined to the breast and abdominal areas.

Side and under wing preening usually occur together. During side preening the position of the head is similar to the above description (Fig. 2). The night herons nibble deeply to the skin but little feather stroking occurs. The under wing is exposed by a slight wing drop accompanied by bending the neck to the side of the exposed wing. The tip of the bill points downward while preening (Fig. 3). The under primary and secondary coverts are passed through the bill in one smooth movement. Most under wing preening is concerned with maintenance of feather integrity. Little feather nibbling was observed.

The feathers of the neck are nibbled and stroked with apparent effort. While the neck remains in the perched position, a sharp bending occurs at the anterior end of the cervical vertebrae. The bill is parallel to the neck while nibbling and in the initial phase of feather stroking. The bill moves from base to tip of the feather in an arc to a vertical position (Fig. 4). The night heron can reach most of the neck feathers except some dorsal areas.

Upper wing and primary preening is accomplished by bending the carpals and lowering the wing. The upper primary and secondary coverts are erected and the primaries fanned slightly. The coverts are nibbled and stroked first. Usually the night heron does not preen all primaries at one session, and on occasion only one primary may be preened during a preening sequence. The primary feather is either nibbled along its entire length or, more commonly, run through the bill in one smooth stroke.

Nibbling of the back and tail feathers is followed by stroking these feathers through the tip of the bill (Fig. 5). The head is turned to one side and the top of the head is turned down at an angle of 45° from the horizontal. This position forces the occipital plumes to an erect position at the base of the skull.

The head feathers are smoothed by placing the head under the wing. The wing

FIG. 3. Preening under wing.

FIG. 4. Neck preening.

is slightly lifted from the body and the neck bent posteriorly until the head is enclosed by the leading edge of the wing. The inverted head is thrust downward by the wing until it is halfway down the back. The head is then vigorously twisted between the body and wing. This sequence is completed in less than a minute.

Green Herons as observed by Meyerriecks (1960) conduct preening for the most part in the same manner as above except for the occasional pulling out of some of the breast feathers and the frequent final act of rubbing the bill over the oil gland.

Care of the feet.—Little attention is given to the feet and legs by the night heron. Only one instance of foot pecking was noted. The aquatic habits of the night heron may so clean the legs and feet that they require little maintenance.

Scratching.—Black-crowned Night Herons scratch the head and neck areas directly (Simmons, 1957) ("Vorherum" of Heinroth, 1930), not by drooping the wing but by bringing the leg straight up and concomitantly lowering the head. The indirect method (Simmons, 1957) ("Hintenherum" of Heinroth, 1930) of head-scratching common to passerines was not observed. The pectinated claw on the middle toe is the part of the foot which makes contact. Each head scratch was accompanied by a slight occipital plume erection (Fig. 6). Scratching did not seem to be associated with a preening bout. It did occur while the bird preened, but more often was an isolated action. The scratching process is similar to the behavior of the Green Heron as described by Meyerriecks (1960), except that he states that scratching of the head occurs at least once during a preening bout and could occur at any time in a bout.

Shaking.—Shaking was observed at the end of a preening bout, or as an isolated activity. The night heron leans forward slightly, erects most of the

FIG. 5. Preening back feathers.

FIG. 6. Scratching.

contour feathers and shakes vigorously while rapidly moving the wings in and out (Fig. 7). The length of a shaking session is from 5 to 10 seconds. Shaking apparently places the feathers in order.

Stretching.—Stretching usually occurs during the preening bout, but was also observed as an isolated incident. We did not notice a tendency for the heron to stretch one wing more often than the other or to stretch, for example, the right wing before the left. The heron shifts his weight to the right (or left) leg and places the head and neck in the perched position. The left leg is lifted until the tibiotarsus is parallel to the abdominal wall and the tarsometatarsus hangs vertically. Extension of the left wing down and out is followed by an outward extension of the left leg. The same but opposite procedure is followed for the right wing stretch.

Defecation.—Defecation may occur either in flight or while perched. Defecation sometimes occurs just a few seconds after take-off, but more commonly the heron will defecate while perched immediately prior to takeoff. In contrast Meyerriecks (1960) states that the Green Heron seldom defecates upon takeoff unless frightened. The defecation position is assumed by rearward dropping of body. The head, neck, and wings remain in the perching position, while the tarsometatarsus moves from an almost vertical to a nearly horizontal position. The young nestlings void into the nest, but about the time of fledging they elevate the rump and defecate over the edge. No attempt by the adult at nest sanitation was noted.

Bill-wiping.—Bill-wiping is an uncommon activity. It usually occurs after a preening bout or after food transfer to young herons. The head is lowered, so that the bill comes in contact with the branch on which the bird

FIG. 7. Shaking.

FIG. 8. Posture during throat pulsation bout.

is perched. A repeated stropping action of the bill against the branch is accomplished with swift strokes. This was the only method of feather removal observed following a preening bout.

Throat pulsation.—Special attention was given to the rapid in and out motion of the gular region which we termed "throat pulsation." It is performed while the heron is in the perched position with the bill opened slightly (Fig. 8). A tendency was noted for the throat to pulsate more often during higher temperatures and in direct sunlight. A study was made of three separate throat pulsation bouts, one lasting 49 minutes and the other two 55 minutes each. The heron would stop and start the throat movements for varying periods of time during a bout. Each period of throat movements was termed a "pulsation session." During the three bouts, there were 42 pulsation sessions. The average length of a single pulsation session was 7 minutes, and the minimum length was 0.25 minutes. These pulsations probably act as a body heat regulatory device.

Yawning.—Yawning occurred irregularly while the herons rested. The night heron remains in the perched position; the bill is opened wide and the eyes are open and bulging slightly. It did not appear to be associated with sleeping and no external factors were observed influencing the yawn.

Resting.—The night heron remains in the perched position for extended periods of time without movement except for some head turning. A major portion of the daylight hours is devoted to this behavior which appears to be resting.

FIG. 9. Pre-feeding behavior of Black-crowned Night Heron.

Sleeping.—Black-crowned Night Herons sleep during some of the daylight hours if there is no disturbance in the heronry. They sleep perched either on top of the buttonbushes, or low in the bushes out of sight. The sleeping heron retracts the neck, drops the wings slightly and stops all throat movement. The eyelids are completely closed, although they may be opened slightly at intervals and then reclosed. After the young have fledged, the adults spend most of the daylight hours sleeping or resting at a roost apart from the breeding heronry.

No sunning posture was observed in this colony, but the sleeping position was usually assumed in direct sunlight. Visiting Great Blue Herons (*Ardea herodias*) did assume the wing spread sunning posture described by Meyerriecks (1960).

FEEDING BEHAVIOR

Feeding of the young.—Observations were made of young night herons approximately two weeks old and older. Feeding methods used by younger Black-crowned Night Herons are summarized by Palmer (1962). The feeding ritual we observed is quite complex and involves active participation of

FIG. 10. Food transfer from adult to immature heron.

both parent and young. The feeding bout varies in duration and sequence of events. Regurgitation was evident in all feeding bouts, although some were more labored than others. Usually only one food transfer occurred during a feeding bout; however, as many as three transfers have been observed. The earliest attempt of the young to grasp the parent's bill was noted by Noble et al. (1938) at about two weeks of age. Bill grasping is an important phase of the food transfer process. The most aggressive young herons will grasp the bill first, pushing the younger nest-mates away. Evidence of the behavior is reflected in the billing that occurs among the young herons throughout pre-flight life. Noble et al. (1938) described the billing as an outgrowth of the feeding responses. If dominance is achieved by the nestlings' aggressive feeding responses, and its maintenance is achieved by billing. then Noble is probably correct. As the birds get older and venture from the nest one of the young herons will assume the highest perch. Billing still occurs. but height assumes a more important role as the birds near flight age.

The details of the food transfer were recorded in a series of still photographs. Both sexes were observed feeding the young. Sex determination was based upon the number of occipital plumes, one or two plumes probably indicating a female, three or four plumes a male (Noble et al., 1938). The length of the feeding bout seemed to be determined by the time required for regurgitation. As the adult enters the nest area, the immature herons move in an awkward fashion toward him. The adult makes a forward thrust ("repelling reaction" of Lorenz, 1938) toward the immature heron in an apparent effort to keep the young heron from grasping his bill (Fig. 9). The forward thrust or "repelling reaction" observed is a swift stab with opened beak and does not appear to be a part of the appeasing ceremony described by Lorenz (1938). During these violent engagements either the immature heron is knocked off his perch or the adult flies to an adjacent branch. If the adult has not completed regurgitation, he resists bill contact until ready to feed the immature heron. The pre-transfer behavior usually lasts for five to ten minutes.

Herrick (1935) noted that herons transfer regurgitated food by a "crossing or juxtaposition of bills, rather than by insertion of the parent's bill in a young one's mouth or contrariwise." This is the method we observed for the actual transfer of the fish. When the adult is ready to transfer the fish, it advances toward the immature heron and permits the bill to be grabbed. A young heron encloses the adult's bill at about a 65° angle with the adult's upper bill to the rear of the immature heron's mouth. The young heron always grasps the adult's bill from the top or slightly to the side. Once bill contact is made the immature heron vigorously shakes the adult's head and both birds flap their wings, presumably to maintain balance during the transfer. The head, neck, and back feathers are erect with the occipital plumes separated and extended. The adult regurgitates the fish forward in the mouth until the young heron can grasp it (Fig. 10). A withdrawal of the two bills follows with the young heron pulling the fish from the adult's mouth. Both adult and immature herons will wipe their bills with their tongues after transfer. Although the unfed young will advance toward the adult until they receive food or the adult flies, all aggressive action between the adult and fed immature heron ceases until the fish has been swallowed.

For twelve hours during a four day period we observed feeding rates at six nests. All hours between 0700 and 1830 were included in the observations at least once. During the twelve hours there was an average of four feedings per nest. These feeding data are meant to be only an indication of diurnal activity.

SUMMARY

A field study of Black-crowned Night Heron maintenance behavior was conducted on the Bass Islands of Lake Erie, Ohio, in the summer of 1963. Descriptions of the behavior patterns associated with locomotion and body maintenance are given.

The breast receives the most preening and the head the least. There is no set preening

sequence, and the preening methods used showed little individual variation. Scratching was observed to be by the direct method and was for the most part an isolated action. Stretching and shaking are employed at infrequent intervals and shaking is used to place the feathers in order.

Sleeping and resting were carried out during the daylight hours. Sunning, which is common to other herons, was not observed, but the herons did sleep in the direct sunlight. Throat pulsation, a rapid in and out motion of the gular region, was also noted during periods of higher temperatures.

Bill-wiping and care of the feet are an uncommon activity of the night heron. Defecation may occur either in flight or while perched but occurs more commonly just before flight.

When feeding, the immature heron's bill grabs the adult's bill at approximately a 65° angle and the food is transferred as the immature heron's bill withdraws from the adult's. There was no evidence of the adult placing its bill into the immature heron's mouth.

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NEW LIFE MEMBER

A recent addition to the roster of Life Members of The Wilson Ornithological Society is Mrs. Kathleen Green Herbert of Middletown, Delaware. A graduate of Mt. Holyoke College and the University of Michigan and a former student at St. Hilda's College, Oxford. Mrs. Herbert is also a Life Member of both the AOU and the Cooper Society as well as a member of British Trust for Ornithology and several other conservation organizations. Her principal ornithological interests have been devoted to the study of the Peregrine Falcon and she has published several papers on this subject including an important paper on the Peregrine in the New York City region written jointly with her late husband, Richard A. Herbert. At present she teaches ornithology in the University of Delaware extension division, and continues her field work and activities in various conservation organizations.

SPECIES AND ABUNDANCE OF DIURNAL RAPTORS IN THE PANHANDLE OF NEBRASKA

JOHN E. MATHISEN AND ANN MATHISEN

RECENT evidence of population declines for several species of raptors has been a subject of some concern both nationally and internationally. Although raptors are the most conspicuous birds in our environment, by virtue of their large size, flight habits, and food habits, little information is available to evaluate population densities and trends over large areas. Data are needed to provide yardsticks for judging population changes over time periods and among geographic areas.

This study was undertaken to provide information on the species and seasonal abundance of raptors in the panhandle of Nebraska for three years (1957 through 1959). Ten years have elapsed since the study was initiated and a replication at this time would be of considerable interest and value. We hope this report stimulates someone to repeat the study now and provide valuable information for helping to evaluate the population status of raptors.

Preliminary findings on our Nebraska study were reported by Mathisen and Mathisen (1957). Similar roadside raptor counts have been conducted by Nice (1934), Allan and Sime (1943) in Texas, Enderson (1965) in Colorado, and Rowan (1964) in South Africa.

METHODS

Most of the observations were made during official travel for the Nebraska Game, Forestation and Parks Commission. On days when observing conditions were good, all raptors seen on either side of the road were identified and recorded. Data included species, location, general habitat type where each bird was observed, time of day, and weather conditions. If positive identification could not be made, the bird was classed as unidentified. Observations were not made on rainy, foggy, or exceedingly windy days.

The number of miles traveled during each observation period was also recorded. Observations were made while traveling on both paved highways and secondary roads during all months of the year, except January 1958. The study period extended from 1 January 1957 through 31 December 1959.

An index of abundance was computed for each species for each month by calculating the number of raptors observed per 100 miles of travel. Future data can be compared on a monthly or annual basis, provided an adequate sample of mileage is obtained.

Information on habitat preferences of the various species appears in the preliminary report (Mathisen and Mathisen, 1957).

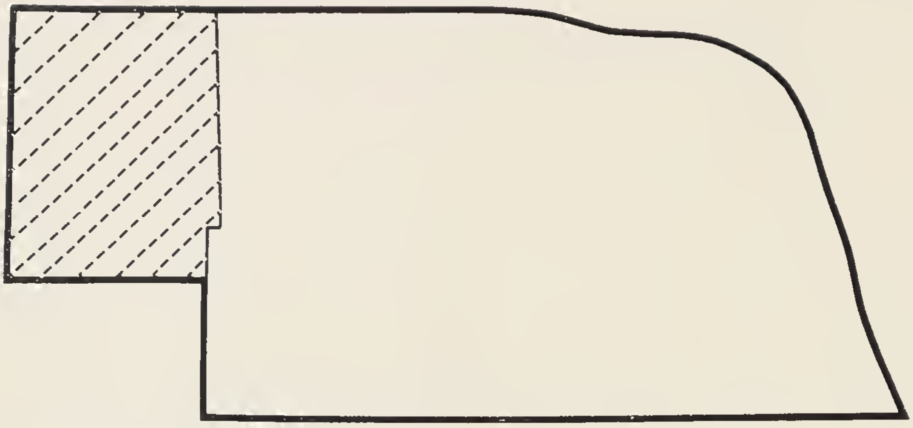

FIG. 1. Location of Nebraska panhandle study area.

STUDY AREA

This study was restricted to the eleven counties comprising the panhandle of Nebraska, an area of approximately 14,000 square miles (Fig. 1). This region may be roughly divided into three general habitat types: (1) cropland, largely winter wheat and other grains, (2) grassland, including the short-grass prairie of the extreme west and mixed-grass prairie of the sandhills, and (3) pine ridge, a rough escarpment with many buttes and canyons supporting open stands of ponderosa pine (*Pinus ponderosa*). Grassland is the most abundant habitat type in the panhandle, with cropland second and the pine ridge least.

FINDINGS

A total of 2,564 raptors were recorded in 53,347 miles of travel (Table 1). Seventeen species were recorded during the study period (Table 2). About six per cent of the raptors were classified as unidentified. Almost 90 per cent of the observations consisted of six species: Marsh Hawk, Sparrow Hawk, Rough-legged Hawk, Swainson's Hawk, Golden Eagle, and Red-tailed Hawk.

TABLE 1

SAMPLE SIZES AND INDEX OF ABUNDANCE OF RAPTORS IN THE PANHANDLE OF NEBRASKA, 1957–59

Year	Miles Traveled	No. Observation Days	No. of Raptors	No. Raptors per 100 Miles
1957	17,807	100	623	3.5
1958	20,852	143	1,072	5.1
1959	14,688	100	869	5.9
Totals	53,347	343	2,564	4.8

TABLE 2
NUMBER OF DIURNAL RAPTORS RECORDED IN THE PANHANDLE OF NEBRASKA, 1957–59

Species	1957	1958	1959	Total
Sparrow Hawk (*Falco sparverius*)	113	283	369	765
Marsh Hawk (*Circus cyaneus*)	164	324	166	654
Rough-legged Hawk (*Buteo lagopus*)	149	213	137	499
Swainson's Hawk (*B. swainsoni*)	65	78	29	172
Golden Eagle (*Aquila chrysaetos*)	24	52	61	137
Red-tailed Hawk (*B. jamaicensis*)	20	20	30	70
Peregrine Falcon (*Falco peregrinus*)	24	11	8	43
Krider's Red-tailed Hawk (*B. j. kriderii*)	3	6	6	15
Turkey Vulture (*Cathartes aura*)	5	3	4	12
Bald Eagle (*Haliaeetus leucocephalus*)	1	4	6	11
Ferruginous Hawk (*B. regalis*)	4	2	3	9
Broad-winged Hawk (*B. platypterus*)		3	3	6
Prairie Falcon (*F. mexicanus*)			4	4
Cooper's Hawk (*Accipiter cooperii*)			3	3
Pigeon Hawk (*F. columbarius*)	1		2	3
Osprey (*Pandion haliaetus*)	1			1
Sharp-shinned Hawk (*A. striatus*)	1			1
Unidentified	48	73	38	159
Totals	623	1,072	869	2,564

TABLE 3
NUMBER OF RAPTORS OBSERVED PER 100 MILES, 1957–59
Values given are monthly averages

	Species*						
Month	1	2	3	4	5	6	All Raptors†
January	0.1	0.8	1.1	3.2			6.1
February	0.2	1.0	1.0	2.7			5.4
March	0.1	1.4	0.4	2.1	tr		4.9
April	3.3	2.0	0.2	0.4	0.3	0.4	7.1
May	1.4	1.0	0.1	tr	0.1	0.4	3.2
June	0.3	0.4	tr		tr	0.3	1.4
July	0.6	0.8	0.1		tr	0.5	2.2
August	1.7	1.0	tr		0.1	0.4	3.5
September	8.4	1.5	0.2	0.1	0.6	0.4	12.6
October	0.4	2.0	0.1	0.2	0.2	0.1	3.5
November	0.1	1.3	0.7	1.9	0.1		4.5
December	0.2	0.7	0.5	2.2			4.1

* 1 Sparrow Hawk; 2 Marsh Hawk; 3 Golden Eagle; 4 Rough-legged Hawk; 5 Red-tailed Hawk; 6 Swainson's Hawk.

† Includes all identified and unidentified raptors observed.

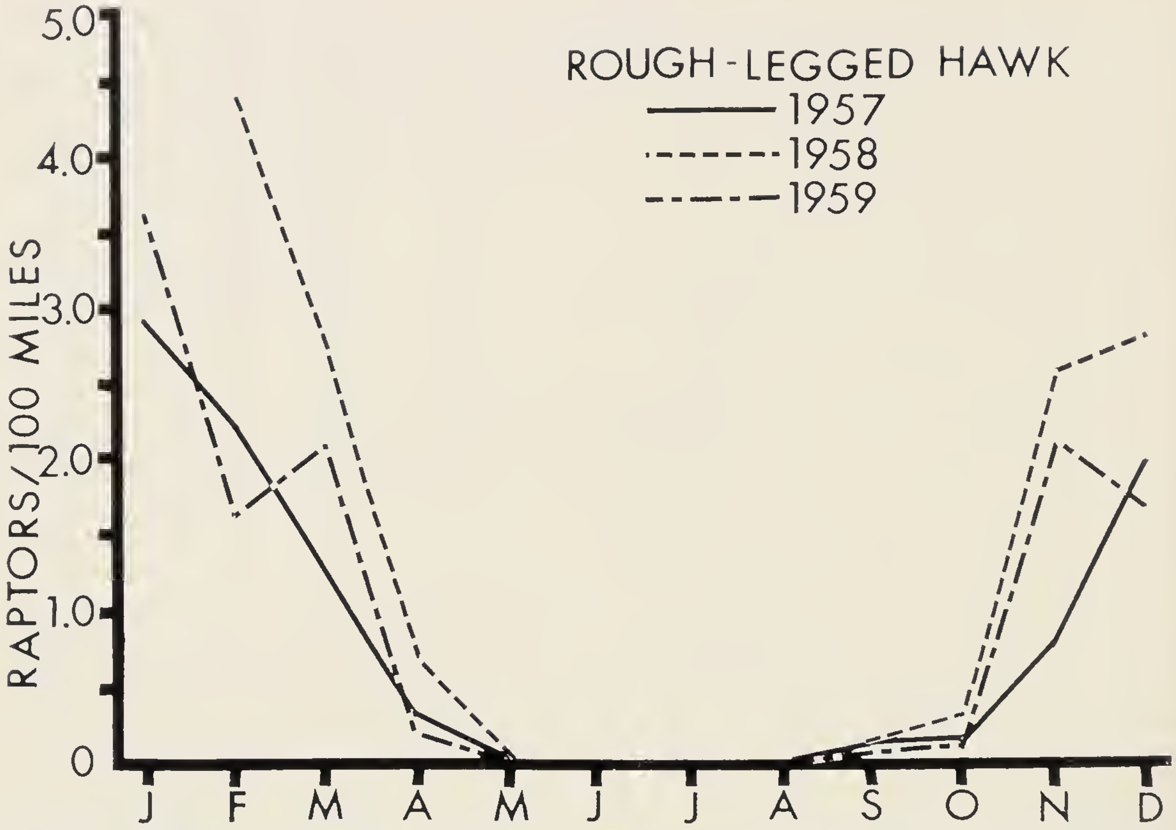

FIG. 2. Monthly abundance of the Rough-legged Hawk in the panhandle of Nebraska, 1957–59.

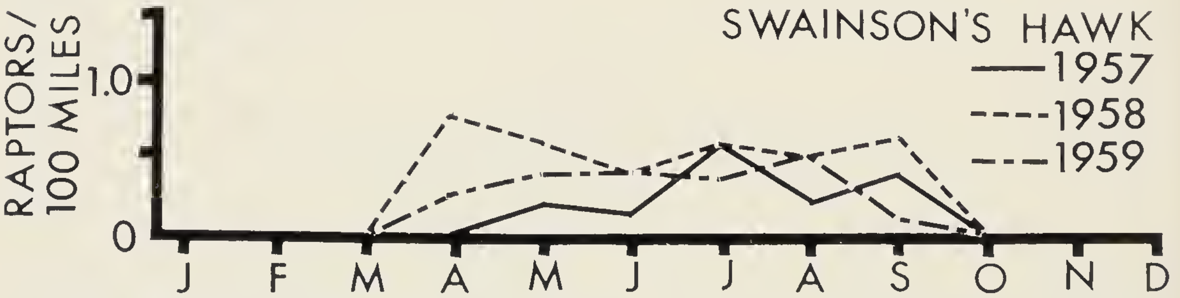

FIG. 3. Monthly abundance of the Swainson's Hawk in the panhandle of Nebraska, 1957–59.

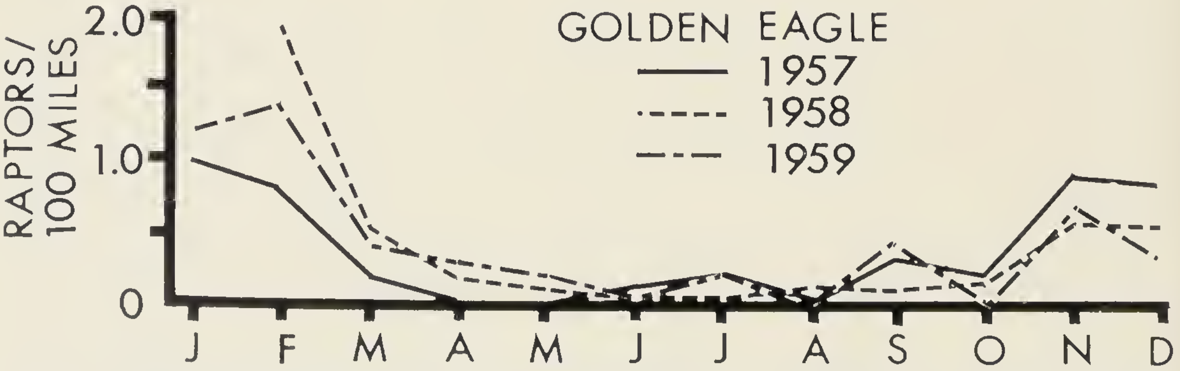

FIG. 4. Monthly abundance of the Golden Eagle in the panhandle of Nebraska, 1957–59.

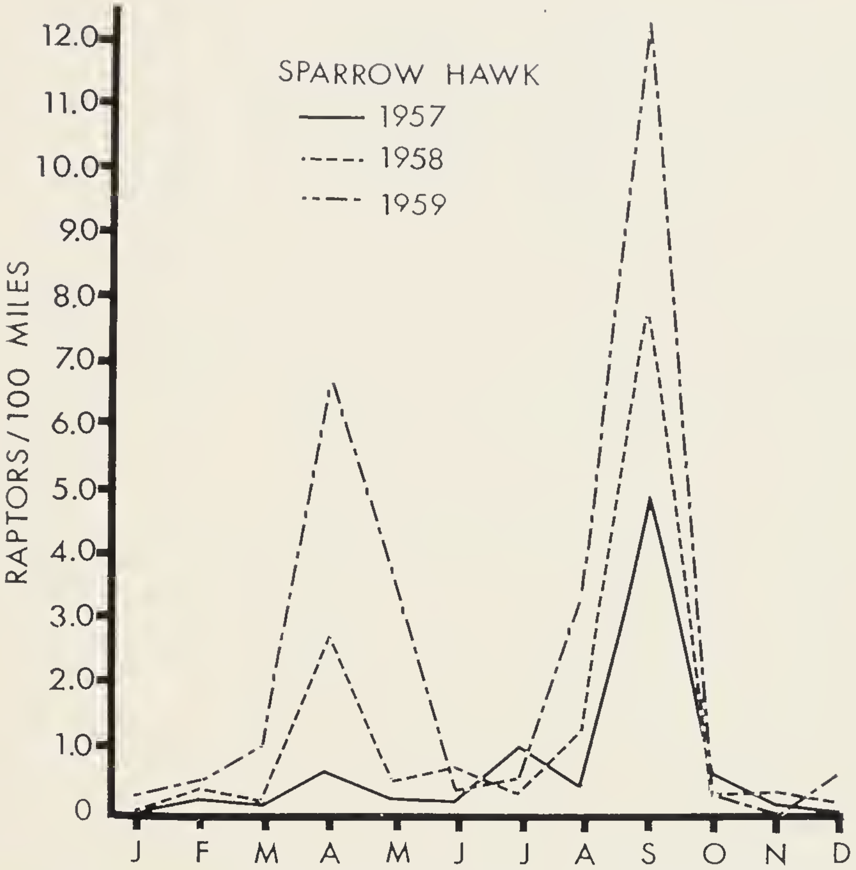

FIG. 5. Monthly abundance of the Sparrow Hawk in the panhandle of Nebraska, 1957–59.

Annual patterns of population abundance for the six major species are presented in Figures 2 through 7. These graphs show the periods of migration and relative abundance of each species for the three-year period.

Average monthly indices of abundance for the six most numerous species and for all raptors observed are given in Table 3. The pattern of seasonal abundance of raptors was similar from year to year with but few deviations. But the magnitude of abundance for specific months varied from year to year. April and September were months of major migrations. More raptors were observed in September than in April each year. The population reached a low point yearly in June or July. In 1957 and 1959 an increase in July was recorded for species breeding in the area, possibly reflecting the increment of young birds. This premigration increase was detected in August 1958.

The Rough-legged Hawk was the major raptor in midwinter in the study area. Its population changes were very similar for the three-year period (Fig. 2). Highest densities occurred in January with a consistent decline through May, after which the birds were not seen for the summer. They reappeared in September and gradually built up to their wintering peak.

TABLE 4
SEASONAL SPECIES COMPOSITION OF RAPTORS OBSERVED IN THE PANHANDLE OF NEBRASKA, 1957–59

	Summer		Fall		Winter		Spring	
	No.	Per Cent	No.	Per Cent	No.	Per Cent	No.	Per Cent
Rough-legged Hawk	—	—	90	10.4	289	52.4	120	14.8
Red-tailed Hawk	11	3.4	34	3.9	—	—	25	3.1
Marsh Hawk	104	32.1	233	26.9	90	16.4	227	27.9
Sparrow Hawk	105	32.4	357	41.3	19	3.4	285	35.1
Golden Eagle	11	3.4	41	4.7	93	16.9	33	4.1
Swainson's Hawk	61	18.8	21	2.4	—	—	49	6.0
Others	32	9.9	89	10.3	60	10.9	73	9.0
Total	324	100.0	865	100.0	551	100.0	812	100.0

Summer: June, July, August; Fall: September, October, November; Winter: December, January, February; Spring: March, April, May.

When the number of Rough-legged Hawks per 100 miles is expressed for comparable groups of months, there were 11.1 in Colorado (Enderson, 1965), 2.1 in Nebraska (our data), and 1.2 in Texas (Allan and Sime, 1943). Rough-legged Hawks were recorded almost five times more frequently in Colorado than Nebraska from September to February.

The Swainson's Hawk was recorded from March through October or November at relatively low population levels (Fig. 3).

The curves for the Golden Eagle population were almost identical for the three years. Peak numbers occurred during the winter months, with highest densities in January and February. Low populations occurred during the summer period, with a slight peak in July and September. A slight peak was also evident in November of all three years. For the same period, there were 1.9 Golden Eagles observed per 100 miles in Colorado (Enderson, 1965), compared to 0.5 seen in Nebraska.

The Sparrow Hawk population followed a similar annual pattern of abundance for the three years, although the magnitude of the peak populations varied (Fig. 5). Large numbers of Sparrow Hawks migrated through the area in April and September. In Colorado, Enderson (1965) recorded 1.9 Sparrow Hawks per 100 miles, compared to 1.3 for this Nebraska study.

The Marsh Hawk was present throughout the year, with peak numbers occurring in April and October in all years except October 1959 (Fig. 6). No peak was recorded in the fall of 1959, even though 1,000 miles were logged for the month on eight different days. For the same months, 5.0

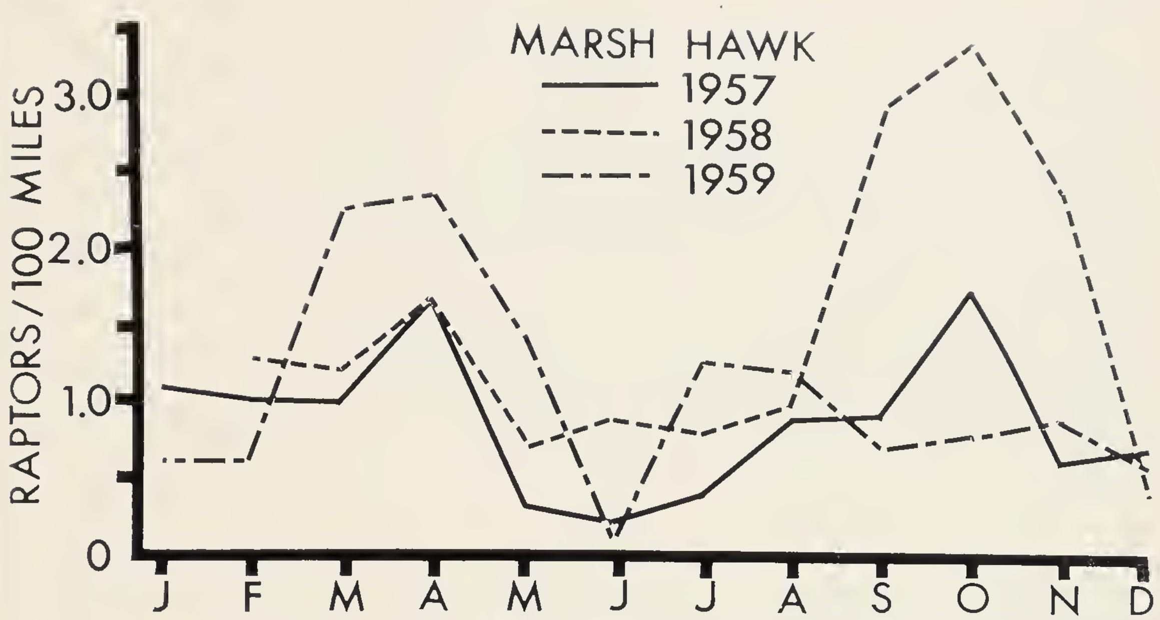

FIG. 6. Monthly abundance of the Marsh Hawk in the panhandle of Nebraska, 1957–59.

Marsh Hawks per 100 miles were found in Texas (Allan and Sime, 1943), 4.5 in Colorado (Enderson, 1965), and 1.2 in Nebraska (our study).

The Red-tailed Hawk was present in all months except December, January, and February (Fig. 7). Migration apparently took place in April and September. The breeding population was at a relatively low level in all years, with greatest numbers present in 1959.

Relative abundance of the six major species of raptors was obtained by combining data for the three-year period and summarizing by seasons of the year (Table 4). A direct comparison implies that each species is equally observable. This, of course, is not the case. The small size of Sparrow Hawks, for instance, and the ground roosting habits of Marsh Hawks makes these raptors less observable from the roadside. Craighead and Craighead (1956) suggest applying correction factors to field data so these two species are more properly represented. Their studies in southern Michigan indicated that doubling the Marsh Hawk observations and tripling the Sparrow Hawk observations would correct for their being less observable.

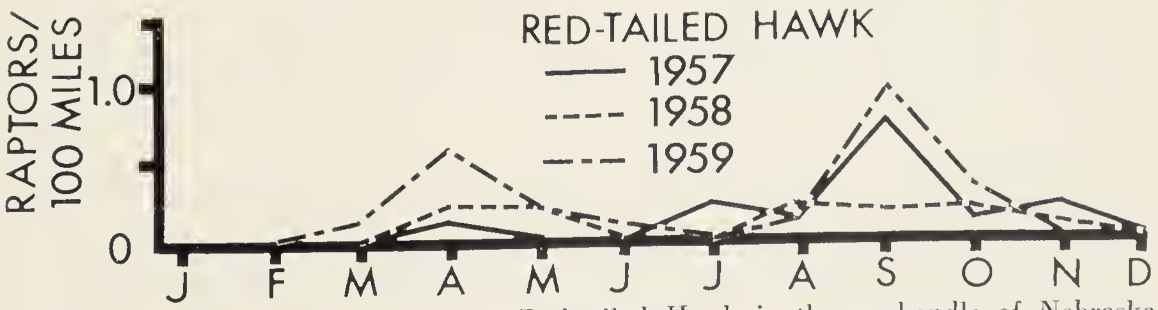

FIG. 7. Monthly abundance of the Red-tailed Hawk in the panhandle of Nebraska, 1957–59.

Data given in Table 4, therefore, probably do not properly reflect the true species composition of the raptor population. Species composition from future roadside counts, however, can be compared with data in Table 4.

The winter population of raptors consisted primarily of Rough-legged Hawks, Marsh Hawks, and Golden Eagles. By spring the Rough-legged Hawks were replaced in dominance by Sparrow Hawks. Other buteos and eagles became relatively scarce.

The summer breeding population consisted largely of Sparrow Hawks and Marsh Hawks. The Swainson's Hawk was the major summer buteo. Species composition in fall was almost identical to the spring period.

SUMMARY

Diurnal raptors were recorded from 1957 through 1959 while traveling by automobile in the panhandle of Nebraska. A total of 2,564 raptors of 17 species were observed while traveling 53,347 miles. The number of raptors per 100 miles was 3.5 in 1957, 5.1 in 1958, 5.9 in 1959 and averaged 4.8 for the three years.

Annual patterns of raptor abundance were, with but few deviations, similar among years. But the magnitude of abundance for certain months varied among years. April and September were months of major migrations.

Major winter raptors were the Rough-legged Hawk, Marsh Hawk, and Golden Eagle. Abundant species in summer included the Sparrow Hawk, Marsh Hawk, and Swainson's Hawk. In spring and fall the raptor population was dominated by the Sparrow Hawk, Marsh Hawk, and Rough-legged Hawk.

ACKNOWLEDGMENTS

We wish to thank the following persons for reviewing the preliminary manuscript and offering many helpful suggestions: L. R. Jahn, J. J. Hickey, F. N. Hamerstrom, F. Hamerstrom, G. A. Swanson, and R. A. Ryder.

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2317 PARK STREET, BEMIDJI, MINNESOTA, 25 JANUARY 1967.

GENERAL NOTES

An Eared Grebe specimen from coastal Virginia.—On 8 November 1966 an immature Eared Grebe (*Podiceps nigricollis*) was seen at the U.S. Army Corps of Engineers' Craney Island Disposal Area, Norfolk Co., Virginia. The writer returned the next day, found an adult in the same place, and collected it. On 12 November the immature was seen for the last time, but could not be collected.

The specimen of 9 November is the first taken in Virginia, the closest specimen locations being New Jersey and South Carolina. This is one of nine specimens of this species from the eastern Great Lakes and the Atlantic coast (Buckley, in press, *Audubon Field Notes*). It was a female (ovary, 17 mm × 5 mm), almost certainly adult from the dark flanks, head and neck, and measured as follows: wing (chord) 126.6 mm; exposed culmen 26.9 mm; bill from nostril 16.9 mm; tarsus 47 mm; tail 33 mm. It was quite fat, weighing 242.9 gms. Soft part colors were: orbital ring and irides bright red-orange; bill: silver grey; legs and feet slate-grey anteriorly, blackish posteriorly; gape flesh. The specimen is now No. 786259 in the American Museum of Natural History collections and was determined by J. L. Bull and E. Eisenmann to be *P. n. californicus* on the qualitative basis of no white at the base of the innermost primaries. All other eastern North American specimens have also been *californicus*, as one would expect (see for example, Dawn, *Auk*, 76:521, 1959; Snyder, D., *Auk*, 71:313, 1954; Snyder, L. and Hope, *Auk*, 67:506, 1950; Woolfenden, *Wilson Bull.*, 69:181–182, 1957; etc.).

Prior to the fall of 1966 there were three sight reports of the Eared Grebe from Virginia, all within a few miles of Craney Island (see *Audubon Field Notes*, 16:316; 19:365; 20:406). After this specimen was taken, third and fourth individuals were reported from the Cape Henry area in December 1966, and from January to mid-April 1967 a fifth (in complete nuptial plumage when last seen) was present at Craney Island (*Audubon Field Notes*, 21:15 & 401, 1967). Another was seen at Craney Island from 6 November 1967 to the date of this writing (7 December 1967; P. A. Buckley et al.).

The status of the Eared Grebe in eastern North America has apparently been changing since the 1940s, and is discussed elsewhere (Buckley, op. cit.). At present, the species must be considered regular in limited numbers on the eastern Great Lakes and along the Atlantic coast; it probably occurs annually in Virginia.

I thank R. L. Anderson for assistance in collecting this specimen.—P. A. Buckley, *Department of Biology, Hofstra University, Hempstead, Long Island, New York 11550, 14 December 1967 (originally received 11 August 1967).*

An Ohio record of the Magnificent Frigatebird (*Fregata magnificens*).—On 30 September 1967, while observing birds in the vicinity of Clear Fork Reservoir, Morrow County, Ohio, Nye saw a frigatebird as it soared or sat in a dead tree. The next day Dr. and Mrs. Edward S. Thomas saw it, and on 1 October Trautman and his wife collected the bird. It has been deposited in the state research collection as OSM No. 13510.

The bird, an adult female, was greatly emaciated, weighing only 1253.2 g without the contents of its alimentary tract, which weighed an additional 356.6 g. These contents consisted of two white crappies (*Pomoxis annularis*) total lengths 256 mm and 175 mm; two yellow perch (*Perca flavescens*) 140 mm and 125 mm; and the posterior portion of a largemouth blackbass (*Micropterus salmoides*) 140 mm in length. These fishes appeared to have been dead before being swallowed by the bird, because there were traces of fungus and evidences of decomposition on two of them. All of the fishes were in the anterior portion of the alimentary tract, the stomach and posterior alimentary tract were empty.

The bird was in fresh fall plumage. If it had been brought northward by a recent hurricane the feathers gave no indication of this.

The above appears to be the third record for the occurrence of this species in Ohio. The first account is the statement by Oliver Davie (Nests and eggs of North American birds. David McKay, Publ.:74, 1898) that "A specimen, which is now in the possession of Dr. Renshaw, of Sugar Grove, Ohio, was taken by Mr. Emmet Adcock in Fairfield County, Ohio, in the spring of 1880." The specimen appears to be no longer extant. This record is of particular interest because it was captured in *spring*; the majority of the more northern, inland and Atlantic coastal records in the eastern United States and Canada have occurred in summer or fall (Bent, Life histories of North American petrels and pelicans and their allies. *U.S. Natl. Mus. Bull.*, 122:315, 1922).

In a letter dated 10 November 1967 from Mr. Emerson Kemsies and from newspaper accounts I learned of the finding of the second Ohio record, a bird that had been "picked up dead in an eastern suburb" of Cincinnati, Ohio on 29 September.—MILTON B. TRAUTMAN, *Ohio State Museum, Columbus, Ohio 43210* AND THOMAS W. NYE, *20 October 1967.*

Atypical behavior of a Green-winged Teal.—On 23 August 1967, while making a field trip to Great Island, near Bauline, Newfoundland, I noted an example of atypical behavior in an adult female Green-winged Teal (*Anas carolinensis*). I left the landing stage at the outport at approximately 9:45 AM and on the way out to the island saw a boat in which three men were jigging cod. A wild, adult female Green-winged Teal, which had been seen on a local pond since early spring, flew out to sea and landed next to the boat, which was lying approximately one-quarter of a mile from the coast. The teal then stayed "on station" around the boat until late afternoon when I was returning from the island. The fishermen who took me out to the island stopped their boat near the one that had been out all day, and we jigged for cod for a period of approximately 20 minutes. During this time the duck swam around our boat, before returning to the original boat. While swimming around the boat the duck was seen to make bill-dipping and occasional nibbling movements, as described by McKinney (*Behaviour*, 25:120–220, 1965). If pieces of paper, cigarette ends, matches, or any other waste material was dropped overboard by the fishermen, the duck immediately ate them.

When the fishermen returned to the settlement in the early evening, the duck flew inland to a local pond. This behavior of flying out to sea after the boat, and returning in the evening, was repeated over a period of several days.—WILLIAM THRELFALL, *Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, 23 October 1967.*

Specimen of the Harlequin Duck in Florida.—B. W. Evermann (*Ornithol. and Zool.*, 11:81–83, 97–98, 1886) reported seeing a Harlequin Duck (*Histrionicus histrionicus*) at Pensacola, Florida. A. H. Howell (Florida bird life. Coward-McCann, New York, 1932, p. 154) mistook Evermann's report to refer to a preserved specimen. The error was repeated by A. Sprunt, Jr. (Florida bird life. Coward-McCann, New York, 1954, p. 82), and probably also in the current A.O.U. Check-list (1957). The fourth edition of the A.O.U. Check-list (1931) listed the species as casual in Florida, but I do not know if that referred to Evermann's sight record or some other record. F. M. Weston (*Bull. Tall Timbers Research Station*, No. 5, 1965; p. 35) recently straightened out the confusion surrounding Evermann's sight record and mentioned several sight records of the species in extreme western Florida on the northern Gulf coast. H. M. Stevenson (*Audubon Field Notes*, 12:273, 1958) mentioned an individual sighted at Haulover Canal Bridge on 3 December 1957. There is no other record for the Atlantic coast of Florida.

During the winter of 1967 I learned that a male Harlequin Duck in nuptial plumage had been seen at Matanzas Inlet, Florida. Knowing that there was no preserved specimen from Florida or the southeastern Atlantic coast south of South Carolina (A.O.U. Check-list, 1957), I thought it worthwhile to secure the specimen and did so on 21 February 1967. The specimen was taken near the line separating St. Johns and Flagler counties. The specimen is No. 1666b in the Florida State University collection at Tallahassee.—Lovett E. Williams, Jr., *Florida Game and Fresh Water Fish Commission, Wildlife Research Projects Office, Gainesville, Florida, 24 October 1967.*

Some observations of social hierarchy in the wild Turkey.—The author observed two instances of social dominance in a flock of 35 wild Turkey hens (*Meleagris gallopavo*) at 5:00 PM 24 December and 8:35 AM 25 December 1966 on the Wesley DeGrodt Ranch in Medina County, Texas. I was with one of Mr. DeGrodt's deer hunters in a blind located 25 yards from a feeding station baited by casting whole kernel corn on the ground under a motte of live oak trees (*Quercus virginiana*).

The Turkeys came in to the feeding station on a dead run on the first afternoon and immediately began scratching among the leaves to feed on the corn. From the size of the birds, they appeared to be all adults; however, the young-of-the-year were probably full grown by this time. Two of the hens had visible beards that enabled me to distinguish them from all the other hens at all times. One had a beard that I estimated to be about 8 inches long because it almost touched the ground as the hen bent over to eat. The other hen's beard I estimated to be about 5 inches long. Neither of the beards was as heavy as that of a gobbler's beard of comparable length. The birds were identified as hens on the basis of their buff-tipped breast feathers.

The hen with the longest beard was definitely the Number 1 bird in the order of dominance over all the other hens with which she came in contact during the course of these observations. The birds were observed feeding the first day for 24 minutes. Neither of the bearded hens led the flock into the feeding area but were close to the last to arrive. The birds fed very actively during the entire period they spent at the feeding station. None of the Turkeys seemed to be aware of our presence in the well-concealed blind 25 yards away, although at least some of the birds constantly had their heads up surveying their surroundings.

The Number 1 bird showed very aggressive behavior toward all other hens that were in her way as she wandered around over the feeding area. She displayed two types of behavior with seemingly no preference for either. One type could be best described as the "peck" in that she merely pecked at the less dominant bird with her beak. The other was the "running lunge" during which she would move quickly toward the offender and lunge with her body at this offender. All birds she confronted in this way hastily began to get out of her way, including the hen with the shorter beard. This second bird in turn seemed to be dominant over all the other hens except Number 1 and displayed the same types of aggressive behavior as did Number 1.

The hen with the longest beard was the last Turkey to leave the area after the morning feeding. The Turkeys left the area in a follow-the-leader style with the Number 2 hen about half way back in the line. The Number 1 hen stayed until the rest of the Turkeys were almost 40 yards away, and then she ran to them and took a place at the end of the line until they disappeared into the brush about 75 yards away.—Samuel L. Beasom, *Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706, 27 September 1967.*

The Whooping Crane from the lower Pleistocene of Arizona.—While studying the avian fossils in the Frick Collection, American Museum of Natural History, I discovered the proximal end of a left tarsometatarsus (A.M.N.H., F:A.M. No. 8410) of a Whooping Crane (*Grus americana*). The fossil was collected in 1939 by Mr. Ted Galusha from lower Pleistocene deposits in Arizona; the locality data are as follows: Dry Mountain locality, San Simon Valley, 20 miles east of Safford, Graham Co., Arizona.

The Whooping Crane has not been recorded from fossil deposits in southwestern United States including Arizona (Brodkorb, *Bull. Florida State Mus.*, 11:153, 1967), the nearest locality previously reported being the Rancho La Brea tar pits of southern California (Howard, *Condor*, 32:84, 1930). The fossil tarsometatarsus further documents the once wide distribution of this species.

Measurements.—Transverse breadth (external to internal) across cotylae 28.0 mm.

I am grateful to Dr. Malcolm C. McKenna for allowing me to report on this specimen; to Dr. Richard Tedford for his help with stratigraphy; and to the authorities of the Division of Birds, United States National Museum, and the Department of Ornithology, American Museum of Natural History, for allowing me the use of their collections.—Joel Cracraft, *Department of Biological Sciences, Columbia University, New York, New York 10027, 13 October 1967.*

Bar-tailed Godwit from Alaska recovered in New Zealand.—Mr. Frank H. Rowson of Kati Kati, Bay of Plenty (North Island), New Zealand, found the skeleton of a banded Bar-tailed Godwit (*Limosa lapponica*) at the mouth of the Tawanga-Harkoin River on 28 October 1967. The bird had been banded by DeLong on St. George Island, Pribilof Islands, Alaska, 31 May 1966. The distance between St. George and the Bay of Plenty, following the Great Circle Route, is 5,288 nautical miles. This is the first recovery of a Bar-tailed Godwit banded in North America and one of the longest over-water movements on record for any species of bird.

The Bar-tailed Godwit had been previously recorded only as a casual visitant to the Pribilof Islands (Kenyon and Phillips, *Auk*, 82:624–635, 1965). The species was not recognized by island residents when it began arriving in sizeable numbers on 29 May 1966. By 30 May there were an estimated 300 godwits on St. George. On 31 May the birds were feeding persistently and a rocket net (Thompson and DeLong, 1967. *Bird-Banding*, 38:214–218) was set. It was camouflaged with moss and lichens torn from the earth in front of the net. After an hour's futile attempt to herd the birds toward the net, two birds discovered the disturbed area and began feeding actively. The rest soon followed, and when the net (70 ft × 35 ft) was launched, 113 birds were trapped and only seven escaped. Size No. 5 bands were used; these were large and had to be overlapped and crimped. This species is normally banded with size No. 3 (male) and

No. 4 (female) bands, but these were not available. Before the supply of No. 5 bands was exhausted, 100 godwits were banded, leg-streamered, color-marked with orange paint, and then released.

That evening flocks of godwits with marked birds among them were observed flying over the bogs west of St. George Village. By the next day all but a few had left. The New Zealand recovery is the only one to date.—*(Paper No. 40—Pacific Ocean Biological Survey Program.)* ROBERT L. DELONG, *Pacific Ocean Biological Survey Program, Smithsonian Institution, Washington, D.C.* AND MAX C. THOMPSON, *Southwestern College, Winfield, Kansas, 26 April 1968.*

"Ploughing" for fish by the Greater Yellowlegs.—A feeding method employed by the Greater Yellowlegs (*Totanus melanoleucus*), but not by the Lesser Yellowlegs (*Totanus flavipes*), is "ploughing" the water in pursuit of fish. Rowan (*Brit. Birds*, 23:2–17, 1929) described it thus: "The species never probes and is frequently to be seen running through the water and skimming the surface with its bill . . . the bill being pushed along steadily forwards." (p. 15). According to Witherby (Handbook of British birds, vol. 4:336, 1940) similar behavior is exhibited by the Greenshank (*Totanus nebularia*), and Lacey (*Brit. Birds*, 37:217, 1944) said further of the Greenshank, that "On five occasions . . . its whole head and body were under water, so that all that was seen was its tail moving along, sometimes at considerable speed."

I first observed and photographed ploughing behavior by the Greater Yellowlegs in 1964 at the Cheyenne Bottoms of central Kansas. There, at 6:00 AM on 5 September, two birds were walking in a shallow, turbid channel bordered by extensive sedge flats. Repeatedly they ran forward, cutting the water with the lower mandible for periods of one to seven seconds. The birds were attracted to surface ripples produced by concentrations of fish; they ran toward and ploughed through these ripples when they appeared. The birds changed direction at times while ploughing, but the usual movement was a straight forward rush. I saw no food being taken. Lesser Yellowlegs feeding nearby kept closer to the sedges and walked about, making repeated single stabs at the water's surface.

On 6 September a lone bird fed near the middle of a roadside ditch containing muddy water between one and two inches deep. A number of times the bird ran forward with its bill open, the lower jaw submerged and the upper jaw above water (Fig. 1A). It also fed by drawing the opened bill to one side and back again through the water. On the next day a bird was feeding in the same spot, running after fish whose presence was revealed by surface ripples. This bird ploughed briefly several times, but eventually caught a fish by simply picking it up. The fish was about as long as the bird's bill and quite flat-bodied. After about seven attempts, the bird finally swallowed it with a single flick of the head.

I again observed Greater Yellowlegs ploughing in clear, shallow water at the southern end of Assateague Island, Virginia, on 29 September 1966. The site was a channel with exposed mud bars supporting some short sedge and other herbaceous plants. Two Greater Yellowlegs were accompanied by about twenty Lesser Yellowlegs. The latter walked on the mud bars and in the water, pecking or briefly probing. By contrast, the Greater Yellowlegs kept largely to the water and walked or ran, at times abruptly changing direction. Although I was unable to see fish or surface disturbance during much of their feeding, the birds sometimes ran 10 or 15 feet in a straight line to a spot where they made a stab or a short ploughing motion in the water. At times the

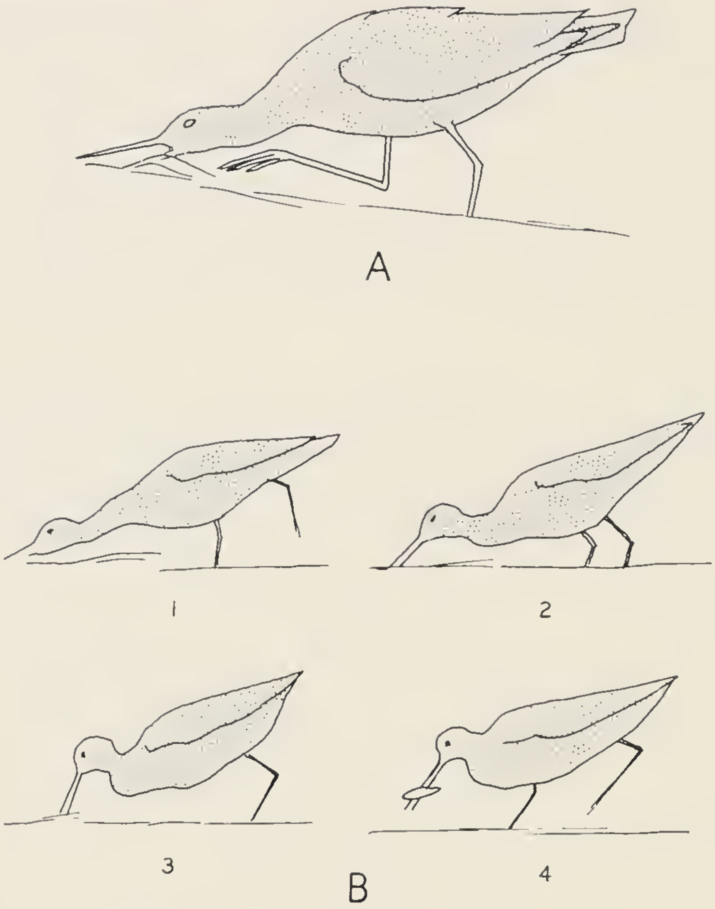

Fig. 1. A.—Greater Yellowlegs ploughing the water while running (drawn from photograph). B.—Greater Yellowlegs catching a fish by ploughing (drawn from successive motion picture frames taken at 30 frames per second).

fish were evidently all about the wading bird, which alternately raised its head, looking down, and stabbed periodically at the water or swept its slightly opened bill sideways. Both of the Greater Yellowlegs engaged in ploughing, covering distances of up to 10 feet with the bill or much of the head submerged. One bird caught a small fish while ploughing (Fig. 1B) whereupon it ceased ploughing and swallowed the fish. The path of ploughing was sometimes straight; at other times the birds turned at right angles toward a mudbar, and once completely reversed direction within less than a second. Changes in direction occurred most often when the head was submerged as if the bird were following groups of fish by sight.

Ploughing by the Greater Yellowlegs shows some resemblances to skimming by the Black Skimmer (*Rynchops nigra*). Both feeding methods sample the food source by cutting the water in simple patterns, relying on chance contact with prey. Both species may also use visible evidence of fish concentrations to direct the ploughing or skimming. Both cut the water with open jaws, at times throwing up a wake from the bill or head. The skimmer doubles its head under its body upon striking prey or an obstacle; I did not observe this in the Greater Yellowlegs. Pursuit of individual fish by a bird with its head underwater is not known in the Black Skimmer.—Richard L. Zusi, *Division of Birds, U.S. National Museum, Smithsonian Institution, Washington, D.C. 20560, 3 November 1967.*

Sabine's Gull in North Dakota.—On 1 November 1966, I collected an immature female Sabine's Gull (*Xema sabini*) at Lake Ashtabula, 10 miles north of Valley City, Barnes County, North Dakota. I first noticed it when it flew from a rocky shore about seven feet away from me. The water of the reservoir, which is approximately 20 miles long and one half mile wide, was quite cold with ice along the shores. The gull's stomach contained several diving beetles of the family Dytiscidae as identified by Dean K. McBride of North Dakota State University Entomology Department. The bird (NDSU No. 2103) has been deposited at the North Dakota State University vertebrate museum. This is believed to be the first record for the Sabine's Gull in North Dakota, although according to Peterson (A field guide to western birds, 1961) it occurs rarely as a transient through the Great Plains.—Roger L. Kroodsma, *Zoology Department, North Dakota State University, Fargo, North Dakota, 16 September 1967.*

Comments on Reproduction of the Common Grackle in central Illinois.—During a cool spring (on 8, 10, and 19 May 1966) in central Illinois (Lake of the Woods Park, Mahomet), 52 nests of the Common Grackle (*Quiscalus quiscula*) were found and observed. They were situated from approximately three to 20 feet above the ground, in small evergreens (mostly spruce), tall white pines, and dense rose hedges. Some of the data obtained on reproduction are presented in Table 1. They may be compared with those of other large samples reported for Kansas (Johnston, *Univ. Kansas Publ., Mus. Nat. Hist.*, 12:575–655, 1964), Wisconsin (Peterson and Young, *Auk*, 67:466–476, 1950), and Ontario (Snyder, *Canadian Field-Naturalist*, 51:37–39, 1937). Climatological and other ecological information are presented elsewhere (Long, *Trans. Illinois Acad. Sci.*, 61:139–145, 1968).

Of 34 nests found on 8 May, 12 contained broods (indicating April breeding), and 22 contained incubated eggs (six of these nests also contained hatchlings). All clutches had hatched (excepting the sterile eggs) before 19 May. On 10 May, broods had left seven of 47 nests. On 19 May, other broods had left, including 10 of 24 fledged broods checked. All of the nestlings were well fledged.

Clutch size averaged 4.21 (2–5; N, 23; mode 5) for 10 May (clutches with hatchlings were included in this sample). It is noteworthy that the frequency distributions are skewed to the left (Table 1).

"Predation" by small boys (see Peterson and Young, op. cit.) was not observed, but probably is at least of occasional importance, especially in warmer weather. Subfreezing temperatures at night evidently caused some mortality. On 10 May, one dead fledgling was found in a brood. A downy bird of a different nest was found dead on the ground. On 19 May, two dead fledglings were found in dense spruce needles next to an empty nest. Still another was found dead dangling by a strand of nylon fishing line incorporated in the nest structure.

Peterson and Young (op. cit.) included deserted eggs with those actually sterile (infertile). Admittedly, it is difficult to distinguish between nonincubated and sterile eggs, but as a rule of practicality eggs in fledged broods may be considered sterile. Only a single sterile egg was found in each of two of 24 fledged broods. In this study four deserted clutches were found, two on 8 May (2, 4 eggs), one on 10 May (4 eggs), and another on 19 May (3 eggs). Three nests were found overturned with eggs spilled out. One new, empty nest (renesting?) was seen 19 May.

It is interesting that concentrations of breeding grackles were not to be found in nearby cemeteries and other parks, even though their vegetation appeared similar

Table 1

Data on Reproduction of the Common Grackle (May, 1966) in central Illinois. On 8 May, 16 nests contained incubated eggs, but some clutches were incomplete.

	Class frequencies of clutch or brood size						
	1	2	3	4	5	Totals	Date May
Number of clutches	0	0	3	6	7	16	10
	0	0	0	0	0	0*	19
Number of nests with eggs and hatchlings	0	1	0	3	2	6	8
	0	1	1	1	4	7	10
	0	0	0	0	0	0*	19
Number of broods	0	1	1	2	8	12	8
	1	0	2	9	7	19**	10
	0	2	3	6	3	14**	19

* No clutches were seen; all fertile eggs hatched, or were occasionally deserted.

** Some fledged birds had left some of these nests.

to that at Lake of the Woods. Nests of two Mourning Doves, three Robins, a Brown Thrasher, and a House Sparrow were also observed at Lake of the Woods.—Charles A. Long and Claudine F. Long, *Department of Biology, Wisconsin State University, Stevens Point 54481, 3 November 1967.*

Allopreening invitation display of a Brown-headed Cowbird to Cardinals under natural conditions.—On 18 June 1966, I observed a behavioral interaction, which I interpreted as an allopreening invitation display, between a female Brown-headed Cowbird (*Molothrus ater*) and a pair of Cardinals (*Richmondena cardinalis*). In 68 hours observation of 10 widely separated pairs of Cardinals in Weakley County, Tennessee, between 29 April and 19 June, this was the only such observation.

I had observed the pair of Cardinals almost continuously since 04:42 cst. At 08:05 they were actively foraging together in a freshly plowed field near a low, narrow hedgerow when, suddenly, a female cowbird flew rapidly towards them and landed on the ground in front of the female Cardinal. The cowbird walked directly towards the Cardinal until their bills were about 5 cm apart. The Cardinal remained motionless for 138 seconds, and the cowbird for almost as long. The cowbird then opened its eyes, which had been closed for more than one minute, and assumed a hunch-backed attitude with bill pointing forwards at a 45° angle to the ground and feathers of the nape slightly ruffled. Maintaining this posture, she repeatedly approached the Cardinal; each time, the foraging Cardinal hopped away. The female Cardinal was approached about 30 times while foraging on the ground or perching in the hedgerow. The male Cardinal was approached once; he immediately took flight. After 5½ minutes, the cowbird flew away, leaving the Cardinals still foraging.

The cowbird was apparently adult. Neither of the Cardinals approached the cowbird, acted aggressively towards her, or made any attempt to preen her when approached.

Similar behavior of cowbirds in an aviary has been described by Selander and La Rue (*Auk*, 78:473–504, 1961). They suggest that under natural conditions such behavior results in reduced hostile tendencies of individual birds that are potential hosts for the cowbird. Harrison (*Behaviour*, 24:161–209, 1965) elaborates on other possible functions. Among captive birds, an invitation display results in flight, attack, or allopreening. Selander and La Rue mention a "positive" allopreening invitation of cowbirds to a dummy male Cardinal placed in an aviary. They suggest that an allopreening invitation display is a regular feature in the behavior of noncaptive cowbirds. The fact that I have observed this behavior only once in three summers' intensive observation of Cardinals, all of which were members of populations microsympatric with the cowbird in both Tennessee and Ontario, suggests that it is rarely given towards this species, which is commonly parasitized by the cowbird in some areas (Scott, *Wilson Bull.*, 75:123–129, 1963; Wiens, *Wilson Bull.*, 75:130–139, 1963). As the cowbird is an easily observed species, the rarity with which observers of cowbird behavior record allopreening or an invitation display (J. Darley, pers. comm., familiar with the behavior in his captive birds, noted it only once in 300 hours of field observation at London, Ontario.) outside the aviary renders the biological significance of such a display questionable. Of course, it is entirely possible that we are observing the initial stages of a behavioral adaptation in a very recently evolved brood parasite.

This observation was made in a field study of the Cardinal supported by a National Research Council of Canada Studentship and a Louis Agassiz Fuertes Research Award from the Wilson Ornithological Society to the author and by an N.R.C. grant to D. M. Scott. I am grateful to D. M. Scott for his critical reading of an earlier draft of this note.—Douglas D. Dow, *Department of Zoology, University of Western Ontario, London, Canada, 13 November 1967.*

A Maine nest of the Scarlet Tanager.—Palmer (Maine birds, *Bull. Mus. Comp. Zool.*, 102:518, 1949) remarks that although the Scarlet Tanager (*Piranga olivacea*) undoubtedly breeds in Maine, he could not find any record of a nest in this state. On 23 June 1967 we located a nest of this species near Sieur de Monts Spring, slightly over a mile from Bar Harbor. It was situated 8–9 ft. from the trunk of a lower branch of a hemlock approximately 30 feet above the ground, among a scattered hemlock grove that had escaped destruction by the disastrous forest fire of 1947. When found, the nest was nearly completed, and on 28 June the female was incubating. Both adults were seen feeding the young on 11 July. The morning of 22 July, the nest was watched intermittently between 7 and 10 AM and three fledglings were seen to leave, two before 8 AM the last about two hours later after considerable coaxing by the adult female carrying food. In mid-June the contour feathers of the adult male appeared completely scarlet, but at the time the young left the nest there were distinct patches of olive-green on the back and greenish yellow on the breast, sides and flanks.—Barbara Patterson and Reginald Allen, *Somesville, Maine, 20 October 1967.*

Lark Bunting in New Jersey.—On 7 September 1962 I captured a Lark Bunting (*Calamospiza melanocorys*) in my net at the Operation Recovery Bird Banding Station at Island Beach, Ocean County, New Jersey. Realizing the rarity of this species, I brought it to Bertram G. Murray, Jr., for verification. He kept it as a specimen which is now in the University of Michigan Museum of Zoology (No. 157,599) and supplied me with the following information.

The bird was an immature female with an incompletely ossified skull and a small ovary (2.5 × 1.0 mm). It had little fat, an empty stomach, and weighed 28.9 g. While this species has been reported several times in the east, this is apparently the first substantiated record for New Jersey.—Mabel Warburton, *300 W. Trenton Avenue, Morrisville, Pennsylvania, 6 November 1967.*

The association of invading White-winged Crossbills with a southern tree.—The quest for food by invading White-winged Crossbills (*Loxia leucoptera*) leads an occasional band into areas where deciduous woods predominate and conifers are few. Growing evidence indicates that a deciduous tree, the sweetgum (*Liquidambar styraciflua*), may be of importance to the survival of such migrants. In Kentucky during the winters of 1937–38 and 1954–55 (see Mengel, Birds of Kentucky, A.O.U. Monograph No. 3:476, 1965), White-winged Crossbills foraged in this species, extracting seeds from the hanging fruits; and the same was true of some birds during the winter of 1965–66 both in West Virginia (Maurice Brooks, pers. comm.) and, as I observed, in southern Illinois.

In structure a sweetgum fruit is exquisitely peculiar, and for this reason a description of its characteristics seems required before considering the implications of the sweetgum-crossbill association.

Lacking scales, the fruit is not in the least conelike except in being pendulent. It hangs, a hard walnut-sized ball, from a 3–4 inch-long stem. Green in the growing season, the ball is actually composed of many small fruits, each bearing two spines which form a single beaklike chamber. The whole ball turns brown with autumn, the spines typically spreading apart to release a pair of winged seeds. However, a small proportion of the spines of some fruits fail to separate; a seed supply consequently remains locked inside certain chambers while the ball remains drooping among naked branches during winter. Interestingly, a near relative of *Loxia*, the American Goldfinch (*Spinus tristis*), alone takes full annual advantage of this benefaction, perhaps because no other member of the regular winter avifauna combines the use of a strong finch bill with the art of clinging up-side-down while adjusting the feet. These attributes appear essential, owing to the toughness and rigidity of the spiny locking device, the length of the stem and the fragility of the brittle connection which in winter secures the stem to its branch. A direct attack on the seed chambers by a bird perching on a fruit—a common practice in fall of both goldfinches and juncos (*Junco hyemalis*)—would tend to sunder the stem connection, plunging the fruit to the ground. Goldfinches reach the seeds by employing various clever techniques; in one the bird first hangs from a twig near a fruit; then uses one foot as a sliding vise which clenches the stem between its base and its branch, drawing the fruit to the bill tips. This method is the one, precisely, which I saw White-winged Crossbills employ in southern Illinois.

The repeated observation of feeding in sweetgums by *L. leucoptera* presents a record which suggests that sweetgum distribution may influence the local winter distribution of the invaders. But two further factors appear to lend a still more special point to this history: first, the northern distribution of the bird as compared to the southern distribution of the tree; and second, the lengthy time intervals between invasion winters.

The sweetgum is absent from the bird's regular range, not occurring as native growth north of southern Connecticut, southeastern New York, West Virginia, southern Ohio, southern Illinois, southeastern Missouri, and Oklahoma. Contact between the two species, more than likely, then, is limited to invasion years. Since the time lapse between two consecutive invasions may well exceed the average life span of a bird as small as a crossbill, the periodic renewal of the sweetgum-crossbill association would seem to depend on birds which have had no previous invasion experience. Different generations of the species evidently can initiate the association anew, and indeed, judging from the parallel actions of birds in West Virginia and southern Illinois during 1965–66, separate bands participating in the same invasion can initiate it independently.

I have no evidence that the association is a historical one, innately resumed, or is not.

However, learned behavior possibly underlies it; if so, a glimpse of the learning process may be provided by the observed record of the species in southern Illinois, an area where mature conifers are not only relatively scarce but often impoverished. On six known occasions, beginning on 18 December, *L. leucoptera* appeared in a grove of ten introduced eastern hemlocks (*Tsuga canadensis*), and of other trees including one sweetgum, two miles north of the village of Cobden, Union County. The largest number of birds counted together was ten; the fewest, five; a solitary male once visited the grove. None was recorded out of the grove and accordingly any or all, without my knowledge, may have foraged continually in sweetgums elsewhere. My single record of such feeding occurred in the grove on 7 February during the visit of five birds. By then the hemlock seed crop had been much depleted. The birds nevertheless were first observed in the hemlocks. At this same time four goldfinches and one Pine Siskin (*Spinus pinus*, a rare winter visitant) fed in the sweetgum. Subsequently three crossbills joined this aggregation, all the species foraging in the manner described above. I have since speculated that perhaps the crossbills were attracted to the sweetgum less by the fruits in the branches than by the stimulus generated by the actions there of their cardueline kin. The characteristic foraging style of one cardueline surely would appear familiar to certain others. I accordingly suspect that the intermittent sweetgum-crossbill association may be an extension, in imitation, of the perpetual sweetgum-goldfinch one.

Another possible source of linkage between the bird and the tree is the appearance of the fruits themselves. While unconelike in structure, they present a set of conditions intermediate between those of pendulent cones among green branches and of the scaled fruits of alders (*Alnus*). This deciduous tree occurs within the regular range of *Loxia*; and its fruits hang in winter from bare branches.

In any case, detailed observations should be attempted on future invading White-winged Crossbills, particularly at points where south-moving expeditions first meet the sweetgums. Do the birds ignore the trees, do some heed them; and to what extent are the birds' later movements influenced by sweetgum distribution?—WILLIAM G. GEORGE, *Department of Zoology, Southern Illinois University, Carbondale, Illinois 62901, 13 November 1967.*

STATEMENT OF OWNERSHIP

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I certify that the statements made by me above are correct and complete. Signed. George A. Hall, Editor.

ORNITHOLOGICAL NEWS

The Wilson Ornithological Society has never had a permanent fixed address. Mail for the Society is frequently sent to the address of any person who has been an officer in the last ten years, and indeed, The Editor received a letter addressed to Oberlin, Ohio which was last the editorial office in 1924. It is a pleasure, then, to announce that as of the immediate present the permanent address of the Society is to be: The Wilson Ornithological Society, c/o MUSEUM of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. The connections between the Society and the University of Michigan are of long standing and we are grateful to the authorities of the University and the Museum of Zoology for generously allowing us to use this address. Persons having business with any of the officers may, of course, address them directly at the addresses given on the inside front cover of this issue, and all matters pertaining to *The Bulletin* should be sent directly to the Editor, but the University of Michigan address will serve as a fixed point of reference through changing officers over the years.

The Second Annual Arthur A. Allen Award for distinguished service to ornithology was awarded by the Cornell University Laboratory of Ornithology to James Fisher of Great Britain on 21 September 1968.

We note the retirement of James R. King as Editor of *The Condor* after three years of excellent service. The new Editor will be Dr. Ralph J. Raitt of New Mexico State University.

Dr. Tom J. Cade has resigned from the Editorial Board of *The Bulletin* to assume other editorial duties. The Society and the Editor wish to thank him for the excellent service he performed, and to wish him well in his new endeavors.

On Page 513 readers will note an announcement of extreme importance to prospective authors of papers for this journal. Starting with the first number of Volume 81 (1969) *The Wilson Bulletin* will make a number of stylistic changes in the matter of citations to the literature. These changes are being made both in the interests of economy and of uniformity among the American ornithological journals. Prospective authors are advised that the printed format of the "Literature Cited" section of papers will be changed to something very close to that used in the other American journals.

The American Institute for Biological Sciences announces that the First National Biological Congress will be held in Detroit, Michigan on 6–10 November 1970. It is planned to hold subsequent Congresses in 1971 and 1972. These Congresses will be concerned with social, educational, and scientific aspects of such important biological problems facing the world as overpopulation and environmental contamination. There will also be a combined program of invited papers for interdisciplinary symposia and original research papers.

Readers are reminded again of the Third Pan-African Ornithological Congress to be held in Kruger National Park, South Africa on 15–19 September 1969. Anyone who wishes to attend the Congress should without delay ask for particulars and entry forms from: The Hon. Secretary, South African Ornithological Society, c/o Percy Fitzpatrick Institute of African Ornithology, University of Cape Town, Rondebosch, C.P., South Africa.

The Eastern Bird Banding Association announces that again this year they will make an award of $100 to a student, graduate or undergraduate, who is using bird banding in an ornithological study. The application for this award should be received prior to 25 February 1969. Further information can be obtained from, and all applications should be sent to: F. R. Scott, Chairman Memorial Grant Committee, Eastern Bird Banding Association, 115 Kennondale Lane, Richmond, Virginia 23226.

With the publication of the final number of Volume 80 it is again my pleasure and privilege to extend appreciation to all those persons whose cooperation and help have made the task of preparing the volume lighter. Particular acknowledgement should go this year to: William A. Lunk who bore the responsibility of seeing that the four color plates were prepared on time and to the standards expected for them; to Treasurer William A. Klamm for preparing the Membership List, surely an exacting initiation to his new job; and to the several reviewers of papers for the symposium on Arctic ornithology who in many cases responded with almost instantaneous reviews. All of the color plates in this volume were subsidized by donors and our thanks is extended to them. It becomes almost routine to acknowledge the assistance of the members of the Editorial Board, and the other ornithologists who reviewed papers, but this service is in large part responsible for making the Bulletin what it is or has been. It has been a real pleasure to dedicate this volume in honor of the 70th birthday of Dr. George M. Sutton, and it is hoped that our readers have enjoyed the series on Arctic ornithology that has featured this affair.—G. A. H.

LOUIS AGASSIZ FUERTES RESEARCH GRANTS

These grants, established in 1947, are devoted to the encouragement and stimulation of young ornithologists. One particular desire is the development of research interests among amateur ornithologists. Any kind of ornithological research may be aided. Recipients of grants need not be associated with academic organizations. Each proposal is considered primarily on the basis of possible contributions to ornithological knowledge.

An anonymous donor gave $500 to found the fund; later donors have provided additional money. The Council of the Wilson Ornithological Society has added funds as necessary to provide at least one $100 grant annually. Two grants have been made in several recent years. In 1969 a single grant of $200 will be made.

Although grantees are not required to publish their studies in *The Wilson Bulletin*, it is hoped that they will submit their manuscripts to the Editor of the *Bulletin* for consideration.

Since its inception, the Fuertes Research Grant has been awarded to 25 persons, many of whom have continued their research work.

Application forms may be obtained from Harrison B. Tordoff, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104. Completed applications must be received by 1 March 1969.

ORNITHOLOGICAL LITERATURE

The Shorebirds of North America. Editor and sponsor, Gardner D. Stout; paintings by Robert Verity Clem; text by Peter Matthiessen; species accounts by Ralph S. Palmer. The Viking Press, New York, 1967: 10½ × 14¼ in., 270 pp., 32 col. pls., two-tone pl. dealing with shorebird plumages. $22.50.

It would be easy to dwell exclusively upon the good features of this handsome book. In it are some of the most completely satisfying paintings of birds I have ever seen. In it is a wealth of distinguished prose and much valuable reference material. But the investigator who has travelled a long way to observe shorebirds on their far northern breeding grounds; who has witnessed their courtship behavior and made rounds of nests weeks on end in an attempt to ascertain which sex spends the night on the nest, which predators are responsible for destroying eggs, etc., who has, in short, lived with the birds during the whole of their brief but exciting reproductive cycle—that person is bound to feel that the book is primarily about shorebirds as transients, as visitors to the United States. Furthermore, when the "average" bird student, eager to be brought up to date about this important avian group, starts to use the book, he soon finds that the index is far from adequate (it applies largely to the "species accounts" and hardly at all to the first 135 pages) ; that the "off-plumages" every observer has to deal with—no matter what the area or season—are neither illustrated nor very fully discussed; that the taxonomy and nomenclature are bewildering in that they involve wholly unexplained departure from that which has been widely accepted for some time; and that there is an unfortunate inconsistency in presentation of subject matter.

In the eleven opening chapters by Matthiessen (pp. 19–135) there is no evidence of attempt to shorten, to save space in any way. In the "species accounts" by Palmer (pp. 143–267), on the other hand, abbreviations are so numerous as to be offensive. Page-size is ample, margins are generous, yet despite this abundance of space we are obliged to read (concerning the Black-necked Stilt) : "Breeds from s. Oregon and n. Utah southward to s. Louisiana and locally s. to n. Brazil and, w. of Andes, to cent. Peru" (p. 152). The captions on virtually blank pages opposite the colorplates might have included meaningful comment on elements of habitat shown in the pictures; or mentioned facts concerning molt (the Lesser Yellowlegs on Plate 16 is obviously molting, yet the caption tells us that the plumage shown is "definitive") ; or discussed behavior. The beautifully drawn Killdeer on Plate 9 is feigning injury. Some users of the book will know this instantly; others may decide that the bird has been shot, or that it is sunbathing. The caption for the plate, instead of making at least one point pertaining to behavior memorably clear, reads as if author and publisher had grimly resolved to keep the wording as short, dry, and uninformative as possible.

The "inconsistency" in presentation that I have mentioned may well be a by-product of today's overweening desire to bring out something patently marketable as rapidly as possible. I have dealt with publishers enough to know how demanding—indeed how infuriating—they can be at times. There is that almighty deadline. The fall catalogue has already announced a publication date. The field force are ready to sell. Review copies must go out. "Yes, we decided that some of the background in that picture was extraneous, so we took some off; what we did doesn't change the picture at all; in fact it looks better than it did. No, there's no time for preparing the sort of index you have in mind; most people won't need any sort of index. This part of the book is dull; use abbreviations wherever possible and we'll liven it up by running it in two columns. The two columns improve readability." I have heard all this many times over. Worse than the publishers are the engravers: "Just leave it to us. When you see our final product you'll agree that we've improved on the original. It will be a lot brighter, a lot more pleasing to everyone!"

Justifiable cynicism aside, let me discuss the work of Robert Verity Clem. Briefly assayed, it is more than exceptional; it is thrilling. I have long had an aversion for composite plates, especially for such impossible assemblages as that in Plate 2 (Common and Red-throated Loons, Greater Shearwater, Arctic Tern, Great Auk) in H. H. Bailey's "The Birds of Florida" (1925)—an unsavory goulash cooked up, alas, by myself! But in Clem's gifted hands groups of assorted shorebirds are wholly acceptable—even those as in Plate 11 (Hudsonian and Marbled Godwits, Golden Plover) and Plates 31 and 32 (phalaropes) in which both breeding and winter plumages are shown side by side. The point of my approval is, of course, that such motley assortments not only might be, but occasionally are, seen together in late summer and fall. Indeed, now that I have observed shorebirds in Oklahoma during the past 15 years or so, I am prepared to see "almost anything" from the end of June through August and September in this part of the continent.

Clem's groupings are pleasing pictorially and sound ecologically. I deeply regret that so few of them show what can conceivably be identified as tundra vegetation. Many of them tell a story. His four Sanderlings and three Semipalmated Sandpipers (Plate 20) have finished their morning feeding and are drowsing off the heat of mid-day. Since all are facing the same way, a light wind must be blowing. His Dunlins, Knot, and Ruddy Turnstone (Plate 25) have been quieted down by fog. Whether conscious or not of the little comedy created, Clem shows his Lesser Yellowlegs eyeing a food item that a Greater Yellowlegs also sees (Plate 16). But Clem does not depend on extremes of posture—grotesque stretching, mad scrambling after food, agonized effort to escape—in giving life to his subjects. He is, in other words (and fortunately), no Audubon.

A fact about Clem's special genius merits emphasis. He paints what he sees. In his plover portraits the highlight of the eye is often so subdued, so muted, as to be almost imperceptible (see, especially, the juvenal Piping Plover in Plate 7). This handling is far from traditional, yet it helps to give his plovers that innocent, mellow facial expression that plovers have. How fortunate are they (and we!) in having a portraitist who knows them so well!

Clem's juvenal Piping Plover just mentioned has dark legs. I must not say that a mistake has been made here, for some juvenal Piping Plovers may indeed be dark-legged; but a juvenal specimen collected 1 September 1968 near Oklahoma City had *orange* legs. I prepared this specimen myself. Its skull and major wing- and leg-bones were not yet fully ossified; the gray plumage of its upperparts was beautifully edged or "veiled" with white; its bill was all dark; but the bare tibial area, tarsi, and toes were of a shade of orange fully as bright as that shown by Clem in his drawing of the adult bird.

The plates showing groups of shorebirds are pleasing; but Clem is at his best, in my opinion, with single birds—e.g., his exquisite Upland Plover and the neglected fence (Plate 14), his Golden Plover on the beautiful rock (Plate 5), and his brooding Woodcock among the suntouched dead leaves (Plate 27). His Common Snipe (Plate 28) was cropped without permission—an unforgiveable blunder (or worse) on the part of the publisher—though the picture as it stands is a superb portrait of both bird and habitat.

Plate 21 (Pectoral, Western, Least, and White-rumped Sandpipers) is for me the least satisfactory of the plates. In my copy of the book the buff on the breast of the White-rump is far stronger than in any spring or summer specimen of either sex in the considerable series before me. The Pectoral and Least are somewhat wooden in appearance and, unfortunately in another way, the White-rump is standing in water considerably deeper than would be at all likely along so flat a shore.

All in all, the Clem plates are an outstanding contribution to ornithology; more than this, they are glowing proof of humanity's appreciation of a wonderful part of the world in which it exists. Of themselves they give "The Shorebirds of North America" a completely valid *raison d'être.*

Matthiessen's several chapters, which appeared in two long installments under the title "The Wind Birds" in *The New Yorker*, in 1967, are excellent reading. They provide a fine accompaniment for the Clem plates. I wish they had been based to a much greater extent than they were on first hand experience in the far north. Peter Matthiessen should have been with me on Jenny Lind Island on 11 June 1966, when, on a gravel slope above the frozen ocean, I happened upon a pair of Sanderlings. The wind was sharp; light snow was falling. The handsome male (brick-red all over the head and chest) and drab female were pecking at the thin grass. They must have been eating tiny seeds, for I could find no gnats or animal life of any other sort in the area they so thoroughly covered. I wanted to ascertain what they were feeding on; but I was so convinced that they were a pair and that they had a nest in the vicinity that I decided not to collect them. Thirteen days later David F. Parmelee found a nest (four fresh eggs) not far from where I had seen the birds. What a time we had at that nest—hour after hour of vigil, partly to protect the eggs from predators, partly to ascertain which sex did the incubating. Not for one minute during a 22-hour period was that nest without a human guardian. The whole experience was memorable (see Parmelee, Stephens, and Schmidt. The birds of Southeastern Victoria Island and adjacent small islands, *Natl. Mus. of Canada Bull.*, 222:224, 1967). If only Peter Matthiessen could have been there!

So full of feeling and on the whole so convincing is Matthiessen's writing that coming upon gross errors is worse than shocking; it obliges us to wonder how many thought-provoking and exciting pronouncements may be misleading or wrong. Take, for example, the statement that the "gular sac" of the Pectoral Sandpiper "has an almost identical counterpart in the prairie chicken, not only in color (orange) and appearance but in resonating effect produced" (p. 82). I have observed hundreds of transient and breeding Pectoral Sandpipers. I have handled many freshly killed specimens both in the United States and in the Canadian Arctic Archipelago. Fascinated by their courtship behavior, I have watched them by the hour. Never have I seen anything that could conceivably be called an orange neck sac ("gular sac" is hardly a correct designation for the flaccid, highly vascularized, subcutaneous mass of tissue that the Pectoral puts to such spectacular use); nor can I find in the literature so much as a phrase that might be construed as description of such a thing. The wonder of a mistake of this sort is that none of Matthiessen's several consultants caught it. I call attention to a related misconception. The Pectoral's "gular sac" is not truly "unique in the shorebirds." In lesser degree the White-rumped Sandpiper has it (see Sutton. The birds of Southampton Island, *Mem. Carnegie Mus.*, 12, Part 2, p. 132, 1932); in still lesser degree the Buff-breasted Sandpiper has it (see Sutton, *Arctic*, 20:6, 1967).

Matthiessen reveals the fact that he has not spent much time *himself* making the rounds of shorebird nests when he says that "chicks must be removed from the scrape and the telltale eggshells as rapidly as possible" (p. 97). Many galliform birds leave a nestful of empty shells when the nidifugous young depart; not so with shorebirds. What happens is this: the parent bird flies off with pieces of shell as soon as the chick is out. It would not surprise me, indeed, to learn that the parent lifts or pries the chick loose and makes off with the shell while the chick still is damp. On scores of occasions I have visited shorebird nests containing whole broods of young near which there was not a sign of egg-shell. Parmelee, Greiner, and Graul (*Wilson Bull.*, 80:17–18, 1968) graphically describe the haste with which female White-rumped Sandpipers make off with empty half-shells.

My criticism of Matthiessen is intended to be severe. He has erred either because his imagination has run away with him or because he has incorrectly interpreted the writings of others. May he not be discouraged. He loves shorebirds; no one doubts that. May he go right on observing them—more closely than ever before. And may he continue to inform us, in his own highly literate way, of what he himself sees, hears, *and knows.*

The "species accounts" by Palmer include much useful material, some of it unavailable elsewhere. Parts of the accounts are presented in the tersest, driest possible way, as if to conform to agreed upon word-limit. The numerous abbreviations oblige us to realize that all extraneous material is to be excised; yet under the heading of "habits" we come upon repeated reference to vaguely identified molluscs, crustaceans, worms, and the like. Why did Palmer not prepare a succinct foreword making clear that shorebirds eat a great deal of animal food and some vegetable food, but that for most species little has been ascertained as to exactly what this food is? Such a statement would have saved a great deal of space. We observers are all to blame for this lack of concise information. I know from examination of Red Phalarope stomachs and esophagi that that species often eats the "rat-tailed" aquatic larvae of some such insect as the syrphid fly *Eristalis tenax.* I made a crude life-sized drawing of the larva in the field. But I have never, until now, published a word about the finding. My friend Harley P. Brown has done his best to identify the creature from the drawing, but specimens are needed. Adding to the sum of knowledge is a slow process. Information is gathered "bit by bit," even as Celia Thaxter and her "one little sandpiper" gathered driftwood, but neither Palmer nor anyone else can add to knowledge with verbose generalities.

Palmer's foisting of an unfamiliar and wholly unexplained classification on his public in this sort of book is unpardonable. Many of his innovations (too numerous to list here) may be quite sound; but they are meaningless to the layman and confusing to the professional. I do not consider myself much of a professional, to be sure, yet I know enough about generic characters to wonder whether Palmer considers *Erolia* an out-and-out synonym of *Calidris* or whether, to his way of thinking, some scolopacids belong in *Erolia* and others in *Calidris.* Palmer's placing of the three phalaropes in the Scolopacidae rather than in a family by themselves is unacceptable to me at this writing, but Palmer may know something that I do not; in fairness to all concerned he should share what he knows and permit his co-workers to weigh this knowledge in their own balances, so to speak.

Palmer's "species accounts" and the captions for most of the plates fairly resound with the word *definitive*, a term used (I take it) for a feathering that, once achieved by the individual, is repeated season by season for the rest of that individual's life. I can't free myself of the feeling that this word, as so used, is pompous and virtually meaningless, especially if it is to be applied to such as an individual as the above-referred-to Lesser Yellowlegs in Plate 16. Attempts to get away from errors of the past are wholly laudable; the coining of new words and phrases is part of this process of moving forward; but unless the new words and phrases are truly an improvement, no progress has been made.—George Miksch Sutton.

GAMEBIRDS OF SOUTHERN AFRICA: BEING A GUIDE TO ALL THE MAJOR SPORTING BIRDS OF AFRICA SOUTH OF THE CUNENE, OKAVANGO AND ZAMBEZI RIVERS. By P. A. Clancey. American Elsevier Publishing Company, New York, 1967: 7¼ × 10 in., xviii + 224 pp., 12 col. pls., 35 figs., 10 maps. $15.75 or R8.00.

In 1912 Major Boyd Korsbrugh published his "Game-Birds and Water-fowl of South Africa," a lavishly illustrated volume containing all then known of this interesting group. This book has long been out of print, and Clancey has taken this opportunity to summarize the taxonomic and biological knowledge accumulated over the past half century and to present it for us in a useful and attractive form.

Clancey's "gamebirds" are defined not on taxonomic lines but on their actual importance to the shooting fraternity. He gives a full discussion of the francolins and quail (Phasianidae), the guineafowl (Numididae), the waterfowl (Anatidae), and the Sand Grouse (Pteroclididae), and then considers in less detailed fashion the Buttonquail (Turnicidae), the Bustards (Otididae), the Painted Snipe (*Rostratula*), two true Snipes (*Gallinago*), and the Green Pigeon (*Treron australis*). Systematic treatment for each species includes: (1) *description*—elaborate and detailed descriptions of each plumage stage from downy young to adult, including sexual differences, and measurements of adults; (2) *distribution*—range in detail within southern Africa (south of the Cunene, Okavango, and Zambezi rivers), and extralimital range; (3) *general biology*—ecology, food, general habits and breeding behavior where known; (4) *nidification*—descriptions of nests and eggs, and dates of breeding. Where more than one subspecies occurs in southern Africa, the best known race is treated in detail. and the others are compared to it.

In his preface, Clancey states that his purpose in presenting his new information is to enable sportsmen and landowners to identify the species that they hunt, and to stimulate in them an interest in the conservation and wise exploitation of their gamebird resources. This is an especially valid approach in southern Africa, where in a vast area with a sparse population, only local measures are effective. The conservation picture in southern Africa at present is satisfactory, although not one to cause complacency. Of all the gamebirds, only the Karkloof Forest Crested Guineafowl (*Guttera edouardi symonsi*) is in danger of extinction. The status of the francolins, quail, and guineafowl as a whole is one of decreasing numbers or even extirpation in heavily populated areas, but of holding their own in unspoiled country. The reduction in numbers is not apparently due to hunting pressure but to the destruction of cover through agriculture or overgrazing. In areas where sufficient cover exists, birds thrive despite high population densities and constant shooting and trapping. This presents a conservation opportunity for the landowner to recreate stands of original cover on his lands to permit the recovery of the gamebird population. In contrast to the upland gamebirds, the waterfowl population has increased over the past half century, primarily through man's activity in building dams for urban, industrial, and agricultural use. With the minimum of protection during the breeding and flightless periods, the waterfowl can be expected to continue to increase as irrigation projects already planned are completed.

Considering that Clancey explicitly aims his book at the sportsman and landowner, much of it seems overwritten. His descriptions are phrased in the technical language of the professional ornithologist, and, for some of the complex patterns of the cryptically colored francolins, are in almost feather by feather detail. Such terms as "medial elliptical zonations," "sagittate markings," "tertials" (even professionals disagree on these), "desquamate," and "accuminate" will convey nothing to the average sportsman or landowner, and Clancey offers no definitions or figures to clarify them. It is true that there are color plates figuring the adults of each species, and these are the primary means of identification, but there is great overall similarity among many of the francolins, and a short paragraph giving the diagnostic and field characters of each species would have been more useful than an elaborate description. Similarly, his terms for the different plumage stages are nowhere defined, and "first basic plumage" will convey nothing to the sportsman. Simply to number the plumages and to state their approximate duration would have been much more informative. On the other hand, the sections on general biology, particularly where it is evident that Clancey is writing from personal experience, are well done and give a clear picture of the bird against its usual habitat and pursuing its daily and seasonal routines. Of special interest to sportsmen are the time and duration of the periods of flightlessness in the waterfowl, when they are most vulnerable to human predation. However, the descriptions of courtship behavior, most of which are taken from the literature, are too interspersed with technical terms to mean much to the layman.

The above criticisms of Clancey's book as directed to sportsmen are not meant to detract from its value as a handbook of the gamebirds of southern Africa. The descriptions and measurements were made afresh for this volume, and the biological sections are careful summaries of what is known of each species and are thoroughly documented. The color plates, all by the author, are well done and attractive, although they have suffered in the reproduction, possibly from an attempt to make these essentially dull colored birds more vivid. Certainly the violet tones on Plate 9 are more striking to the eye than faithful to the birds. Nevertheless this is a volume that will be of value to all who are interested in gamebirds.

Although technically published in New York, the actual printing and binding were done in Cape Town. This may explain, but it certainly does not justify, the 40-per cent-increase in the U.S. price.—MELVIN A. TRAYLOR.

PRELIMINARY SMITHSONIAN IDENTIFICATION MANUAL: SEABIRDS OF THE TROPICAL PACIFIC OCEAN. By Warren B. King. United States National Museum, Smithsonian Institution, Washington, D.C., 1967: 7¾ × 10⅛ in., xxxii + 126 pp., 11 pls. (bl. and wh. drawings) and many distributional maps. No price stated.

The aim of this manual is "to fill the needs of ornithologists, fishermen, oceanographers, and ocean travelers who want a guide to identification and distribution of seabirds they may encounter at sea." The manual covers the area between latitudes 30°N and 30°S, including the Hawaiian Islands, Bonin Islands, south to the Kermadec Islands and Easter Island. Migrants from outside the area are included, and rare vagrants are briefly treated. The area includes 28 island groups and 107 species.

I would prefer to have the area covered by the manual extend farther east toward the American continents and farther west into Malaysia. Perhaps the reason for its present boundaries has to do with the present Smithsonian banding scheme in the Pacific. The larger area would give a more general picture of distribution and movements, especially of the wide-ranging species, even though the inclusion of the Humboldt Current area would not have conformed with the title of the manual.

The introduction consists of excellent, concise discussions of seabird distribution, oceanographic surface water zones, their representative birds, and the principles of marine ecology and seabird migration. These are followed by guides to at-sea identification, methods of preserving and shipping specimens, a brief note on landbirds at sea, and references to groups of seabirds. All these are cleverly simplified and readable. Material on general matters was taken from its sister-volume on Atlantic seabirds by Dr. G. E. Watson; material dealing only with the Pacific is original.

The principal part of the manual consists of keys and specific descriptions of morphological characters (length and wing span are given in inches), flight techniques, food, marine habitat, and distribution with very useful maps. These accounts are concise and up to date. For example, *Oceanodroma matsudairae* is stated as migrating south to the Indian Ocean, a fact first reported by Bailey in 1965. Also, *Pterodroma longirostris* is treated as a species, in which is included the race *pycrofti.* The aim of the guide is field identification so, understandably, the literature references for the above-mentioned are not given, but the scientific value of the manual for the serious bird student would be raised considerably if such references were given.

The figures showing color patterns of seabirds in flight are fairly complete for each species. They show with sufficient accuracy the characteristic dorsal and/or ventral patterns of different ages or sexes. It may be pointed out that two (darker and paler) types of dark phase *Puffinus pacificus* are illustrated in addition to the white-breasted phase without comment in the text. The size difference between Sooty and Slender-billed Shearwaters is not shown, and the underwing of the former is too uniformly white. (There is a variable amount of white in the underwing of Slender-billed Shearwaters—Kuroda, *Misc. Rept. Yamashina Inst.*, 28:194, 1967.) The tails of the Streaked and Wedge-tailed Shearwaters are more cuneate than shown. Dorsal patterns of skuas (jaegers) would have provided a better comparison of the relative amount of white in the primaries of each species. (The white on the ventral wing surface of *Stercorarius longicaudus* is too large.) The juvenal plumages of *S. pomarinus* and of frigatebirds should be added. Excellent drawings of the gradual change with age of the body and dorsal wing patterns of *Diomedea albatrus* were recently published by Mr. Norio Yanagisawa (*Yacho*, 32:123, 1967). These should be consulted to supplement the manual.

The final part of the manual is a very useful appendix which consists of seabird lists of the 28 island groups with known status for each species, a brief note on general status of our knowledge of the seabirds of the island group, and reference literature.

In conclusion, this manual of 126 pages is concise and well documented with keys, plumage patterns of birds in flight, clear distribution maps, and avifaunal lists by island groups. It should certainly prove to be a very useful and accurate guide for the sailors, marine ornithologists, and ocean travelers for whom this booklet was aimed. Photographs of representative species and treatment of waters surrounding the area covered by the manual would make the guide more complete. I would like to end this review with congratulations to the author for such a fine work.—NAGAHISA KURODA.

THE BEHAVIOR OF BICOLORED ANTBIRDS. By Edwin O. Willis. University of California Publications in Zoology, Vol. 79, 1967: 127 pp., 3 pls., 21 figs. $3.50.

This paper represents a major advance in our understanding of tropical forest birds. There is so much in it that it is hard to know what to single out for special mention; and there is a lot to learn from it not only about the birds themselves, but also about how to tackle a piece of ornithological field work in the tropics and how to write it up afterwards.

Dr. Willis studied his birds over a period of six years, mainly on Barro Colorado Island, Panamá, with briefer observations for comparative purposes elsewhere. He does not give the grand total of hours spent watching them, but by 1963 he had put in nearly 1,400 hours and his observations continued until 1966. Bicolored Antbirds (*Gymnopithys bicolor*) are specialized followers of army ants and rarely ascend more than a few feet above the ground. And as they tend to be concentrated at certain points within the forest, they can be caught in mist nets, and all their activities can be observed by a human observer at ground level. Moreover, soon after they have been banded they become very tame again. Another great advantage is that the behavior of their associates, the army ants, is already well understood. Thus Bicolored Antbirds are in many ways ideal subjects for detailed study, and the author took full advantage of the fact. He got to know his birds individually, and was able to make sense of the outward confusion characteristic of bird parties as they follow the ant raids.

He shows that there is an elaborate hierarchical system of dominance among Bicolored Antbirds at the ant swarms, and that this is related to the birds' territoriality. Territories are however not "defended areas" from which conspecifics are excluded; they are areas in which the territory-holder is dominant to other individuals. As an army ant swarm crosses from one pair's territory to that of another, the dominance relationships of the birds concerned may be reversed within the space of a few yards. The territorial system thus revealed leads the author to a stimulating discussion of territories in general, and he suggests that the Bicolored Antbird's system may be paralleled in many other species which are usually thought of as nonterritorial.

In describing the Bicolored Antbird's various postures Dr. Willis goes into great detail as to the angles of flection of the limb joints and neck, the orientation of the body, head, and tail, and the position of the feathers of the various tracts; so that I wondered at times whether all these minutiae could be relevant to the main theme. But in fact they are: they lead up to an analysis of display postures which, it is suggested, may be more fruitful than the more usual interpretation in terms of conflicting drives. It would not do justice to what the author calls "the rule of angles" to attempt to discuss it in a few words. The rule itself can be stated simply, that "in aggressive behavior, angles at the extremities are closed and ones nearer the center of the body are opened; in submissive behavior, the reverse is true." The author's development of this theme should be read by anyone interested in the origin and significance of displays.

Detailed description of the Bicolored Antbird's stance and movements is also highly relevant ecologically. One learns that its habit of clinging to vertical perches near the ground and catching its food in the way it does is based on subtle structural adaptations. At the same time, the fact that another antbird of about the same size but with longer, thinner legs, *Myrmeciza longipes*, frequents thicker undergrowth where there are more horizontal perches, takes on a new significance. I believe that detailed studies of this sort, which illuminate the finer structural and behavioral adaptations of tropical forest birds, will throw more light on the general question of bird species diversity than will more superficial, quantitative analyses of bird faunas and vegetation structure.

The presentation and style of this very fine paper are up to the standard of its content. The author is not afraid to make the reader work hard. Sometimes I felt that it would be easier to follow some of the discussions if there were more of the connecting words and phrases that guide one through an argument—"hence," "on the other hand," and so on. But there is a danger in the over-use of such words, as they tend to draw the reader along a predetermined argument uncritically, and their avoidance may have been deliberate. The drawings, maps, and diagrams are very clear, but it would have been an advantage, and not just an adornment, if there could have been a color plate of male and female Bicolored Antbird. It would often have been a help to have a clear visual image of a species that nobody interested in tropical forest birds can now afford to ignore.—D. W. Snow.

The Parrots of Australia: A Guide to Field Identification and Habits. By William R. Eastman, Jr., and Alexander C. Hunt. Illustrations by William R. Eastman, Jr. Livingston Publishing Company, Narberth, Pennsylvania, 1966: 7¼ × 10 in., xiv + 194 pp., many paintings in col. and photos in bl. and wh. and col. $12.50.

The subtitle of this book states that it is a guide to field identification and habits. But the size of the book and its price suggest either a scholarly monograph or an art work. A cursory examination, however, shows that it is neither of these things and indicates that it should be judged as a naturalist's guide.

It is a matter for praise that the attempt should be made because Australia is lacking in first-rate books on natural history. For birds there is no book equal to the Peterson guides, or "A Field Guide to the Birds of Britain and Europe," though "The Birds of Western Australia" by Serventy and Whittle is a fine work. A book devoted to a small taxonomic group of birds and reduced further by concerning itself with those of one continent is of very different scope from the field guides I have mentioned. One might well ask: What might one expect of such a book?

The student of natural history has three major interests. The first is the study of the adaptation of the organism. He wants to know to what degree it fits the environment where it is found. For the student of avian natural history today, adaptation tends to be very largely the observation of ecology and behavior. In the second place, this interest requires some aid to species recognition. The third major interest is in the origin of the organism. How did it arrive in the habitat where it is found; where did its adaptations form; what are its relatives and how is it related to them in space and time? These, I believe, are the sorts of questions running through the minds of all naturalists. It is these questions which a book on natural history must seek to answer and it is these questions which a naturalist will try to answer himself if he has access to a suitable book. The degree to which the bird watcher can, and wishes to, contribute to a deepening of understanding of birds should never be overlooked. After all, deep interest comes from familiarity or accurate detailed knowledge. A good book on natural history will pave the way for new discoveries and deepen the understanding of bird watchers.

Measured against these criteria this book falls far short of the ideal. One would expect in the introduction that some attention would be given to the place of the Psittaci among birds generally, even if only to draw attention to the problem and to stress here the possibility of new light being thrown on the problem through accurate descriptions of behavior. Next, one would want to see some introductory description of present-day ideas of the classification of parrots. There is nothing on these matters, except what can be deduced from the arrangement of the species and groups in the book. Here there are some peculiar associations and groupings. For example, such diverse genera as *Probosciger*, *Eclectus*, *Calyptorhynchus*, and *Kakatoe* are grouped together under the heading Cockatoos, while the closely related genera of platycercines (*Neophema*, *Psephotus*, *Lathamus*, *Barnardius*, *Platycercus*, and *Purpureicephalus*) are each taken as separate groups. In my view such treatment will confuse the naturalist and orient him to expect relationships where they do not exist, and to fail to see behavioral and ecological relationships where they do exist. The banding together of the Quarrion, Pileated Parrot (*Purpureicephalus*) Budgerigar, Swift Parrot (*Lathamus*), and Bourke Parrot (*Neophema*) as an "individuals" group has nothing to commend it.

The naturalist normally has little chance to examine the literature on a group and when he seeks further information about a group in a new book he expects to find some sort of summary or reference to contemporary ideas about evolution and the species problem and how it is affecting the recognition of species and subspecies of the group. In this book the naturalist learns very little of contemporary authoritative ideas such as those of Condon and of Cain, in spite of slight references to some matters by the junior author in his preface. To neglect entirely such an interesting example of a cline as that of the *Platycercus elegans* superspecies is to deprive the naturalist of one of the most interesting examples of this phenomenon in evolutionary studies.

Leaving the taxonomic side of natural history and turning to the geography of parrots, much the same adverse criticism can be advanced. There is nothing to tell us how parrots are distributed on the continents, nor why a book about them in Australia should be of such great interest. When it comes to a summary of the habitats or formations of Australia, on which notes on individual species might be based, we find a classification adapted from one which applies satisfactorily only to southeastern Australia, when an acceptable one for the whole of Australia exists in a readily accessible work, "The Australian Environment," compiled by CSIRO. The classification includes a set of "non-natural habitats." Among this set occurs what must be a unique parrot habitat—"tanks, ground-tanks or dams, watering troughs." This poorly presented but important section is supported by a series of fuzzy photographs. One of these illustrates a completely new category in community classification called grass savannah, and in the illustration of this strange new formation we see trees! The so-called *Banksia* blossoms on page 14 are actually bottle-brush spikes of *Callistemon*; not only is the genus wrong but the family also. There are, in this section of the book, a large number of serious errors too numerous to mention here, and the general impression left with the discerning reader is that it would be unwise to try to make use of this part of the work.

The naturalist at this point would like to have a brief survey of some of the salient behavioral, ecological, and morphological features of parrots, so that his attention might be focused on interesting similarities and differences among these birds. This is almost entirely lacking. It is especially sad when so much has been learned of the behavior of Budgerigars by Dr. Barbara F. Brockway.

Finally, we may turn to the main part of the book where the authors seek to show us how to recognize the species and to tell us systematically about their habits. The reader will anticipate from the strictures already put before him that here also the book is very disappointing. The paintings are unlifelike. The colors are frequently inaccurate and the postures sometimes verge on the grotesque. The plate illustrating the *Neophema* group may be the worst. The colors of the female Red-backed Parrot make identification impossible, and I doubt if the Many-colored Parrot could be recognized from the illustration. The photographs are all poor, invariably lacking sharpness. The notes have the merit that they are succinctly set out, and the detail is easily found, but serious inaccuracies appear. For example, the notes for two species on page 24 referring to the plate opposite are interchanged so that correct identification is impossible. Under habitat we find categories such as wet scrub, dry woodland, and brush not listed in the introduction.

As already stated, this is a large and expensive book. It has many imperfections and inaccuracies. The most glaring of these appear to be the work of the senior author who is also the illustrator. The junior author is known to have a good knowledge of the Australian parrots, especially in respect to aviculture. This may account for the notes being markedly better in level than the rest of the book. It is sad but inescapable that this work is ostentatious and at the same time unreliable and superficial. A really worthwhile naturalist's guide to this very colorful and extremely interesting array of species has unfortunately not yet been written.—J. Le Gay Brereton.

The Ray Harm Nature Sketchbook. Written and illustrated by Ray Harm. World Publishing Company, Cleveland and New York, 1967: 8½ × 11 in. (opening lengthwise), vi + 138 pp., 4 col. pls., 88 pencil and wash drawings. $7.95.

This book is made up of a miscellaneous gathering of folksy paragraphs recounting the artist-author's experiences with a wide variety of wildlife from angleworms to foxes with some botany mixed in and even how to make basswood branch whistles and persimmon pie. In fact these "nature notes" together with most of the illustrations originally appeared in the *Louisville Times* as a nature column. It is copiously illustrated with at least one large drawing on each of the double page spreads. It is divided into major sections covering the four seasons.

Many of the drawings are excellent but there is considerable variation in quality. The author boldly attempts some difficult subjects such as the Indigo Bunting feeding young on page 34 or the Woodcock striking a tree on page 79 without too much success. Occasionally he makes a mistake not too infrequently found among bird artists of failing to get the proper proportions of head, body, and tail as in the Blue Jay drawing on page 73, or the Pileated Woodpecker on page 89. He appears a bit weak in his knowledge of anatomy in the colored Ring-necked Pheasant painting opposite page 26 in which the neck is unpleasantly arched. On the other hand, some of his bird drawings are excellent such as the baby Robin on page 36, the Black-and-white Warbler on page 11, and the Purple Finch on page 100. I was somewhat bothered to find the Purple Finch drawing repeated in a slightly larger size on page 130. He exhibits excellent copying ability in the fruit and seed drawing and his snakes are consistently well drawn.

Although there are a few errors in his natural history statements, the great majority contain convincing details indicating that they are accounts of actual happenings as he saw them in the field. I might challenge his portraying a crow carrying a young bird in its claws. Do they not almost invariably make off with such prey in their beaks? Here again I find, page 41, the description of how a female Wood Duck flies full speed into its nesting cavity. Many writers have made this comment whereas I have watched Wood Ducks enter nesting cavities literally hundreds of times and I have yet to see this happen. I find they normally brake their flight a bit as they approach the hole; they alight at least momentarily on the edge of the hole, then tip up and enter the cavity.

Where the author mentions facts derived from reading, he unfortunately fails to mention the sources of his information. For instance on page 95 "a banded Golden Plover covered a distance of over 2,000 miles in two days over water." If this surprising flight is actually authenticated, I would appreciate the reference.

I am sure that the amateur naturalist will find a great deal to interest him in Mr. Harm's Sketchbook even though the $7.95 price for a book with only four colored plates seems high even in these days of rising prices.—W. J. Breckenridge.

Hawaii's Birds. By Hawaii Audubon Society. Hawaii Audubon Society, Honolulu, 1967: 5 × 7 in., 88 pp., 72 col. illus., 4 maps. $2.00.

This attractive little paperback, a product of the Hawaii Audubon Society, and especially its past-president W. Michael Ord, is a completely revised edition of an earlier work ("Hawaiian Birds"). It is profusely illustrated, and each of the 74 species described is accompanied either by a colored photograph, some of them excellent and most of them reproduced quite well, or a reproduction of the magnificent plates from Wilson and Evan's classic "Aves Hawaiiensis" (1890–1899). These latter illustrations, 19 of them in all, picture most of the native land birds, including 13 of the extant drepaniids, and are probably the best illustrations of these birds to be found anywhere at modest price. The presentation of the material is crisp and orderly: a full page is devoted to each species, and contains, in addition to the illustration, brief statements on the distribution, description, voice, and habits of the bird considered. Following this section are three lists of other birds encountered in Hawaii: 41 species of casual or accidental migratory birds; 33 species of introduced gamebirds, with comments on their current status; and 13 recently introduced birds, mostly exotic estrildine finches seen in urban Oahu. The book concludes with maps of the four largest islands, with suggested bird-finding trips on each of them.

The major limitations of the book are its omissions. It fails to mention several of the birds found on the Hawaiian Leeward Islands. Such birds as the Bonin Petrel (*Pterodroma hypoleuca*), Sooty Storm Petrel (*Oceanodroma markhami*), Laysan Duck (*Anas laysanensis*), Millerbird (*Acrocephalus familiaris*), and Laysan Finch (*Psittirostra cantans*) should certainly be mentioned, even if few people have access to them. Harcourt's Storm Petrel (*Oceanodroma castro*) should be listed as probably occurring, at least on Kauai, where its calls may be heard. Certainly a list of extinct birds belongs in any work on Hawaii—such a list would also underscore a brief conservation plea in the preface by Dr. Andrew J. Berger. In spite of this, however, the book (available from the Hawaii Audubon Society, Box 5032, Honolulu, Hawaii 96814) is a bargain, and will be most useful to anyone interested in the birds of Hawaii.—Cameron B. Kepler.

Hummingbirds. By Walter Scheithauer. Translated from the German by Gwynne Vevers. Thomas Y. Crowell Company, New York, 1967: 8½ × 10 in., 176 pp., 76 col. photos, numerous marginal drawings, map. $10.00.

Seventy-six color photographs illustrate a fantastic variety of poses of birds in flight and perched. All show exceptional craftsmanship by the photographer, as well as great patience, for an average of 100 exposures were made in each instance before a satisfactory photograph was obtained. High-speed photography tends to be dull because the wings of birds are frozen in positions which the eye never sees. These photographs are endlessly varied as the hummingbirds twist, turn, fan their tails, and shift their wing positions. The iridescence of their plumage is captured and reproduced to a high degree.

Even perched birds show liveliness and character. On page 43 is a perched Long-billed Starthroat that was, so the author-photographer states, "a little bored." While watching hummingbirds in Madera Canyon in southern Arizona, I have seen these tiny birds, particularly pugnacious Rufous Hummingbirds, similarly stare at me with slightly narrowed eyes and wondered what went on in the cryptic brain of each one.

The variety and interest of the photographs are enough to make this a thoroughly satisfactory volume.

The text, quite as interesting as the photographs are beautiful, is the result of years of research about hummingbirds. The galaxy of names, the marvels of hummingbird flight, their energy and habits are presented vividly. Explicit directions for keeping these tiny birds in captivity are included together with the author's food formula and those of several zoos that have housed them successfully.

Finally the camera and light equipment used and the successful techniques of high-speed photography of captive hummingbirds are given.

The species illustrated are listed according to their scientific names on page 7. Since most readers will undoubtedly be laymen, the absence of common names in this list is somewhat frustrating. It is easy to remember Green Thorntail, for instance, but difficult to remember *Popelaria conversii.*

It is difficult to conceive of a reader who will not be enchanted by "Hummingbirds," but a word of caution is in order. Note the high loss of birds due to travel, their specific requirements in the matter of temperature in their housing, the exacting food needs and the care which they must have daily. Hummingbirds are imported from Central and South America by pet shops and they bring prices beginning at $50. This presents a genuine threat to the hummingbirds and should not be encouraged. Unlike many species of cagebirds, hummingbirds do not breed in captivity, and the drain on the population of these beautiful birds, trapped in their native lands, could be fatal. Only qualified zoos and scientists with the patience to devote unstinting care to the shining birds should be permitted to import them. This reviewer hopes the enthusiastic readers of "Hummingbirds" will be content to grow flowers and perhaps supply bottles of sugar water to attract these fascinating birds to their gardens and enjoy them there as incredibly colorful birds with amazing powers of flight that carry many on annual journeys of many hundreds of miles.—HELEN CRUICKSHANK.

WORLD OF THE GREAT WHITE HERON: A SAGA OF THE FLORIDA KEYS. By Marjorie Bartlett Sanger. Devin-Adair Company, New York, 1967: 7 × 10 in., x + 146 pp., many line drawings by John Henry Dick. $10.00.

In this book the Great White Heron appears as the leading character in an enormously varied semi-tropical ecological area: the Florida Keys. But the heron is presented as but one of the species of birds at home there while some of the colorful fish, the corals, sea urchins, rare crocodiles, the plants and insects as well as the complex humans, past and present, whose lives have left an imprint on the history of the area. To many, these people may actually overshadow the herons, for the Florida Keys attracted under five flags a truly amazing array of *Homo sapiens.*

Damage to the Keys and its life by hurricanes is a recurrent fact of life. On Labor Day, 1936, the worst hurricane ever to strike the Western Hemisphere not only killed hundreds of people, wrecked the railway built under fantastic difficulties by Flagler, but almost decimated the Great White Heron population. Only 146 survived the storm that swept the vegetation from their nesting islands.

In 1938 the Great White Heron National Wildlife Refuge was established. Then in September, 1960, Hurricane Donna swept across the upper Keys. Again many Great White Herons fell victim. By 1965 they had apparently recovered, as 2,100 were counted. Recently they survived an attempt by private industry to use the shallow waters for shrimp farming which would have involved digging a maze of deep canals where many species of herons feed.

Interest is added to this accurate, informative book by the illustrations by John Henry Dick. These not only depict the variety of the birds that inhabit the Keys country, but many of their companions in it.

To all who plan a trip to the Florida Keys, this book is a "must" for complete enjoyment of that colorful region, and wise travelers will take the book with them. But whether bound for the Keys or not, any arm-chair explorer will delight in the vivid story of the Keys where the tallest white heron in the world is at home.—HELEN CRUICKSHANK.

PUBLISHER'S STYLE IN AMERICAN JOURNALS OF ORNITHOLOGY

The editors of the The Auk, Bird-Banding, The Condor, and The Wilson Bulletin have agreed to make some minor stylistic revisions leading to identical or very similar practices in the four journals in matters, principally, of abbreviations and bibliographic citations. The main objective of this concordat is to make it possible for authors to learn and to apply a single style in the preparation of manuscripts intended for publication in American ornithological journals. The following practices and standards will apply henceforth.

For bibliographic citations in a terminal list of references, authors should use forms stipulated by the Style Manual for Biological Journals, Second Edition (Council of Biology Editors, published by the American Institute of Biological Sciences, Washington, D. C., 1964).

For bibliographic citations in texts not having a terminal list of references, authors should conform with these examples: Crowell (Auk, 85: 265, 1968), or (Crowell, Auk, 85: 265, 1968). Citations of publications having three or more authors should be given in the form, for example, "Jones et al.," in all cases in the text. Consult current issues of the journals for further details.

Abbreviation of mensural units should conform with the C.B.E. Style Manual except in the case of thermometric units, where the degree sign is to be retained, as, for example, 20°C (not 20 C, as given by the Style Manual).

Clock-time is to be designated in the 24-hour system and written, for example, as 08:00 or 17:25 (not as 0800 hours, or 1725 hours).

In cases in which both the common name and the Latin name of a bird species are given in a paragraph heading (for example, in regional lists of species), the common name should be given first.

The Auk, Bird-Banding, The Condor, and The Wilson Bulletin will retain numerous idiosyncrasies in publisher's style, but the editors believe that the concessions to uniformity mentioned above will significantly aid authors in the preparation of manuscripts, while not appreciably diluting the distinctive flavors of the four journals.

INDEX TO VOLUME 80, 1968

By Mildred Stewart and Tanya Hall

This index includes, in addition to names of genera, species, and authors, references to the following topics: Anatomy, banding, behavior, breeding, distribution, ecology, food habits, fossils, habitat, hatching, hybrids and hybridization, incubation, measurements, migration, molts and plumages, mortality, nesting, parasitism, physiology, populations, predation, preening, taxonomy, territory, voice, weather, and weights.

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