

# BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

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VOL. XXXII

January, 1961

No. 1

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## STUDIES OF THE BREEDING BIOLOGY OF HORNED LARK, WATER PIPIT, LAPLAND LONGSPUR, AND SNOW BUNTING ON BYLOT ISLAND, NORTHWEST TERRITORIES, CANADA

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### INTRODUCTION

This paper is divided into three parts. The first part reports detailed observations on the breeding biology of the four species. I have included many details because they show ecological factors deserving discussion, and behavior differences suggesting unexpected geographical variation. The second part discusses ecological questions such as how the four species survive together without competition, what adaptations allow them to breed successfully in the Arctic; and what is the relation of large northern clutch-sizes to annual production and the short breeding season. The third part compares the courtship behavior of Lapland Longspurs with studies of other buntings, specifically Andrew's (1957) aviary studies. These comparisons suggest either that there are unusually large geographical and interspecies differences among buntings, or that their evolutionary relations are not clear. There appear to be adaptive changes in territorial behavior during the early part of the longspur's breeding cycle.

The 1954 Bylot Island Expedition spent from 12 June to 29 July at the mouth of the Aktineq River, southern Bylot Island, approximately 73° North Latitude, 79° West Longitude, District of Franklin, Northwest Territories, Canada. Bylot Island is on the border between the Low and High Arctic areas, and is just north of the north coast of Baffin Island (see map in Miller, 1955).

Short descriptions of the trip (Drurys, 1955) and of the area (Van Tyne and Drury, 1959) have been published. A popular account of certain aspects of the expedition has been published as *Spring on an Arctic Island* by Katharine Scherman (1956).

The observations in this paper were made by William and Mary Drury, and Dr. Benjamin Ferris, who concentrated their time on the breeding birds; and by Josselyn Van Tyne, who contributed information gathered on daily collecting trips. No collecting was done in a study area of one square mile.

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The study and preparation of this paper was made possible by a sabbatical half-year at Harvard University in 1955. Since the first draft, time and expenses associated with publication have been available through the Hatheway School, Massachusetts Audubon Society. Josselyn Van Tyne's sickness and untimely death prevented preparation of a joint report and delayed publication.

The accompanying map (Figure I) shows the vegetation of the study area and nests. A field map of the study area, showing elevations and names used in the text, has been published with the faunal list (Van Tyne and Drury, 1959), and in Drury (1960).

Subspecies identifications and comments are to be found in the faunal list.



Figure 1. MAP OF THE STUDY AREA, showing the vegetation types and location of nests discussed in the text.

**PART I: SPECIES ACCOUNTS**  
**HORNED LARK**

*Eremophila alpestris* (Linnaeus). (Eskimo: Kah-oh-rúd-lee-rah or Kah-óh-dlee-rah).

**HABITAT**

Two nest territories and the areas occupied by 22 pairs were all in the most exposed places of the uplands, almost free of vegetation. These areas were on hilltops, ridges, old beaches, or frost-heaved areas where most of the surface was tan, angular gravel. All were the first places free of snow, and the typical plants were: black, crustose lichens and dead mosses, Gray Lichen (*Stereocaulon paschale* [L.] Ach.), and clumps of Purple Saxifrage (*Saxifraga oppositifolia* L.), and Poppy (*Papaver radicum* Rottb.). Arctic Willow (*Salix arctica* Pall.) and Bell Heather (*Cassiope tetragona* [L.] D. Don), grasses and Grass Rush (*Luzula confusa* Lindeb.) grew in mats in the hollows and on slopes.

**DISTRIBUTION AND DENSITY**

Hoyt's Horned Larks (*E. a. hoyti*), although not numerous in any spot, were the most widely distributed bird, except that Snow Buntings occurred in the mountains above the icecap. There were four pairs of larks in our study area. The centers of their territories were about 400 yards apart. I have reported census data for the four passerine species dealt with here in Van Tyne and Drury (1959).

**TERRITORY**

*Song.* Larks were singing when we arrived, and continued to sing until 26 to 28 June; then frequency dropped and we heard none after 3 July. The birds sang over: the west end of Kungo Hill (Drury, 1960); the Upper Phalarope Ponds; and Tui-Tui Tabletop. Each songpost was constant and over the center of a territory. We agree with Pickwell (1931, 1942) that only one bird was in the air at once, but we have no indication that singing larks flew over a neighbor's territory. We heard the "recitative" (Pickwell) rarely in the evening, and rarely heard any song given from the ground. These were short bursts, and seemed to be preliminary to a flight song. Pickwell points out that human intruders are greeted with a flight song, and a dispute at Golden Plover Creek described below may have been caused by our approach.

Just before a bird flew up to sing, he stopped, standing unusually erect with horns raised and feathers sleeked (Figure 2) on a tuft of grass or a rock. He used the same take-off perches regularly. The posture and movement contrasts with the crouched, shuffling amble of a lark feeding undisturbed (Figure 2). The bird rose with undulating flight, silent, sometimes as if in spirals but really "tacking" upwards. When he began to sing, he sailed with spread wings and tail (Figure 2), or dropped with nearly closed wings. Between songs he climbed for 10 to 20 beats. In this way he hung nearly in place, but moved up and down singing short-lisping phrases, Pickwell's "intermittent song," more or less continuously. Pickwell (1931) gives about five minutes as the maximum time for a song flight. In our subjective impression, the song is mellower than the rather dry song of a "Prairie" Horned Lark (*E. a. praticola*) and more like that of the northern subspecies (*E. a. alpestris*). The bird

performed the same reckless drop to the ground after singing. Birds sang 150 to 200 feet over Kungo Hill. Early morning, evening between 2000 and 2200, and cloudy, windy days, were favored for singing. In a wind, the singing bird soared with wings half-closed and tail widely spread, flying always into the wind. Under such conditions they often sang at about 50 feet.

**AGGRESSIVE BEHAVIOR**

We saw one boundary quarrel on the west side of Golden Plover Creek on 21 June. A bird from overhead dove at the bird feeding on the river bank and drove it rapidly about 40 yards in a zigzag course towards Kungo Hill, then rose again to give a flight song.

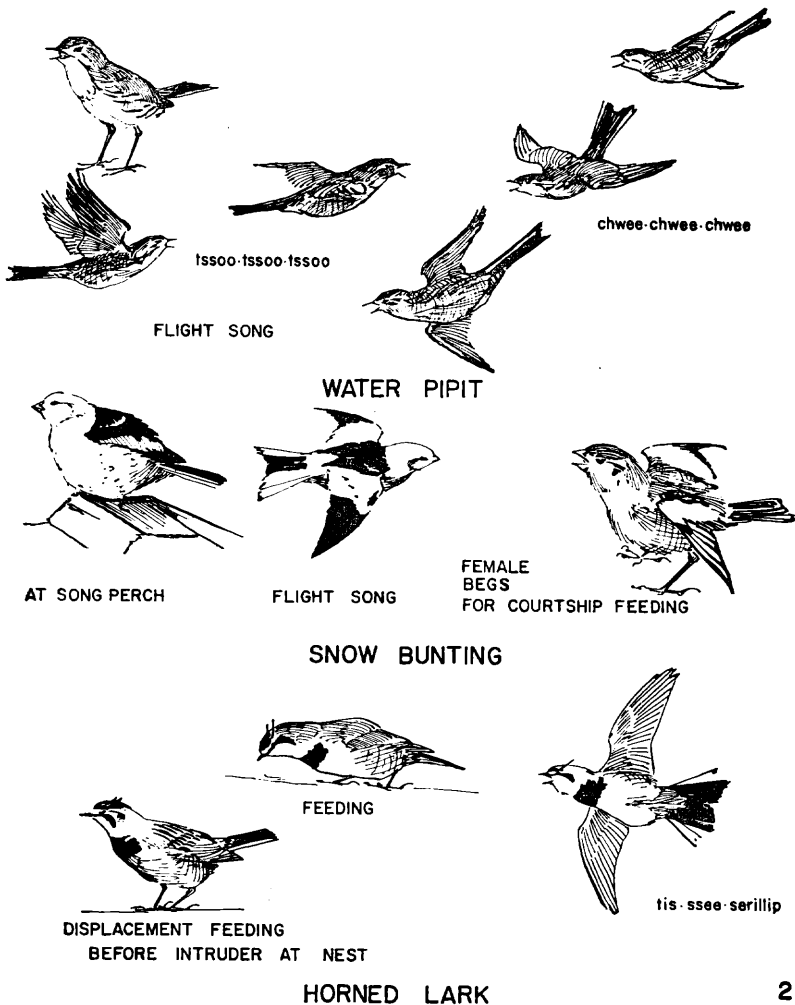


Figure 2. WATER PIPIT, SNOW BUNTING, AND HORNED LARK. Displays.

On 14 June two larks fed freely with five Snow Buntings and five Lapland Longspurs on the still wet, grassy crest of the Bluffs at the western edge of their territory. This persistent flock behavior may have been correlated with the lateness of the 1954 season. Only 10 to 15 percent of the land surface was free of snow at this period in 1954, whereas D. V. Ellis tells us that at the time of his visit, 1 June, 1955: "There was very little snow on the ground by the (camp) site."

#### NEST AND EGGS

During the first week (12 to 20 June), the males were either constantly singing aloft or closely following the females. According to Pickwell, these actions indicate nest building as much as does nervous activity of the female. We did not find any nests until the young had hatched.

Nest sites and construction of *hoyti* agree with those of Pickwell for *praticola* and DuBois (1935) for *leucolaema*, but differ from those of *alpestris*. Townsend and Allen (1907), Sutton (1932), Soper (1946), Wynne-Edwards (1952), Sutton and Parmelee (1955) describe the nest of *alpestris* as sunk in growth of lichen or moss, perhaps under a hummock, but definitely *in* the vegetation. The two nests we found were on bare ground, on a steep slope, and in a shallow excavation with no evident relation to a clod. They were on the upper edge of continuous mat plant cover and had southern exposure. The lower side of the nest was built of small, flat stones and pieces of dirt or clod held together by drying and by lichen thalli (compare DuBois, 1935). The nest lining was tightly woven of gray, dead grasses and Grass Rush, with four to six feathers. The floor of the nest was dirt.<sup>1</sup>



Figure 3. HORNED LARK YOUNG IN NEST NO. 2. Young are four days old and were not seen to be brooded during the day.

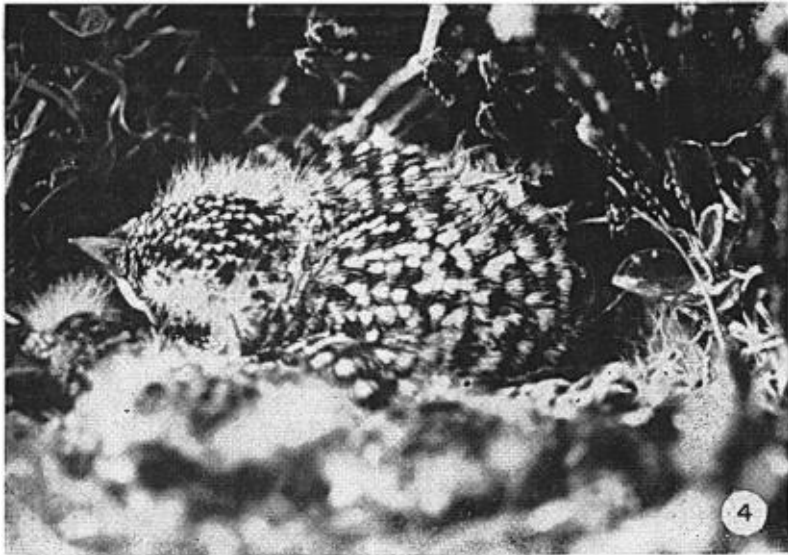


Figure 4. HORNE LARK YOUNG IN NEST NO. 1. Young is six days old.

*Clutch-Size.* One of our nests had four and one five eggs; the four families found out of the nest each had five young.

#### HATCHING AND CARE OF NESTLINGS

1. *Feeding.* We did not see larks brood their young on the nest during the day. They did not fly directly to the nest, but lit at a spot about 20 yards away and ran, stopping as if to feed, along an irregular route to the nest. The giving of food to the young was so rapid that it seemed to be a continuation of feeding unless one knew of the nest site. After feeding, they ran 10 feet or more, stopped once or twice, then flew to a rock, dropped the fecal sac they usually got, and wiped their bill. Both parents fed the young.

2. *Development of the young.* Pinfeathers were evident the third day amid the yellow-buff down. The nestling skin was brown. The inside of the mouth of the nestling for the first four days is yellowish, reddish below the tongue and bill rami. In this period the young gape at any disturbance. After their eyes are open (between the third and fourth day), the nestlings press themselves flat and still into the bottom of the nest on approach of a human. Fourth day young are shown in Figure 3. Sixth day young are shown in Figure 4. They keep this behavior until they leave the nest. For the first week after leaving the nest, even when able to fly, the young will allow approach to within 15 to 20 feet. The parents' *jrreeeet* alarm note makes them crouch until disturbed individually.

<sup>1</sup>Detailed descriptions of the nests, their construction, topographic locality and vegetation surroundings, are on file at the Hatheway School, Drumlin Farm, South Lincoln, Massachusetts. They are omitted here because of their bulk and because they are of very specialized interest. We have descriptions for all species treated in this paper. They can be consulted on request.

The young were five days out of the nest (6-11 July) before they flew about 30 yards, but five days coincides with the minimum for the species. Our observations agree with Pickwell that the fledged young, barely able to fly, hop instead of walk.

3. *Nestling period.* The nestling period was eight-nine days compared to 9-12 days in five nests in *leucolaema*, DuBois (1935).

#### REACTION TO PREDATORS

When we were near their nests, the larks fed nervously and rapidly, covering a large area and circling around the nest and intruder. When feeding undisturbed, they fed creeping and walking here and there over the barren dirt of "frostings" (Washburn, 1956) and wind-cleaned areas.

When there were eggs, or eggs and young in the nest, the female left the nest when we first appeared over the skyline at a distance of 250 to 300 yards, "casual abandonment" mentioned by Pickwell (1942). Her flight was low and direct and followed the same route each time. We found no distress display at the nest, but found it frequently with parents with flightless or weakly-flying young. When with their young the parents sat very close, then sprang from the ground with noisy wingbeat. The male was much less aggressive and under these circumstances often rose ten to fifteen feet into the air and sang a few short, atypical phrases.

On 30 June larks started to give a different alarm note, a contralto shorebird-like *jrrrreeet*; the regular alarm call is *tseeeep*.

#### WATER PIPIT

*Anthus spinoletta* (Tunstall). (American Pipit). (Eskimo: Engeoók-jéeyook).

#### HABITAT

This species was almost entirely restricted to the sun-soaked ravines cut into the Bluffs west of camp. Soper (1928, 1946); Sutton and Parmelee (1954a); Wynne-Edwards (1952) agree that this species is restricted to steep slopes, where the sun can have maximum warming effect. We found pipits at this, the most northern recorded nesting site, to be closely correlated with the most mesophytic vegetation, richest in species of plants.

#### DISTRIBUTION AND DENSITY

Along the mile-and-a-half stretch of the Bluffs west of camp, there were seven areas where parents scolded. Each group was separated by a gap of at least two valleys.

#### TERRITORY

*Song.* Pipits were in song on 12 June. Various authors (Sutton and Parmelee, 1954a; Soper, 1928) record a song which changes in quality or accent. Others (Dixon, 1938; Pickwell, 1947) record songs that change only in tempo, accelerating rapidly as the bird dives from the top of its flight. Townsend and Allen (1907) and Lewis (*in* Bent, 1950) record a trilling song. We heard uniformly two-parted songs given on the ground and in the air. Just before starting to sing, the bird ran nervously, fitting onto rocks where he sang briefly, and sleeked his body

feathers (Figure 2). As he flew up, usually to the level of the crests of the Bluffs, he called *tsoo-tsoo-tsoo-tsoo* and beat his wings in a nervous, shallow beat. Then he glided down with primaries closed and secondaries open, tail furred or partly open, and immediately changed his song to an accelerating *chwee-chwee-chwee-chwee* (Figure 2). He lit again on a conspicuous rock or ridge and stood with neck stretched up and feathers pressed flat, scolding *tseep* or, as often, repeated his song from the ground. In the ground songs, the *chwee-chwee* was more common.

On 29 June, a pipit flew into a neighbor's territory calling the usual flight call *chip-chip, chip-chip-chip*. As it trespassed, the territory holder trilled loudly, dropped off its high perch at the crest of the ridge, and dove at the newcomer who fled. Shortly one bird returned, sat on its usual tussock perch, and called *tseep-tseep, zzeep-zzeep-zzeep*. On another occasion, we heard a parent give the trilling song while carrying insects. This song seemed associated with imminent attack.

Song stopped during the first week of July. We heard song once 20 July.

#### AGGRESSIVE BEHAVIOR

On 15 June we saw many chases in several ravines west of camp. Two birds met and had a brief fight; then one chased the other at break-neck speed in and out of the ravines, up and down from the Bluffs to the beach, round and round, then they just vanished into a ravine. In some cases three birds were involved.

#### TERRITORIES STUDIED

Each pair of birds fed in four or five valleys along a distance of about 100 yards and 200 feet high. Sometimes when feeding, silent birds intruded into neighboring territories without fights. At other times, seemingly without relation to the progress of the breeding cycle, intruders were vigorously attacked.

#### NEST AND EGGS see Table I

The nest was built entirely of grasses.

#### REACTIONS TO PREDATORS

We found parents with young in late July. A *zzeep* scold-note and nervous walking around in the low vegetation, accompanied by vigorous tail-bobbing while they seemed to feed in the matted growth was associated with alarm at the nest. Such alarmed birds did not run and dart, however, as they do when really feeding. On returning to the nest, the disturbed parent characteristically "fed" along the edge of the slump terrace sheltering the nest, then hopped down and entered the nest.

When we first saw parents carrying food to young in late July, we heard a new alarm note, *zing-zing*.

#### FEEDING

Occasionally these birds fed on the frost-heaved barrens on the slopes of Kungo Hill or on the meadows at the crests of the Bluffs, but they usually fed in the edge of open areas, walking in and out of the tufts of grass, through mats of Bell Heather, patches of Locoweed (*Oxytropis Maydelliana* Trautv.), and Vetch (*Astragalus alpinus* L.). They seemed





to like the taller growth, where they fed threading their way through, ducking under branches, stepping over low growth. At other times, they fed by searching over the surface and catching insects by short runs and flights.

Occasionally, when flying around in pairs feeding, they gave a call similar to that of a Common Redpoll (*Acanthis flammea*)—*dik-dik*, *dik-dik*, *dik-dik-dik*.

### LAPLAND LONGSPUR

*Calcarius lapponicus* (Linnaeus). (Eskimo: Kúngnuktah).

According to Frazer Rowell (1957), our breeding records for this species are the farthest north; but the A.O.U. Check-list (1957) lists breeding at Dundas Harbor, Devon Island, and at Thule, Greenland, in Latitude nearly 77° North. Nests reported from Taimyr Peninsula and New Siberian Islands (Tugarimov and Tolmatshev, 1934; and Birula, 1907; in Grote, 1943) are as far if not farther north in Siberia.

#### MIGRATION AND ARRIVAL

Longspurs were present when we arrived. For the next three days their numbers increased and the number of females increased rapidly. They were not paired on arrival, as suggested in Russian articles (Michel, 1935; Tugarimov and Tolmatshev, 1934; and Birula, 1907; in Grote, 1943) for populations in the far north of Siberia.

During the first week, groups fed together and seemed to revert readily to flock behavior and the flock call. On 14 June, four male and one female longspurs fed in a flock with Snow Buntings and Horned Larks on a grassy area at the crest of the Bluffs on the south end of West Ridge. Grote says that in Siberia, flocks are maintained while the tundra remains mostly snow-covered.

#### HABITAT

Longspurs occupied the thick, moss-floored vegetation of dry places in the uplands, primarily on the east- and south-facing slopes, not the bogs. Their distribution was similar to that of Bell Heather, but Bell Heather grew over large areas where we found no longspurs.

#### DISTRIBUTION AND DENSITY

This was the most numerous nesting species around our camp. It was, however, nearly equalled in numbers by Baird's Sandpiper (*Calidris bairdii*), and was less widely distributed over the island than Horned Larks. Where longspurs occurred, they were crowded together.

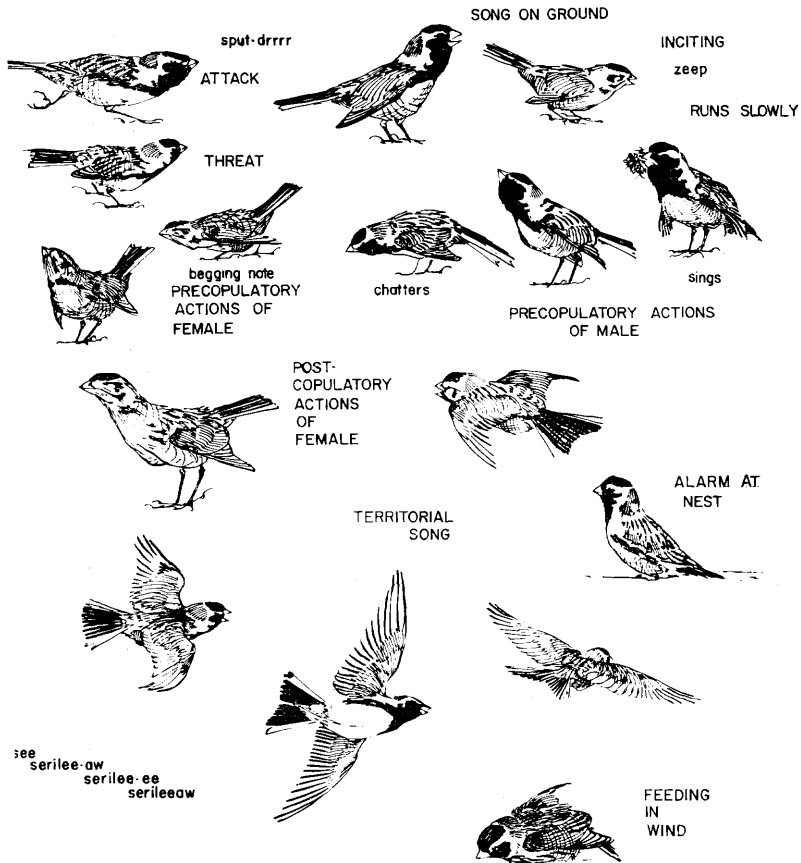
A survey of territories in mid-July—nests, parental alarm, or flightless young—indicated at least 27 nests on our study area, and at least 60 in the seven square miles between Eclipse Sound and the snout of the Aktineq Glacier on the west bank of the river.

As others have found, longspurs became inconspicuous at the end of July, but we saw no obviously molting birds, nor any flocking or migration.

**TERRITORY**

*Song.* When we first arrived, full song and territorial disputes were going on over the radio masts at Pond Inlet, but were sporadic on Bylot Island. Song increased in intensity and frequency at camp 15 June, and was general, and territorial disputes vigorous, by 17 June. Males took up territories between 15 and 25 June.

The males sang: (1) a partial, abbreviated song on a raised hummock near the nest site; (2) a full but not rapidly repeated song on two or three song perches on rocks or some conspicuous break in slope; (3) a whispered song on the ground near the female; and (4) a flight song. When males were singing on the ground, the primaries were lowered, bill raised obliquely, tail barely cocked, crown feathers sometimes raised, back feathers sleeked, and belly and flank feathers slightly fluffed



LAPLAND LONGSPUR

Figure 5. LAPLAND LONGSPUR. Displays.

(Figure 5). The whispered song had the same elements as the full song, but was usually shorter, given only in close company of the female and before nest building started. The usual (90 percent) full song was a flight song, in which the male rose with regular wingbeats to a height of 20 to 40 feet, then floated to the ground (usually to a rock or other conspicuous spot), singing several songs in rapid succession. His course on the way down was usually a semicircle and as often on set wings as on quivering wings ("moth flight" of Hinde, 1953). When the wind blew 10 to 14 knots, males hung suspended, occasionally beating their partly-folded wings, spread their tails wide, and sang five or six songs in one flight (Figure 5). Many time males sang as they rose from their song perches, especially in a song duel and when suddenly responding to border aggression. When doing this, their wingbeat was rapid and shallow. As I interpret the descriptions in Bailey and Niedrach (1938), the Lapland Longspur's flight song is like that of the Chestnut-collared Longspur (*Calcarius ornatus*), but differs in several details from that of McCown's Longspur (*Rhynchophanes mccownii*). The flight song is an intense, vibrant display, in contrast to the undulant flight and lispng song of Snow Buntings.

We found little individual variation in song, which our field notes describe as liquid, wheezy, and like a Bobolink (*Dolichonyx*) heard in the distance, Soper (1928), and Sutton (1932). Songs started with a ringing and metallic *zing*, followed by a rolling and rapidly descending *zizeleeaw*; then a rolling, sustained *zizelee-ee* (ending with the highest note of the song *ee*), and closed with another rapid rolling and descending *zizeleeaw*. We found no variation in phrasing with the progress of the season.

Our birds had two or several song perches on their territories; in contrast Salomonsen (1950-1951) reported single song perches in Greenland. They chose any rock or conspicuous place as a song perch, and appropriated piles of dirt we made in excavating frost forms on their territories. The male at nest No. 5 sang from the dirt pile before I finished the hole, but he had no suitable rock or ridge, and was under pressure from Nos. 1, 6, 10, and 12 (Figure 7), and his female was building.

Notes preliminary to ground and flight songs included: the alarm note, *dzeeu*, and *tsuk* (perhaps the "twuu" whistle of Frazer Rowell, 1957). We cannot be sure whether they are preliminary notes to the song, or expression of alarm at our intrusion, because longspurs were stimulated to give their flight song by our approach.

All observers agree that singing decreases rapidly after the female starts to incubate: two males were singing 28 June from 2000 to 2200; at midnight on 3 July one longspur was singing from the late nest (No. 6). He sang whenever we approached, for four days after the clutch was complete, and then rapidly decreased his singing. After the clutch was complete, nearly all singing was in flight. Grote (1943) reports that late season song in Siberia was on the ground. Singing was sporadic until one to two days after the young had hatched, by which time it had ceased even as an expression of aggression to a human intruder. We heard no songs after 10 July. Grote reports that in Siberia the song period lasts about three weeks.

#### AGGRESSIVE BEHAVIOR

As with McCown's Longspur (Mickey, 1943), once a male Lapland Longspur started to sing, he stayed on territory except that some birds foraged on the beaches or the camp area while most of the tundra was under the snow. The Russian papers reviewed by Grote report the same.

We saw many territorial disputes between 16 June and 20 June in the area of the territories of nests Nos. 6, 7, 5, and 12 (Figure 7). Disputes consisted of vigorous answering song flights or a dashing pursuit, ending in a short, very fast flight, and such a rush at an intruding, singing male often ended in a song flight or rapid return to the ground within the territory.

On 14 June while the first Bell Heather areas were emerging from the snow, three males disputed an area below the 35-foot beach and 25 yards east of the site of nest No. 6, where territories Nos. 6, 5, and 12 came together (Figure 7). One flew up from the ground and dove at the others, or ran low, as if creeping, with his head lowered and thrust forward, "wrists" barely protruding, feathers sleeked (or ruffled only on upper rump), and bill partly open, as he called *sput dirrrrr*. He held his chin up, so that the black throat and light bill were conspicuous when facing us (Figure 5). One bird did nearly all the rushing. He attacked the other two males when their side was toward him. The victim flew away with a shallow, quivering wingbeat ("moth flight"). A female was present during this posturing. We saw no actual fighting, but Michejev (1939, in Grote, 1943) describes fighting on the ground and in the air, biting and pulling out feathers. It was difficult to see the posture taken by the bird rushed at, but those we saw held horizontal



Figure 6. LAPLAND LONGSPUR FEMALE OF NEST NO. 6. Shows the close association of the nest with overhanging growth of Heather.

posture creeping through the grass. These rushes are typical expressions both of supplanting attacks and head-forward threat as Hinde (1953, 1954) and Andrew (1957) have described them. We did not see any raising or waving of the wings, or bill snapping. These have been recorded from McCown's Longspurs (Mickey, 1943; DuBois, 1937b),

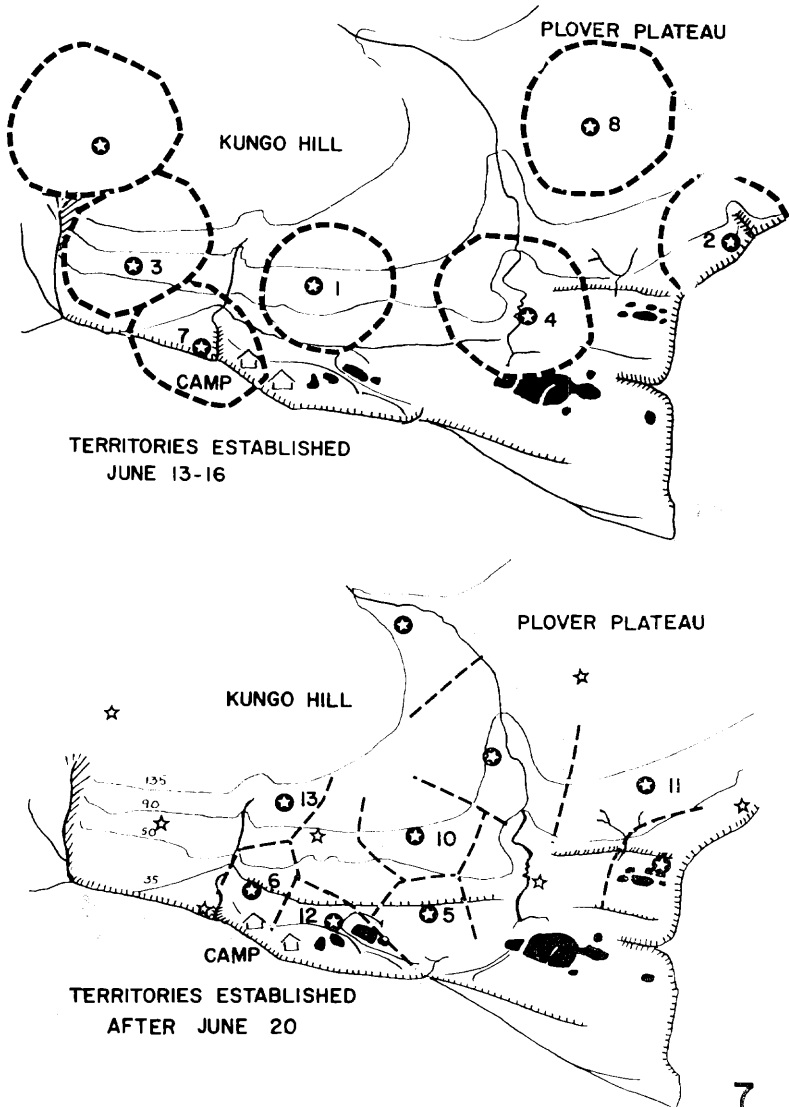


Figure 7. TERRITORIES OF LAPLAND LONGSPURS.

A. Clutches completed June 22-25.

B. Clutches completed July 1-4.

Chestnut-collared Longspurs, and other Emberizines. The note we recorded as accompanying the head-forward posture seems to differ from the "chaa" reported by Andrew (1957). We have recorded a note "chreep" (below), which must be the same.

We saw no territorial disputes after 1 July, which may explain the disagreement summarized in Frazer Rowell (1957) about territoriality. Territory was expressed, but disappeared as incubation progressed.

*Tolerance of Non-aggressive Trespassing.* Some birds did not show conspicuous hostility and in several cases silent males were allowed to trespass into territory No. 6, our camp.

On 26 June the male of territory No. 12, chasing the female from territory No. 12, came over territory No. 6 and the chase passed over the male of No. 6. Male No. 6 crouched in a sleeked horizontal position, lowered his head, thrust it forward, bill up (Figure 5), and gave a vibrant *chreep* that sounded like a begging note; then he rose at once into the air and sang. The pursuing pair was already on its way back into territory No. 12, and male No. 12 sang as soon as he crossed the boundary. In contrast, on 27 June the pair from territory No. 12 moved through the territory of pair No. 6 to the vicinity of the cook tent, which was a favorite feeding area. As they flew over the owner, they gave the winter flock call, a rattling *chi-chi-chi-chi-chi*, and this was answered at once by the resident male, who did not chase or sing until they had moved on. Wynne-Edwards (1952) reports lack of hostility on common ground. Without further testing under favorable conditions in the field, I cannot say whether this is simply non-attack when the trespasser did not sing or act aggressively (Tinbergen, 1939), or whether the winter call is a formalized act of non-hostility. Kluijver (1951) and Hinde (1952) have described for the Great Tit (*Parus major*) a large area in that resident species in which property interest exists but which is not territory in the limited sense. Trespassing is tolerated in the larger "domain." This principle may apply to longspurs, but I doubt it.

In the period of 22 to 28 June the pairs from territories Nos. 5, 6, 7, and 12 all visited the center of camp, although pair No. 6 spent most of the day there and the female of pair No. 6 became so tame she would feed on corn meal spilled between Van Tyne's feet while he prepared bird skins. Mickey (1943) reports that McCown's Longspur did not defend its territory against other longspurs feeding or going through.

#### TERRITORIES STUDIED

On the warm, south-facing Bell Heather-covered slopes north of camp, there were ten nests and territories in an area of four acres (100 yards from nest No. 7 to nest No. 13, and 170 yards from nest No. 3 to nest No. 4 (Figure 7). They were much more crowded together than those recorded by Wynne-Edwards (1952) at the head of Clyde Inlet, where nests were 250 yards apart and territories were of five to fifteen acres. Grinnell (1944) found nests at Churchill to be 200 yards apart. Mickey (1943) found no nests of McCown's Longspur less than 85 yards apart. Territories in our camp area were a half-acre or less, probably a quarter-acre in the case of nests Nos. 5 and 6. Our territories are thus comparable to those studied by Frazer Rowell (1957), or those reported from Russian articles reviewed by Grote (1943)—Michejev reported

100 nests in a square kilometer of hummocky tundra (their preferred habitat).

The territory of nest No. 6 is an example of size, and location of song perches. The male marked his territory most clearly in the few days after the female started to incubate (4 July). It extended up Kungo Hill about 30 yards from the nest (under the crest of the 35-foot beach) to a song perch on a rock outcrop at the 70-foot beach, then 10 yards to the bank of Snow Bunting Creek. From there his territory extended along the 70-foot beach 30 yards to a bare patch on a shoulder of the hill above the nest. He had a second song perch on the bare ground there and a third on the bare beach surface 20 yards east of the nest. Thus his territory was a trapezoid, all sides with natural borders, 30 yards by 40 yards by 30 yards by 20 yards. He came in flight to sing over the westernmost tents of our camp, but did not perch there and, (as above), allowed non-aggressive trespassing in that area. His territory seemed to consist of an area of 1,000 square yards. Even if the area is extended to include the camp area, it covered 1,800 to 2,000 square yards—still less than half an acre. Territories of nests Nos. 1, 5, 7, 10, and 12, although less clearly mapped because there was no pressure on at least one border, were close to the same size. The undisputed borders had been along large snow patches during territory establishment. The twelve territories which we studied most carefully each covered less than half an acre.

#### COURTSHIP

*Pair Formation.* The males' actions are similar to those of McCown's Longspurs. When a male was associating steadily with a female, his singing decreased in frequency though not in vigor. This was not a cessation of song, but rather diffusion of actions by additional activities.

Pursuit flights were obviously mutual affairs and, I believe, closely associated with pair formation. They were longer, slower, and with less zigzagging than territorial skirmishes. If the male caught up, there was a burst of rapid zigzagging, but if he fell far behind, the female slowed down until he overtook her. We saw these flights before any displays on the ground and throughout the period of ground displaying. Male No. 6, displaying to his female, ran across in front of her or up to her side, standing at about a 60° angle to the horizontal, with his breast feathers fluffed out, head held high and bill pointed slightly up, wings about half spread, drooped and quivering. While he ran in this way he was singing his regular flight song. The female ran slowly ahead of him, crouched in a horizontal position with her head partly lowered, wings partly spread, tail cocked just above horizontal, calling *zeep, zeep* (Figure 5). She and the male often pecked stiffly at the ground. These displays coincide with those described by Andrew (1957), but he points out that in most Emberizines the male takes a horizontal position in this situation. The chestnut nape "emphasized" the stiff bow by the male. The female ran around and ahead of him; then flew; if he did not follow, she came back and repeated her actions until he did chase. During the chases she landed several times, ran along the ground, then flew again, fast and darting, or slowly and on quivering wings. During the period of pursuits, because their attention was on the females, males sang less often and chiefly on the ground. Flight songs were conspicuous in the morning (0600 to 1000) and evening (1700 to 2200).



On 17 June we saw a female on three different occasions (or perhaps different females), after being chased by male No. 6, cross into territory No. 12 or fly out of No. 6 into territory 7. The male did not pursue, and returned to the ground before he sang. The male whose territory she next visited usually took a short time to notice her arrival, but when he did, he flew to her at once, singing (in the case of male No. 12), and a pursuit followed.

This pursuit may have been territorial rather than sexual, or this may have been a vacillating female, or we may have missed some of the details. Tinbergen (1939) was convinced that such sexual flights in the Snow Bunting took place only with mated birds, although he observed one female to be pursued by two males.

I have no details on the changes in the male's aggressive postures toward the female after pair formation and before copulation. We saw no sign of courtship feeding.

*Pre-copulatory Actions.* Above nest No. 3 on 21 June (1800 to 1900), I saw the male rise with fluttering flight straight up into the air, flying with difficulty because of a wad of dark material in his bill (Figure 5), a collection of leaves of Grass Rush, Black Mane Lichen (*Alectoria nigricans* [Ach.] Nyl.), and dead Bell Heather branches. Before flying, he stood vertically, bill horizontal or pointed up, wings drooped at his sides, and tail spread and lowered. He sang with this material in his bill and succeeded in getting about 20 feet off the ground, then sang as he fluttered down again. He picked up even more material, and hopped onto a stone. He had so much in his bill now that he could not get off the ground, but he could sing. He stood a few moments and readjusted the material in his bill, put it down and picked it up again; then he pointed his bill up and fluttered his wings without getting off the ground. This may be the wing waving of Mickey (1943) or wing vibrating of Andrew (1957). Michel in Grote describes both male and female fluttering up together. After several tries he hopped off the stone, and walked and hopped between clumps of Bell Heather and Arctic Willow, picking up the darkest sprigs. The female crept hesitantly in a horizontal position through the grass as if feeding, but her tail was slightly cocked up and her wings occasionally spread and quivering. Andrew (1957) suggests two possible origins for this: (a) ritualized feeding action (out of context); or (b) ritualized picking up nesting material (not out of context).

When approaching the female the male held his head high, neck extended and bill horizontal, with all the accumulation of dark material in his bill. He dropped the load and pointed his bill straight up, showing his black throat, while he dragged his wings as he walked up to her. His tail was half spread and tilted down. Then he lowered his head, ruffled his scapular, back and rump feathers, and widely spread his tail (Andrew's "fluffed run," 1957). She crouched with head low, tail cocked up, wings quivering and partly spread. He fluttered over and, without hovering, mounted on her back in the same position he had assumed in front of her, and copulated. After copulation he hopped off and walked in front of her in the same crouched position, while she stood up, raised her bill straight up and cocked her tail as high as possible, chattering.

## NEST AND EGGS

*Nesting Sites.* Although longspurs were among the early arrivals their nesting sites in the great majority of cases were under a patch of creeping Bell Heather (Figure 6, nest No. 6).

Our observations suggest as do Wynne Edwards' (1952) that one year's nesting is often near a previous year's nest site. Our nests Nos. 3, 4, 7, and 8 were placed within 20 to 50 yards of previous nests. Nests Nos. 3 and 8 were placed in Bell Heather, as were their associated nests. Nests Nos. 4 and 7 were placed under Arctic Willow, an unusual site at the Aktineq, and both associated with a previous year's nest under Arctic Willow.

*Male's actions during nest building and egg laying.* Song was vigorous though less frequent than before pairing. He answered his neighbors' songs, but usually he directed his songs toward her, while he followed the female, who was gathering nesting material and feeding seemingly without attention to him. When she went to the nest while building or during the irregular periods of incubation before the clutch was complete, he followed. When he lost sight of her during the egg-laying period, he began to sing (as described by Tinbergen (1939) for Snow Bunting and Nice (1937) for Song Sparrow). While she sat on the nest before the clutch was complete, he was seldom more than five feet away; but as soon as the clutch was complete he stopped following her and made song flights again over his whole territory, returning from his flights to a song perch rather than to her. He fed aimlessly while following her, but not in the stiff way as when alarmed.

*Nest-Building.* Females did all nest-building. The female at nest No. 5, on 25 June, built the lining of her nest with white feathers which she collected walking and hopping along among the Grass Rush tufts and Bell Heather on the edge of the barren ground on the 35-foot beach level. She, like other females, gathered nesting material inside her territory: dead grasses for the bulk of the nest, and white feathers or willow cotton for the lining, as Mickey (1943) observed of McCown's Longspur. Frazer Rowell points out that in some nests, the feather or cotton lining may be absent. The female hopped into a crack in the Bell Heather-covered ridge on the downslope of a frost-crack on the edge of the beach and into her nest, where she pushed the feather or clump of grasses into the side of the nest. Then she sat in the nest and wriggled back and forth with semicircular movements similar to those used in settling on the nest, kicking her feet and quivering all over. I saw no forward and backward movement of the bill ("tremble shove") to work the material in. After briefly wriggling in this way, she flew away to the upper edge of the barren beach ridge. On the average, she returned to the nest every two minutes from 1400 to 1530. When she came from the nest she often stretched her neck, spread the feathers on her belly, exposing the bare skin, spread her wings, and cocked and partly spread her tail. This agrees with observed correlation of nest-building with soliciting in Reed Bunting, *Emberiza schoeniclus* (Howard, 1929), and Snow Bunting (Tinbergen, 1939).

While she fed and gathered material for the nest (occasionally calling *cheep* like begging young), the male walked around with head up and tail partly cocked, occasionally picking up brown grass only to drop it.

TABLE II  
Data for Lapland Longspurs

Nest No.	Date found	Contents when found	Final clutch size	Date completed	Eggs known to have hatched	Obs. or est. first hatching	Obs. or est. last hatching	Obs. or est. first leaving	Obs. or est. last young in nest	Days to leave	Young known or guessed to leave successfully
1	19 June	3 eggs	6 (2 dst)	22 June	4	2-3 July	5 July	12 July	14 July	2	3
2	19 June	1 egg	6	24 June*	5	4-5 July	6-7 July	14 July*	15 July	2	4
3	21 June	2 eggs	4	23 June	4	5 July	6 July	14 July	14 July	1	4
4	25 June	6 eggs	6 (1 dst)	---	---	---	---	---	---	---	---
5	25 June	building	4	30 June	---	---	---	---	---	---	---
6	28 June	building	5	4 July	5	14 July	15 July	24 July	24 July	1	5
7	30 June	5 eggs	5	25 June*	4	6 July	7 July	16 July	15 July	X	1
8	2 July	6 eggs	6	25 June*	6	5 July	6-7 July	15 July	16 July	1	5
9	2 July	4 eggs	4	---	4	12 July*	---	---	---	---	(1 collected)
10	4 July	5 eggs	5	30 June*	2	10-11 July	10-11 July	19 July	19 July	X	2
11	4 July	3 eggs	3	30 June* 1 July	3	10-11 July	12 July*	20 July	21 July	2	3
12	4 July	4 eggs	4	2 July*	4	11 July	13 July	20 July*	21 July	2	4
13	4 July	4 eggs	4	3 July*	3	13 July	14 July	22 July	22 July	2	3
14	7 July	4 eggs	4	2 July*	4	11-12 July	13 July	22 July	21 July	1	4
15	8 July	3 eggs	3 (1 dst)	4 July*	2	14 July	15 July	24 July	23 July	X	2

\* Accurate to within 24 hours  
X Young seen all to leave at once.  
obs --- observed  
est --- estimated  
dst --- destroyed

TABLE III  
LENGTH OF TIME IN NEST OF LAPLAND LONGSPUR EGGS

	Nest No. 1	Nest No. 2	Nest No. 3	Nest No. 6	No. of days in nest before hatching
Individual egg's number (Numbered in sequence of laying)				5 (10½)	10
		6*		4 (12½)	11
	5 & 6		4	2 & 3	12
	4		2 & 3	1	13
			1		14
		1			15
					16

Table of the number of days that individually numbered eggs were in the nest before hatching.

\* Estimated by age of young; the day they hatched was missed.

They both gave low calls, inaudible beyond 20 yards: a reedy chatter, the winter rattling call, and the *chip-chip* flock calls. The male immediately appropriated as a perch the pile of dirt from a test pit and sang every one to three minutes, or whenever the female hopped into the crack and onto the nest. When the nest was destroyed (presumably by an Eskimo dog) on 2 July, the male stopped singing and the pair disappeared.

Our observations on nest material agree with Blair (1936), Grinnell (1944), Sutton and Parmelee (1955b), and Wynne-Edwards (1952). Most nests were tightly woven of dead grass-like leaves and stems and were lined with a few feathers (two to about twelve) and willow cotton (*Salix* sp.). Nests on the uplands were made of grasses and Grass Rush, and those on the edges of marshes were of sedge parts. Early nests were lined with white feathers; late nests (Nos. 6, 10, 12, and 13) were lined with both feathers and willow cotton.

When the female left the nest during the incubation period, the male joined her, or stayed near the nest while she was gone and called in alarm when an intruder entered his territory.

*Clutch-Size.* Early nests (hatching 3-9 July) contained consistently larger clutches (6, 6, 6, 6, 5, 4) than later nests hatching 10-15 July (5, 5, 4, 4, 4, 4, 3, 3).

Table II summarizes the observed data on fifteen nests studied.

TABLE IV  
NESTLING PERIOD OF LAPLAND LONGSPURS

	Nest Numbers															No. Days Young in Nest	Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		
No. young 8 days		1									1					Number of young 8 days in nest	2
No. young 9 days	3	4	3			2	4		2	1	4	2	2	1		9 days in nest	28
No. young 10 days			1			3	1	1			1		1	2	1	10 days in nest	11

Table of number of days as nestlings. The young were not individually marked.

Our egg-laying dates (first egg 17 June and clutches completed 22 June to 4 July) are clearly later than the dates of the peak of first egg dates in Finmark (56 percent between 11-20 June), as reported by Shaaning in Løvenskiold (1947), and in Clyde Inlet, Baffin Island (clutches completed by 6 June) by Wynne-Edwards (1952). They fall within the spread summarized in Frazer Rowell (1957); and they come at the end of the period reported by Michejev (in Grote, 1943): Timan Tundra, 10-20 June; Murman Coast, 14-20 June; Kolyma region, 25-26 June; mouth of the Lena, 25 June to 4 July for full clutches.

#### ACTIVITIES DURING INCUBATION

We have no record of males incubating, although the strongly developed chestnut collar and blackish throat of several females misled us. DuBois (1937) shows that females of Chestnut-collared Longspurs also may have partially male plumages.

The female at nest No. 6 spent three or four periods of 15 minutes on the nest three days before the clutch was completed. She was on the nest about half of the day on which the second from last egg was laid, nearly all of the day on which the next to last egg was laid, and all day when the last egg was laid. Frazer Rowell commented on the start of incubation (sitting) with the laying of the first egg. Michejev (1939) reports the beginning of sitting (by the female alone) after the laying of the last egg. DuBois (1937b) reported that incubation starts when the last egg is laid in McCown's Longspur. Mickey (1943) found that in one case the female incubated all day when three eggs were in the nest although the clutch of 4 was not completed until two days later. He found females "erratic" in respect to starting incubation. It would be very interesting to keep a record of the temperature of the eggs during the whole period.

Males and females stayed in their territories during incubation. On 80 visits (after the clutch was complete) to 14 nests we found the female off 18 times or two absences per seven to nine visits for each nest (a consistent percentage and not skewed by exceptional "absenteeism"). Frazer Rowell reviews the typical behavior of a female and male during the incubation period.

*Recognition of Damage to Eggs.* While marking the eggs at nest No. 13, we knocked a piece of dirt into the nest. The female returned while we watched from 30 yards, picked the dirt out, flew 20 yards with it, landed, and dropped it. Two eggs were punctured in marking them in nest No. 1, and these were both discarded by the same afternoon. At nest No. 4 six eggs formed the complete clutch from 25 June (when it was found) until 30 June. On 1 July only three eggs were present, and one of these was damaged in marking. On 2 July the damaged egg had been discarded and the nest was deserted 5 July. In contrast to these nests in which damaged eggs were discarded (and none of the remains ever found), infertile eggs (one each in nests Nos. 2, 7, and 13, and three in nest No. 10) were left in the nest until the young left or we removed the eggs (nest 10). Removal of eggs during the laying of the clutch and after the clutch was complete had no effect on the number of eggs laid.

*Resistance to Cold.* During the height of the thaw, 26-27 June, the bottom of nest No. 1 was soaking wet, the eggs cold, and the female not seen. This was the fourth to sixth day after the clutch was complete.

The female was back on the nest on 28 June and the four eggs then present all hatched. Perhaps the young bird with one foot undeveloped, which was found dead outside this nest on 7 July, had its development damaged during the period of wetting, but otherwise no complications resulted.

*Incubation Period.* Incubation was measured from the laying of the last egg to the hatching of the last egg (marked): 13 days in nest No. 1; 12 or 13 days in nest No. 2; 13 days in nest No. 3; and 10½ days in nest No. 6. (See Table I for a summary of incubation periods.) The records in this table support (by the incubation periods indicated) our observations that the female spent more and more time on the nest as the clutch increased. DuBois (1935) found the incubation period in Chestnut-collared Longspur to be 12½ days; Mickey (1943) found it to be 12 days in McCown's Longspur. Michejev reports incubation period of 10 days, but Grote in his review suggests scepticism.

*Fertility of Eggs.* We found 10.9 percent of the eggs (6 of 55) to be infertile. This is larger than the 5.3 percent reported by Sutton (1932) from Southampton Island (53 nests, all with 6 eggs; in 17 one each did not hatch). It is much smaller than the 25 percent reported by Sutton and Parmelee (1955) from southern Baffin Island (of 97 eggs, 22 did not hatch). Wynne-Edwards (1952) reported the hatching of all 29 eggs.

#### HATCHING AND CARE OF NESTLINGS

*Hatching Period.* Eggs hatched in the same 24 hour period in nests 3, 6, 7, and 13 and over a 48-hour period in nests 1, 11 and 14, and possibly over 64 hours in nest 2. Wynne-Edwards (1952) reported that hatching occupied from two to four days, while Sutton and Parmelee (1955b) reported three nests hatching within a day (up to 5 eggs), and three nests (4 to 5 eggs) hatching over two days. Frazer Rowell reports one nest hatching within twenty-four hours, and three nests over a period of ninety-six hours. DuBois (1935) found the hatching period to be two days in Chestnut-collared Longspur.

*Feeding of Nestlings.* When the young hatched, the male shared equally with the female in feeding the young. In nests number 3, 6, 8 and 12 the male was more active than the female in feeding during evening and morning. Frazer Rowell shows that the female was the steadier feeder on the last day of the nestling period. She actually fed more, although when he was feeding, the male made as many visits as she did. Frazer Rowell points out that in the first few days after the young hatch, the male does most of the feeding. Such changes in behavior may explain the variation in male and female concern and feeding described by DuBois and Mickey. Grote (1943) reviews 15 Russian articles, one of which reports that both parents feed the young 20-22 hours a day, stopping only 2-5 hours at midnight.

At nest No. 12 the male fed the young as often as did the female during the day, and he seemed to be alone in feeding them in the evening of 19 July when the young were 6-8 days old. Between 1915 and 2010 that evening, he fed them at the rate of once every four to six minutes. At nest No. 6 the male also fed the young as regularly as did the female. Over a two-hour period (2000 to 2200), when the young were 3-5 days old, the male only was feeding them and came on an average of

once in 6 to 10 minutes. In each case the male foraged in his own territory in the Bell Heather on the edge of the 35-foot beach. Michejev report agrees with ours that parents gathered food usually about 20-30 meters from the nest, seldom beyond 40 meters (yards).

*Development of Young.* The young had some dark brown down on the dorsal tracts when they hatched. They gaped at any disturbance on the second and third day. Their eyes first opened on the third or fourth day, and the tips of their first back feathers began to appear. By the fifth or sixth day, they looked at an intruder and often gaped. They crouched in the nest during the last day or two.

Our observations agree with Sutton and Parmelee (1955b) that the nestlings are essentially silent in the nest. We occasionally heard a quavering *cheep* as if a food-begging cry from young that had left the nest. The loud *chee-chee* (or, as we wrote it—*pseep*) reported by Sutton and Parmelee was given when we picked up the nestlings in their last days in the nest, or when we caught them after they had left the nest. When the young were leaving the nest, the parents were very concerned about the first one to leave, but usually showed only mild alarm if intruders frightened the last young from the nest and it hopped "on all fours," stumbling and tumbling over the ground, *pseeping* in alarm.

Frazer Rowell offers the interesting information that all young were ready to leave the nest at the same time, even though in one nest one egg may have hatched four days ahead of the last egg to hatch. More than enough food may provide a partial explanation of this.

*Nestling Period.* Table IV summarizes the number of days the young spent in the nest. The great majority of our birds left after nine days in the nest. These nestling periods are consistently shorter than the between 10 and 11 days recorded by Grinnell (1944) from four nests at Churchill, Manitoba. They fall within the limits (8-10 days) reported by Grote (1943) from Michejev.

In contrast to these reports of longer nestling periods from more southern areas, our observations agree closely with those of Wynne-Edwards (1952) and Sutton and Parmelee (1955b) that the nestling period is 9 to 10 days. All these observers found, as we did, that the young left the nest 3 to 5 days before they could fly. Grinnell (1944) and Nicholson (1930) indicated the same without comment. Frazer Rowell's chart does not allow me to analyze the history of all nestlings individually, but indicates nestling period 8-11 days, chiefly 9 days, if I read it correctly. DuBois (1937a) found the nestling period in Chestnut-collared Longspur to be about 10 days; and Mickey (1943) and DuBois (1937b) found it to be 10 days in McCown's Longspur.

*Leaving the Nest.* Wynne-Edwards (1952) reported that the young left the nest within 48 hours of each other. Our information includes four nests in which the young left the nest within 24 hours of each other, and five nests in which the young left within 48 hours of each other.

Our observations agree with Frazer Rowell that the nests were left clean, not invariably foul as Haviland (1916) reported. Frazer Rowell reports in detail the behavior of the female and young at the time of leaving.

TABLE V  
LAPLAND LONGSPUR NEST SUCCESS

Nest No.	Total eggs	Eggs for whose damage we were responsible	Addled Eggs	Young we took	Young lost through presumed natural causes	Young produced
1	6	2			1	3
2	6		1	1		4
3	4					4
4	6	1 (6)	Deserted, presumably after disturbed by dog.			
5	4	4	Destroyed by dog.			
6	5					5
7	5		1		3 (disturbed?)	1
8	6			1		5
9	4					4
10	5		3			2
11	3					3
12	4					4
13	4		1			3
14	4					4
15	3	1				2
Total	69	13	6	2	4	44

We have no accurate data on how soon after leaving the nest the fledged young can fly, but it was about 3-5 days. Young stayed in their parents' territory for these days and then drifted through other territories to gather, as Frazer Rowell says, in damp areas. Grote reports that they gather in hummocky areas while they can only fly weakly and are somewhat protected from heavy predation by harriers, merlins and jaegers in the hollows. Once strong fliers, the young are less exposed to predation and move to brushy places by ponds and streams. They are completely independent at 10 days.

*Nesting Success.* Table V summarizes the nesting success of the 15 nests we studied. We found a total of 69 eggs, of which we or a dog (there because of us) destroyed 10. Of the remaining 59 eggs, 6 were infertile, and 5 abandoned because of disturbance by the same dog; one young was deformed and pushed out of the nest; and 3 young disappeared from a nest (which was six feet from a well-travelled path at camp). In total, 42 young left the nest; we took two specimens. Eight (perhaps 9) of the 15 nests successfully fledged all young from the full clutch. Thirteen nests, or 86 percent, had one or more eggs hatch, and four was the average number of young that hatched per successful nest. Seventy-five percent of the eggs produced fledged young.

Grinnell (1944) reported that of 12 eggs, 6 nestlings left the nest. Sutton and Parmelee (1955b) reported that of 75 chicks, 62 left the nest successfully. Wynne-Edwards (1952) reported that of 29 eggs, all hatched—5 young were abandoned when wetted, 1 died, and 1 was killed accidentally after it left the nest. Presumably 22 young left the nest.

#### REACTIONS TO PREDATORS

*To Humans.* The first indication of the presence of a nest, and a constant accompaniment to the nest-checking rounds, was the male's alarm



note—a wheezy *dyew* or *dzeeu*. It was given in the presence of a human intruder and was given by several longspurs when a Peregrine (*Falco peregrinus*) flew over. Sutton and Parmelee (1955b) recorded this note as *whee-ye* or *ear*. Grinnell (1944) recorded this note at Churchill as *hee* or a metallic *kittyoo*. In Greenland Nicholson (1930) reported a shrill “*pipe*” (usually double). This seems to be more variation than expected for different ears hearing the same alarm call, but in each area the alarm note is reported to be consistent. We have heard the same note on the wintering grounds, and the bird takes the same head-up posture when giving the call there. The male’s alarm was sounded for his territory rather than specifically for the nest, since no increase of concern was shown as we approached the nest, but he hopped to an exposed perch or fed in a formalized, nervous way within 15 to 20 yards of the nest. Males often flew hesitantly, low over the tundra from place to place in this situation. If the female was on the nest, his concern was much more marked and increased if one approached the nest directly. These actions agree with what DuBois (1935) found in Chestnut-collared Longspurs, and in McCown’s Longspur (1937b).

Females varied in tameness at the nest, but on the average they would flush from it at about 20 yards when we came to the nest directly. They usually flushed at about five yards when the nest was first found. Then they flew about 20 yards low over the ground, as often in straightaway flight as in a quivering, hesitant flight. When they lit, they usually shook themselves and started to feed nervously, occasionally stretching their heads high to look at us. Irregularly under these circumstances, the female was heard to call a rapid *pitze-pitze*, which is probably the note recorded by Nicholson (1930). On a very few occasions, the female hopped and fluttered over the ground, jerking her wings and spreading her tail as if “injury-feigning.” Grote’s review (1943) agrees that the male stands watch while the female incubates, but he suggests much more conspicuous distraction display for both male and female than we saw.

The female at nest No. 2 was very tame from the first, and allowed us to approach within six feet. The females at nests Nos. 5 and 6 were equally tame, especially after several slow approaches were made to photograph them. After this, they, too, allowed approach to within six feet. Nest No. 5 was destroyed, but No. 6 went on to successful completion, and toward the end of incubation the female sat until we stretched a hand out over her.

*To Birds and Mammals.* Tinbergen (1939) suggested that the noisiness of Snow Buntings while in the nest in Greenland might reflect a lack of weasels there. Longspurs, like Snow Buntings, were essentially silent in the nest on Bylot Island, where weasels were present.

On 25 July we watched a female longspur, presumably from nest No. 10, being pursued by a Long-tailed Jaeger (*Stercorarius longicaudus*). As described in our account of the jaeger (Drury, 1960), one made a series of passes at her while she fluttered upslope and downslope, back and forth across the river. She had increased trouble with the steady wind and finally dashed into the large stones in the bed of the river. After hovering a minute or two over these rocks, the jaeger turned and glided off.

## FEEDING

Longspurs fed primarily on the edges of dense vegetation or in the areas of sparse clumps of plants on the margins of barren spots. They fed almost completely on the ground, creeping, walking and hopping, and picking their food off the dirt. During June their food was chiefly plant (probably grass and sedge) seeds. When they started collecting food after the young hatched, they searched thicker vegetation, and many collected food along the frost-heaved ridges in the boggy areas or in the thick Bell Heather and Net-leaved Willow (*Salix reticulata* L.) areas in sheltered, moist areas under solifluction lobes on raised beach edges. Grote (1943) describes the shift from grass seeds to insects as insects become numerous and active through the season. He quotes from Michejev who studied food brought to young: chiefly Diptera and Hymenoptera and only a few spiders.

## SNOW BUNTING

*Plectrophenax nivalis* (Linnaeus). (Eskimo: Kah-óh-dluk-tah).

## HABITAT

Snow Buntings nested in steep ravine sides, overhanging creek banks, and barren ridges nearly free of plants. In contrast to the reports from Greenland, and central and southern Baffin Island, this species was not the most common bird, and it was less widely dispersed than the Horned Lark in the plateau area on the southwest part of Bylot. Our surveys showed 31 pairs (Van Tyne and Drury, 1959).

## DISTRIBUTION AND DENSITY

We found four nests and four more territories in our study area: One territory was on the steep face of the West Ridge at the head of Golden Plover Creek; one east of the mouth of the Little River; and two along the cut banks of the Aktineq River at Ptarmigan Flat (perhaps nest No. 5).

## TERRITORY

Many Snow Buntings were singing at Pond Inlet on 11 June, and we saw one territorial squabble. On Bylot 13 June, Snow Buntings were silent and we did not see territorial activity for several days.

Tinbergen (1939) showed that once pairs are formed, song drops to a minimum, unless the female disappears. We arrived in the later part of his fourth period—paired but not yet nest building.

*Song.* The singing of two males at camp was at its maximum 20 to 27 June, and indicated continuing territorial competition as late as the evening of 2 July. This was, we assume, the recurrence of song while the female is laying and when she starts to incubate. Two males sang while accompanying females carrying nesting material, on 23 June. After singing a while from a perch, the males sang as they left or arrived back on their song perch (Figure 2). They sang in the air if they met a female or another male. There was marked individuality of songs. Of these, the male from nest No. 4 and that from nest No. 2—immediate neighbors—were the most similar. The male from nest No. 3 sang a consistent song of *prrr-tsa-tsu-tsee*, *prrr-tsa-tsu-tsa*, *prrr-tsa*.

Songs became abbreviated in late June and were shorter than we expected at all times. Presumably we did not hear the full songs of the early part of the cycle. Male No. 3 sang until 8 July, but disappeared when that nest was destroyed.

#### AGGRESSIVE BEHAVIOR

We saw territorial fights on the Bluffs near nest No. 4, and between nests Nos. 2 and 3. The male from nest No. 3 avoided going west of the right bank of Snow Bunting Creek where his female built her nest. He had a song perch on a large rock three-quarters of the way up the east (or left) side of Snow Bunting Creek.

The male at nest No. 4 ignored a singing male pipit and a Hoary Redpoll (*Acanthis hornemanni*) which perched and twittered within ten yards of him on the stony ridge, and later took his perch and chattered when he flew down to chase away a male bunting from the west. Other territorial males ignored singing longspurs and shorebirds.

#### LATE FLOCKING

On 14 June, a flock of two male and three female Snow Buntings, four male and one female Lapland Longspurs, and two Horned Larks fed in the grassy meadow between the general snow cover and the top of the Bluffs just west of camp. The vegetation was chiefly Grass Rush, Sweetgrass, Arctic Bluegrass (*Poa rigens* Hartm.), and Water Sedge (*Carex equatilis* Wahlenb. var. *stans* [Drej.] Boott), with patches of mosses, Avens, and Arctic Willow.

#### COURTSHIP

While snow cover was general, Snow Buntings fed together in pairs, and inspected sheltered holes wherever they could be found. On 30 June while the female was off the nest, male No. 3 sang sporadically and preened on his song perch. She fed along the banks and when she came into sight, he glided from his perch down to her and called a weak *zzeeeep*. He followed a while, then she hopped in front of him and cried wheezily, opened and raised her bill, and waved (rather than quivered) her wings (Figure 2). Presumably this was food begging. There were 4 eggs in her nest.

#### NEST AND EGGS

All the nests we found were in hollows, cracks, or tunnels excavated in silt or sandy banks with one exception—under a cracked boulder. Our previous reading led us to expect nests in piles of stones. All sites were free of snow by 15 June.

The lack of suitable sites may be responsible for the relative scarcity of Snow Buntings at the Aktineq as compared with the published reports from other areas. Very few suitable rock piles were present even in the Bluffs which were of friable and poorly consolidated shales and sandstones. Many authors have suggested that Snow Buntings are attracted to a permanent Eskimo camp. On 3 July we found two nests within five yards of each other in the stone wall of the nearest permanent Eskimo house, on the shore at Sermilik seven miles east of camp.

We saw a female carrying nesting material on 13 and 23 June, and found a partly built nest on 20 June. We found the first completed clutch on 23 June. Another clutch was completed 3 July. Of the full clutches we found one contained 5 and two contained 6 eggs.

## ACTIVITIES DURING INCUBATION

*Attentiveness.* We saw the female of nest No. 3 leave the nest to feed during the morning (10-20 minutes between 1000 and 1200), afternoon (5-12 minutes twice between 1630 and 1800), and one about midnight.

Parmelee (Sutton and Parmelee, 1954b) observed that the male fed the female on the nest. We did not see the male ever go into the nest. When the female returned from a feeding excursion, she flew fast and directly, lit a few feet from the hole, and went in—quite in contrast to her aimless movements while feeding.

## HATCHING AND CARE OF NESTLINGS

In the only successful nest we studied, all young hatched on 6 July. They stayed in the nest 12-13 days.

Both parents fed the young, which were usually silent in the nest. We heard them chatter only when the parent actually was in the nest. Tinbergen (1939) says that in East Greenland, young chattered loudly while the parents were away.

Once they had left the nest, the young chattered hoarsely and loudly when fed, and had a characteristic *pit* or *swit-swit* note. We found two young with a male at the head of Lark Gully, when the female was with the other young at the nest. This indicates dispersal and parental cooperation in care of the young, as Tinbergen mentions. The same day, and for three days afterward, 18-21 June, there were two pairs of parents and eight young in the stony creek-bed on the west side of West Ridge.

## REACTIONS TO PREDATORS

Snow Buntings flew endlessly around and around with hesitating flight, low over the ground. They settled briefly and fed stiffly and nervously; then flew on again, perching on exposed rocks. The female called *cheep* occasionally. Usually the female was more demonstrative, and the male followed her or remained perched on a rock and occasionally called *pirrit*. The male acted as concerned as the female if she were absent.

On 28 June the male and female fluttered doggedly after a weasel as it went up the west bank of Snow Bunting Creek and moved between their nest and the snowbank. The female fluttered so close when the weasel was near the nest that it rushed her twice. The nest was destroyed by a weasel.

## FEEDING

Snow Buntings fed on the edges of barren beaches, ridges, or steep slopes kept open by frost action. When feeding they crept along through the sparse vegetation, especially among clumps of grass sedge and rush. Most of their food was taken from the bare surface of the soil, but they also pecked repeatedly at last year's grass heads.

**PART II: DISCUSSION OF ECOLOGY****I. SPECIES SEGREGATION AND DISTRIBUTION RELATIVE TO SUITABLE HABITAT.**

What elements of habitat segregation allow these species to exist together without competition for territory, cover, or food?

1. In plants, there are seldom numerous representatives of the same genus in one habitat which is subject to environmental extremes; and we found the same to be true for the birds of Bylot Island. Snow Bunting—Lapland Longspur, and Black-bellied Plover—Golden Plover, seem to contradict this. But also it is true in plants that when two members of a genus do occur together in the high north, they are closely related—as in *Saxifraga*, *Ranunculus*, *Salix*, *Draba*, *Antennaria*, and *Potentilla*. When organisms widely separated from each other converge evolutionarily on a common habitat, their many differences of structure and behavior will tend to keep them from competition, as Darwin pointed out.

2. We saw no overlap or competition for food among the Passerines. In general, longspurs and pipits fed in thicker, moister vegetation; and larks and buntings in drier sites. Pipits fed mostly on insects, on or flying above the vegetation. The others fed on material in or under the vegetation, longspurs in or below mossy, heather-grown areas, and buntings and larks in sparse, grassy areas. Our few observations on food brought to the young indicate that they were fed many two-winged flies and spiders. Presumably, this reflects an abundance of supply.

All except larks readily accepted trespassing by birds who showed no territorial behavior. This action and the over-riding effect of flock calls are valuable adjuncts to allow a section of the population to crowd together in hard times.

3. The four species differ most conspicuously in selection of nest sites: warm, sunny ravines for the pipit; exposed barrens for lark; well-vegetated slopes for longspur; and holes in exposed ridges or rock piles for bunting. These indicate complete ecological segregation even though there was no shortage of the last three types.

4. Larks had large territories and tended to spread out over wide areas of the uplands—not concentrating in favorable valleys as did pipits and longspurs. This difference in dispersal reduces competition. The sunny, steep valleys occupied by pipits did not overlap the lower sunny slope territories of longspurs. Snow Buntings were widespread, like larks, and in our area were influenced by restricted nesting sites so that the two seldom overlapped.

5. None of the species occupied the total area of habitat suitable for it. Lapland Longspurs were most conspicuous in this. They were crowded into certain places (mosaic distribution), and occupied only a small percentage of the total suitable area. There are at least three reasons for this: *First*—The birds settled on areas free of snow when they first arrived (Figure 2 in Van Tyne and Drury, 1959). These places were on south-facing slopes at low altitudes and were not widespread. *Second*—Mickey (1943) commented (McCown's Longspur) on the aggregation of nests in seemingly uniform grassland habitat. Svardson (1949) discussed the aggregation of Wood Warblers (*Phylloscopus sibilatrix*) at the limits of their range in Sweden. He and Andrew (1957) agree that the song of a male not only attracts females, but also attracts other males to set up neighboring territories. The natural behavior then leads to aggregations of territorial males over and above that forced on them—in our case by general snow cover. *Third*—We found several nests associated with a previous year's nest (especially those in which a peculiarity of construction indicated that they were made by the same bird). This

suggests that females tend to return year after year to the same small territory in this species as in many others.

## II. COMPARISON OF ARCTIC ADAPTATIONS OF PASSERINES.

What are the features of their biology which allow these passerines alone to occupy this area?

A. The behavior of the Lapland Longspur which enables it to occupy the tundra habitat is shared in detail, as far as I can discover, with the other longspurs. Indeed, the tundra at Bylot Island resembles the topography (rolling uplands and deep-sided, sharply-cut river valleys) and vegetation aspect of the grasslands of the high plains. Territory type, song display, restriction to territory, female incubating before the clutch is complete, short nestling periods, and young leaving the nest before they can fly, are shared with McCown's Longspur, and many are shared with Chestnut-collared Longspur; yet they are features which would be assigned as adaptations to the arctic habitat were it not for the excellent studies by Mickey (1943), and DuBois (1935, 1937a, 1937b).

1. Tolerance of crowding is of advantage to the species in a year such as 1954, because thereby many pairs were able to breed successfully when only a small area was available at the physiologically proper time for nest-building.

2. With Lapland Longspurs, one adaptation is physiological. The tolerance of the eggs in nest No. 1 to soaking for two days (26-27 June) in ice melt-water is remarkable, allowing successful reproduction in areas with a "late" spring. DuBois (1937b) tells that being buried two days under the snow killed the eggs of a McCown's Longspur, which extended incubation nine days beyond the normal period. Birula (1907) describes the destruction of Lapland Longspur nests by melt-water floods and by late snowstorms in Siberia.

3. The ability to arrive on the breeding ground and then feed for a week or two until suitable nesting sites becomes available, even though this is after the peak laying periods in more southern parts of the species' range, contributes also to local success. This feature of arctic nesters was discussed by Lack (1933), and treated in detail by Marshall (1952). Grote (1943) mentions it in his review of the Siberian breeding of Lapland Longspurs.

4. The short period taken for the nesting cycle is another important quality, using longspurs as an example: eggs hatched 3-15 July, and the young stayed in the nest 8 to 11 days, and left still unable to fly. This concentrates the breeding cycle (a) by shortening at the beginning in response to a late thaw, and (b) by shortening toward the end by successful independence of fledged young. Presumably the ecological pressures discussed by Pitelka, Tomich, and Treichel (1955) are important in hurrying the later end of the cycle. Those authors discussed the need for the predators' young to become independent while food is abundant. The prey of longspurs is soft insects, rather than lemmings. Nice (1937) showed the influence of temperature on the start of laying in Song Sparrows, and since her studies, others have shown similar effects in other species, most recently Snow (1958) in the European Blackbird (*Turdus merula*). This, coupled with effects of stimulation by the male and nesting site, presumably controls the start of females laying, and decreases the chances of her starting "too soon."

5. The difference in clutch-size from the southern portion of the range, Churchill, Manitoba—4-5 eggs (Grinnell, 1944), to the northern part—6-7 eggs (our records, 1954; and those of Wynne-Edwards, 1952), conforms with the usual tendency; but we notice that in McCown's Longspur the total annual production will be greater since, as Mickey (1943) says, they tend to raise more than one brood a year of 3-4 eggs. The average for McCown's would be seven young per year which is the unusual maximum for Lapland Longspur. At the southern part of the breeding range of Lapland Longspur, there are nearly 20 hours of daylight which is as much as our longspurs actually used (Palmgren, 1935; Grote, 1943; Franz, 1949; Karplus, 1952; Hoffmann, 1959). Because of the adequacy of time "to feed more young" where the clutch-size is smaller, and the greater annual production in two-brooded more southern species, it is hard to see that the "reason" for Lapland Longspurs nesting so far north is that they are able to produce more young. The period during which the young were in the nest (8-10 days) is not decreased in the Arctic as compared with McCown's and Chestnut-collared Longspurs. Interestingly, we found the same types of birds (larks and plovers) sharing the tundra habitat that Mickey (1943) found sharing the grasslands with McCown's Longspur.

The same ideas apply to larks and Snow Buntings, but it is hard to see how a bird so dependent on insect life as the pipit survives late snows at this place. Our observations indicate that pipits are at the extreme of their tolerance, but suggest that larks are capable of nesting much farther north. The nest sites, behavior, and feeding of larks suit them at least as well as longspurs and Snow Buntings; yet they do not go further north while longspurs go north to Ellesmere Land and Snow Buntings are reported to range over all land surfaces free of snow, farther north than any other land bird. The difference may be related to the degree of dependence upon insect food when they arrive on the breeding ground.

I find no obvious characteristics of productivity which make it advantageous for longspurs to nest in the Arctic. Their various habitat-correlated behavior patterns are equally suited to grassland areas to the south. Certainly the ability to maintain physiological preparedness until the final stimulus of suitable nest sites appear, together with the concentration of the breeding cycle into one brood, are factors which allow this species to nest farther north where it lacks competition. Probably the explanation is that by nesting in the Arctic the species escapes competition—the tool of selection—and any species which can live there automatically has an advantage by lacking competition. We should not look, then, for the reasons why the species has an advantage in living in the Arctic, but look for the features which allow it to live there. Most important of all is the fact that they do occur there. Historical accidents and source of population to occupy the area have led to their presence. Once an organism occupies an area, we may show why it can, but we have no hints on why, for instance, the closely related other longspurs or pipits or buntings do not occupy the area. To say they are excluded by competition is no answer unless we have details.

B. All four species have well-developed flight songs. But they readily sing from elevated perches, Horned Larks from telephone poles, and

Snow Buntings and Lapland Longspurs from radio masts at Pond Inlet.

C. All four species walk and have a well-developed hind toe with an exaggeratedly long claw. All four live on treeless areas where the wind blows most of the time. Having no shelter from such a wind, small birds will need firm footing, and the additional long hind toe should supply this. Another purpose might be to supply a larger foot for walking on the snow. This correlates with their walking rather than hopping—an advantage on a soft surface. In my experience, tracks of larks and Snow Buntings on the snow do not sink as deeply as do those of Tree Sparrows or Song Sparrows. Walking or creeping also avoids buffeting by the wind.

### III. CLUTCH-SIZE AND LATITUDE

Lack's work on clutch-size (1947, 1948a, 1948b, 1954) is the foundation of our knowledge of this subject, but I am unsatisfied with his explanations of the large clutch-size in the northern part of a species' range. It is clear that if the phenomenon is present both within populations and between separate species, there must be a selective advantage. On the other hand, our observations suggest doubt that the larger clutch-size results in larger annual production. How do the clutch sizes and total annual productivity of these species vary with latitude?

For example: Information available in Bent (1942) for Horned Larks provides comparison of the clutch-size of this species over its North American range—from the hot deserts of northern Mexico north to our Bylot nests, which are the farthest north recorded. The subspecies from the hottest part of the range have an average clutch of three eggs: (*actia* (2-3-5), *adusta* (3), *enertera* (3), *merrillii* (2-3, rarely 4), *occidentalis* (3); the subspecies of the western and coastal grasslands have a clutch of 3-4: *insularis* (3-4), *giraudi* (3-4), *leucolaema* (3-4), *strigata* (3-4); wetter prairies and the northeast usually have four; *alpestris* (3-4-5), *flava*, Old World (2-4-5), *praticola* (2-4-5); the northern birds, of which only *hoyti* is adequately represented, have 4-5.

The annual production of individual females is actually not larger in the north than in the two- or three-brooded populations farther south. The clutch-size seems instead to be a telescoping of the breeding season.

The following are clutch-sizes for Lapland Longspurs: Hatched between 3 and 9 July—4 (6), 1 (5), 1 (4). Hatched between 10 and 15 July—2 (5), 5 (4), 2 (3). We found no nests with clutch-size of 7, which Wynne-Edwards reports from the head of Clyde Inlet, but he found completed clutches 6 June. Perhaps this is because 1954 was a conspicuously late season (we found the first completed clutch on 22 June). If the rule applies that later nests have smaller clutches, our nests fall into the pattern he found, because our nests should be compared with his later nests (completed 19 June to 2 July and containing three clutches of 5 and two of 4). On this basis, our earlier nests have larger clutches than the contemporaneous nests at Clyde Inlet, but the latitudinal distances are too small to be as effective as seasonal differences in influencing clutch-size; and the fact that early clutches are laid by adults and thus are larger than later clutches presumably laid by first-year females, must be taken into account. The clutch-size in these two places is larger than that reported from Frobisher Bay by Sutton and Parmelee (1955b): 3 (3): 9 (4): 9 (5): 1 (6). Sutton (1932) found



most nests (all but 7 of 78 nests) on Southampton Island (64° N. Lat) to contain 6 eggs. Grinnell's (1944) four nests at Churchill, Manitoba (about 59° N. Lat.), contained 4 to 5 eggs. Blair (1936) reported 3 (7) and 1 (6) from East Finmark (70° N. Lat.). Frazer Rowell (1957) reported 1 (4), 7 (5), 3 (6), and 3 (5+).

The clutches of Snow Buntings 1 (5) and 2 (6) were smaller than those reported from the northern part of their range and they were later than usually recorded. Pleske (1938) reported 5 to 7 eggs from Taimyr Peninsula, Siberia. Nicholson (1930) reported 1 (7), 2 (6), 1 (5), and 3 (4) from southern Greenland. Manniche (1910) reported that the most frequent clutch-size in northeast Greenland was 5 or 6, seldom 4, and only one nest of 3. Sutton and Parmelee (1954b) report: 1 (4), 11 (5), 1 (6), and 3 (7) from Frobisher Bay, southern Baffin Island. Tinbergen (1939) reported: 1 (3), 2 (5), and 4 (6) from east Greenland.

Tinbergen reported most clutches complete by mid-June; the nests Sutton and Parmelee found after 19 June were already completed; and Wynne-Edwards (1952) reports young after 25 June.

*Why larger clutch sizes in the north? Recovery from Disasters.* For a species to occupy a huge area of productive habitat, its breeding biology must allow it to meet the vicissitudes of that habitat, and it is obvious to those who visit the far north, that heavy mortality comes from periodic disasters on migration or accidents on the breeding grounds such as late snowstorms. Natural selection can be expected to have detected a factor obvious to a human. For natural selection to act, however, it must act on the advantages which allow the population to occupy the favorable habitat, not to balance mortality, as Lack (1954) pointed out.

In the north, species must have a breeding potential to allow recovery from periodic catastrophes, and there is selective advantage of large clutch-size to allow rapid recovery of the population. In contrast, in stable and uniform habitats, and especially where there are resident populations, too many young in each nest will be selected against, since it attracts specialized predations and parasitism, and leads to competition among the members of each large brood. The studies available on breeding potential suggest (*viz.*, Lack's (1948b) work on Starlings, *Sturnus vulgaris*), that a species will produce just as many young as it possibly can bring through to maturity. Absence of a second brood, and lack of competition for abundant food when the young are becoming independent and the parents are molting, allow arctic species to bring more young through. Larger broods will be successful as long as they produce more young to migrate. Large clutch-size has the advantage of allowing recovery from disasters—but that is not enough. How is the clutch-size enlarged, and why are clutches smaller farther south? Is productivity greater? Longer daylight alone is not the explanation for the larger broods in the north, because of the daily cycles of activity we and many others have observed (Palmgren, 1935, 1949; Franz, 1949; Grote, 1943; Karplus, 1952; Hoffmann, 1959). Birds at 74° latitude use no more daylight than those at 55° latitude (20 hours), and across this latitudinal range, the longspurs' clutch-size varies "according to the rules."

*Geographical Variation in Clutch-Size and Daylength.* In the geographical variation of clutch-size, it is important to separate releasers from selective advantages. There is abundant evidence of larger clutches in the north and an obvious environmental co-variant is daylength. Our longspur nests and those of Wynn-Edwards (1952) show that within limits, the later the start of the clutch, the larger the clutch until a peak is reached, and then the clutch decreases, and this is known for many species. In the case of Kent's Island Tree Swallows (*Iridoprocne bicolor*)—(Paynter, 1954), later arrivals find a longer length of day than birds nesting to the south. If birds arrive later in an area slightly farther north, they find much greater difference in daylength than expected, on a latitude basis. I am convinced that this is the "releaser." The length of day is one of the stimuli which starts the mechanism of egg production, but it does not necessarily control the upper limit of clutch-size. Nice (1937), Snow (1958), and others have discussed temperature as a stimulus.

I doubt that *the* reason the clutch is larger is ability to feed all the young. Lack's data on the clutch-size of the European Robin, *Erithacus rubecula* (1953) offers evidence enough itself to throw doubt on this. My data on Horned Larks agree that it is misleading to apply only this hypothesis. The variations approximately follow latitude or daylength, but many other factors vary with latitude in the same way. Large brood size is not involved in the most characteristic of northern breeders—the shorebirds. Long day is just one factor obvious to man.

I suggest that large clutch-size is a secondary factor; that in the north selection operates on concentrating the brood into one annual nest. Ray (1913) suggested the same effect for Tree Swallows at higher altitudes in California. In the south, as with larks, it is an advantage to spread broods over a long period—two or three broods of two or three young. The young would not survive a breeding season of March-September on Baffin Island, and thus larks there can have only one brood. Selection is not simply of large broods, but of a single annual brood, which must be large enough to maintain the population. I suggest that there are inherent limitations to total annual production within the species and that these limit the size of the single brood, because the total annual production in the deserts of Mexico is the same as that in Baffin Island. In studies of the selection of brood size, annual production must be considered as a factor; i.e., average clutch-size X average number of broods. In the far north, production is suited to the short season, but production is not necessarily greater.

Date of arrival, relative to length of day on arrival, still may be environmental clues or time-givers in the annual cycle, but they are not the factors leading to a larger clutch-size. This is supported by Baker's (1938) evidence that there is no general tendency for birds to breed everywhere at the same daylength, nor for birds to breed when the days are lengthening particularly quickly.

If we speak of telescoped broods or clutches being selected in higher latitudes, it may help answer some of the questions raised by the theory of daylength cause: such as a larger mean clutch-size in Connecticut than on Cape Cod at the same latitude for Tree Swallows (Paynter, 1954); or a larger clutch-size in Switzerland than in England for Swifts (*Apus apus*), (Lack and Lack, 1951).

The contradictory clutches in Lack's study of the European Robin are smaller where the population tends to be resident. In approaching this and other problems of variation within a species, we should start at the center of the range and ask not only why it is larger to the north, but why it is smaller and subdivided to the south.

*Abundance of Food and the Period of Maximum Demand.* To examine Lack's hypothesis that the successful feeding of the young in the nest is a selection force on clutch-size of passerines, we need to follow the weights of individual nestlings to see how they compare as they leave the nest, and then follow color-banded birds that have left the nest to see whether and how long the "runt" survives. This can be applied to certain groups only, because in some—herons, hawks, and owls—the late or weakling young die and are eaten or trampled into the nest floor.

Snow (1958) has done this for European Blackbirds and has shown that it was really impossible to correlate the breeding of this species with any particularly abundant prey species. The stimulus of rising temperature led to the maximum number of egg clutches being actually present when the chief food—earthworms (*Lumbricus*)—was abundant. Young in the nest came later, at a time when worms often were harder to obtain and parents had to seek other food. The artificial situation of the Botanical Garden, where Snow's studies were made, may have a different annual supply of food than the more natural situation of woodland Blackbirds which, as Snow pointed out, were not so decimated by May droughts. The May and mid-summer droughts hardened the soil surface and largely removed the source of worms.

The critical period of the population relative to its food supply should be considered to extend from hatching of young until the young are independent and the parents have completely molted. No one period in this time is the critical one. The whole population makes the maximum demands on the food supply when all young have been produced and the parents are molting (Pitelka, 1958). Furthermore, in the life of the individual fledgling, a critical time is when the parent has stopped feeding. In early broods, the female may stop feeding fledglings to lay her next clutch (Tinbergen, 1939). If the young she has been feeding are not self-sufficient they die. During this period after leaving the nest and while the parents feed, the young who have inherited behavioral mechanisms for finding, killing, and eating food have to learn (and very rapidly) what food is and where to find it. Ruiter's (1952) studies with Jays (*Garrulus glandarius*) show that the bird blunders onto the caterpillar first, and when it has a "picture in mind" of what to look for, it will seek out the food. But for young to learn their food, the prey has to be "superabundant" for the trials and errors of the young to happen on the prey often enough for them to learn, by "reinforcement." Carrick's (personal communication) work on food of birds in Australia shows extreme individual differences which must depend upon this sort of conditioning.

The point is that: larger broods in higher latitudes are correlated with daylength and depend upon ability to feed the young in the nest must be extended to feeding the young out of the nest—indeed, must include the period when the young are independent and the parents are molting before migrating. Pitelka (1958) made this point in discussing the molt of Lapland Longspurs.

**PART III: DISCUSSION OF BEHAVIOR**

A. *COMPARISON OF BEHAVIOR OF LAPLAND LONGSPURS WITH OTHER BUNTING AND FINCHES.* Do our observations on the behavior of the two buntings help to clarify their taxonomical relationship? Complete descriptions of the behavior of Emberizine finches are few but they suggest several comparisons. The display postures of Lapland Longspurs seem closer to the Yellowhammer (*Emberiza citrinella*) than to the other Emberizines, including Snow Bunting, but are more similar to those of Snow Bunting and other European Buntings than to the American Emberizines (Song Sparrow, *Melospiza melodia*, and Tree Sparrow, *Spizella arborea*).

They lack the wing-waving described in McCown's and Chestnut-collared Longspurs, but they include wing-vibrating (Andrew, 1957). They differ from the Snow Bunting in the nature of the song flight, and in that the longspur "emphasizes" his breast while the Snow Bunting "emphasizes" his back (Tinbergen, 1939) in displaying to the female. There are also differences in song period. In Snow Bunting, copulation stops after the first egg is laid, and the male no longer accompanies the female. The female Snow Bunting starts incubation one to three days *after* the completion of the clutch, instead of one to three days *before* completion of the clutch as in the Lapland Longspur. Food foraging in Lapland Longspurs was restricted to the territory, and much less so in Snow Bunting.

The aggressive and courtship actions agree with general patterns for European buntings described by Hinde (1955), and with specific patterns described by Andrew (1957) for Lapland Longspur. "Supplanting attack" and "sleeked head-forward threats" were shown in the border disputes, and in the first encounters with the female (male fluffed—of Andrew). Later, and with no transition that we observed, the male assumed an upright posture with drooping wings and under-feathers fluffed out when parading before the female (bill-raised run, courtship displays, of Andrew). In our observations the wings were not vibrated in this posture, but we must have missed this detail. In contrast to Andrew we found this as much associated with the song period as the fluffed run.

According to Hinde (1953), drooping wings and parading showed sexual drive, while the upright posture and fluffing of feathers showed drive to flee. More recent work has led Hinde and his students to believe the upright posture is associated with sexual drive (Andrew), since this posture is assumed during copulation. The two were combined in the pre-copulatory behavior of longspur males. The combination of upright posture and bill-up parading showed off the male's black throat and white belly (the posture must have preceded the plumage, as Lorenz (1941) has suggested).

Exaggerated upright posture, drooping and vibrating wings, and handling of nesting material by the male preceded copulation (wing-quivering and nest-site display; bill-raised run, Andrew). My observations suggested that this wing-vibrating was an attempt to fly up rather than a ritualized part of the display, and I saw it only immediately before copulation. The male crouch, with head lowered and rump fluffed—just before, during, and after copulation—is described by Andrew

only under bill-raised run, and not in this context. Hinde (1952) strongly supports the idea that the rise of sexual drive in both male and female suppresses the drive to attack, and that since the male's sexual tendency grows faster than that of the female during most of the courtship and nesting period, he is subordinate to her. Hence, following the upright posture by the fluffed and horizontal posture at the peak of "conflict" may show the strength of the male's thwarting because he is subordinate.

The differences found when my notes are compared with Andrew's suggest (1) a variety of specific postures of particular "meaning" which can be combined in various ways or (2) variations in postures between populations or (3) greater sexual drive in the males I studied because of the lateness of the season, and the advance of their condition before the females were receptive. I prefer to avoid assigning motivations until more is known of specific situations in which the displays appear.

Points of interest in placing Lapland Longspurs' displays properly in comparison with the displays of other finches are: (1) song flight (which is to be expected in a tundra region); (2) horizontal head-forward posture of aggression; (3) lack of bill-snapping, wing-raising, pivoting or twisting, or courtship feeding; (4) symbolic handling of nesting material; and (5) unusual posture of the male just before copulation. These are differences, while the rest of the postures fit into the general pattern, sleeked head-forward posture, supplanting attacks, head-up posture and fluffed posture—the main elements found by Hinde (1953, 1954, and 1955).

**B. CHANGES IN MALE BEHAVIOR AND TERRITORY ESTABLISHMENT OF LATE ARRIVALS.** What explanation can we offer for the two separate periods of territory establishment in our areas? The male Lapland Longspur's hostility changes (1) when he has been joined by a female, (2) when the female has started building the nest and laying eggs, and (3) when the female has started to incubate. The aggressive tendency of the male sinks as his sexual drive rises; at the same time his singing and response to his neighbors' activities change. Eventually he seems to lose interest in territory borders, just as the pressure is highest, if the "reason" for territory is food. We recorded changes in territories of Lapland Longspurs indicating that this change allows the establishment of territory by males which arrived later or those which are unable to establish territories early in the season (Figure 7). Later arrivals take up territories in undefended areas as the aggressiveness of the territory holders fades or is concentrated onto a smaller area. Meyerriecks (1959) has documented this change in territorial defense and its effect on territories in colonial Green Herons (*Butorides virescens*).

Of the sixteen nests of Lapland Longspurs in half of our study area, seven clutches (Nests Nos. 1, 2, 3, 4, 7, 8, and 1 unnumbered) were completed early (22-25 June)—(Figure 7a), and all of these nests were about 100 yards apart. Nine clutches were completed late (1-4 July)—(Figure 7b).

These birds were not banded, and we do not have detailed observations on the change in behavior of individuals; but the evidence is clear that there were two sets of territory establishment nine days apart.

The later nests were placed inside the area included in the five earlier territories.

Smith (1950) described the late arrival of Yellow Wagtails (*Motacilla flava*) in England at an area where three territories had already been established. The newcomer established himself in five acres (half of the total area) where there were two territorial males whose females had nests and were incubating. At the same time a single male, whose nesting activities had not proceeded as rapidly, held five acres and excluded the newcomer.

The functions of territory are complex, and authors have differed on whether the mechanisms are simple or various (Symposium, *Ibis*, 1956). One feature often neglected is that selection acts on maximum successful breeding of the whole population rather than on especially successful breeding of a few individuals. The late breeding of yearling birds is so universal that it suggests selective advantage for the population as a whole. This advantage may come from the increased opportunities for the inexperienced birds to establish territories when the experienced adults have passed their peak of hostility. Young birds which have not established a territory in a previous year are at a disadvantage unless they can choose a time when the hardened campaigners will, for various reasons, be "willing" to let them insinuate their territories among those of the mature segment of the population. Usually it has been assumed that once a territory is established, it remains constant for that breeding season, and late arrivals can only carve out a territory by dint of special aggressiveness. Most theories on the function of territory relative to food for nestlings (Lack, 1948b) depend on this premise. But what does it mean to the biological function of territory if the "any defended area" (Noble, 1939) is a great deal smaller when the young hatch than when the single male first established his territorial boundaries? There is danger of confusion of proximate vs. ultimate causes, and dispersion must be carefully separated from territoriality if we consider the main selection to be concerned with the food supply.

Furthermore, there are adequate "needs" to lead to the phenomenon of territory expressed in courtship behavior. Tinbergen, Lorenz, Lack, and their students have shown the "need" for a male to act aggressively in many cases in order to effect sex recognition. This, combined with site tenacity (*Ortstreu*) leads to a courtship explanation of territory as Tinbergen suggested (1957). But I do not suggest that food is not an evolutionary advantageous effect also. Territory can be expected to have different expressions and different selective advantages in every group in which it is expressed.

I presented a report on Lapland Longspurs, including the idea just discussed at the meetings of the American Ornithologists' Union at Cape May in September 1957, and in response to questions I said that I thought the idea had already been published; but since then Meyerriicks and I have not been able to find it in print.

**C. SELECTIVE ADVANTAGE OF MIGRATION IN TERRITORY ESTABLISHMENT.** Although there are many selective advantages in migration, our studies of longspurs suggest another, the apportionment of available breeding territory. On the average, mortality comes in large

juvenile failure and a steady death rate of adults (Nice, 1937; Kluijver, 1951; and summary in Lack, 1954). Recent population studies have shown that the great peak of juvenile mortality in resident species comes between July and October, even though migratory dangers do not exist. As Kluijver (1951) has suggested, mortal dangers for resident species result from the emigration of juveniles into strange habitats, seeking to establish their own territories. Such young often occupy less desirable habitats, such as the pine woods, in Kluijver's studies. Snow (1958) has data which show that another important peak in mortality occurs during territory establishment and the early part of the breeding cycle in the European Blackbird.

In a wholly migratory species, when the returning population takes up territory in spring, newly territorial birds do not face an entrenched wintering population with inexperienced young at a maximal disadvantage relative to the experienced adults. This must be an advantage to the population as a whole, since it allows more adjustment among the arrivals and less absolute exclusion. It may be that for the year-crop, migration is an advantage in spreading out the population—balancing the migration hazards which become then no worse than those hazards met by juveniles leaving their parents' territories when neighboring birds are in a phase of temporary ascendancy of territorial behavior (Lack 1953, Nice 1937).

#### D. LONGSPUR NEST SITE SELECTION.

Longspurs at the Aktineq built their nests consistently under the decumbent branches of clumps of Bell Heather (Figure 6). How can this observation be rationalized with the nearly universal description of the nesting of this species in low, rolling, wet, hummocky tundra, under a tuft, or in the side of a moss or sedge hummock (Blair, 1936; Dalgety, 1936; Grinnell, 1944; Nicholson, 1930; Soper, 1928 and 1946; Sutton, 1932; Sutton and Parmelee, 1955b; and Wynne-Edwards, 1952)? Haviland (1916) found nests from the wettest to the driest habitats on the Yenesei River, and A. Murie (1946) found them on gentle slopes covered with *Avens* (*Dryas integrifolia* M. Vahl). Grote (1943) reports longspurs nesting on all sorts of tundra in Siberia—wherever there is plant cover—but agrees with Birula (1907) that the species is characteristically a hummock-tundra bird. Only one nest at the Aktineq (No. 12) could be said to be placed in a low, wet place, and No. 11 was in a frost-crack on the edge of a wet area.

Bell Heather grew in shallow depressions on slopes which (after the barren and exposed ridges) were the first free of snow, and longspurs chose the edges of the Bell Heather patches first free of snow on slopes facing southeast, south, or southwest, from which the snow melted very early. Among 26 nests found, there was only one exception concerning exposure. Birula (1907), Michejev (1939), and Tolmatshev (1934) report nests facing south, east, or southeast and sheltered from the wind by hummocks, grass or low heaths. In the Siberian areas studied a south-east wind is almost unknown in summer. Frazer Rowell (1957) reviews the literature on nest sites of this species. DuBois' (1935) descriptions indicate that the nests of Chestnut-collared Longspurs are similarly sheltered, in contrast to the exposed situations of McCown's Longspurs' nests. The breeding sites we found are similar to those found by Havi-

land and Murie, presumably because the wet meadow sites were snow-covered too late in the species' breeding cycle and because the species, displaced from ideal nest sites, selected a form resembling the overhang of a tussock.

At the Aktineq, 14 of 19 nests were directly associated with Bell Heather, but at Ooyarashukjooet (Miller, 1955) only 2 of 6 nests were so associated. Nests at Ooyarashukjooet were overhung by Avens, Arctic Willow or a clump of Grass Rush and placed in frost-cracks, under solifluction lobes (Washburn, 1956), or on the sides of a raised beach ridge where no Bell Heather grew. In the Aktineq region, steeper slopes, less marked with deep frost-cracks and mounds, provided fewer hummocks, and the best available form was provided by the decumbent growth of Bell Heather. The regular frost patterns with steep-sided cracks at Ooyarashukjooet supplied the proper forms, as did tussocks near lemming mounds and plant cushions on the sand bars.

This seems to indicate that longspurs nest in a sheltering overhang facing toward the south and that actually Bell Heather as such did not matter. It was a form requirement rather than a species relation. Observations of other authors farther south and in Greenland (Salomonsen, 1950-51) refers the species to the verge of high arctic areas where Crowberry (*Empetrum nigrum* L.) is replaced by Bell Heather), indicate that the species does not belong to a particular vegetation association. Rather, it takes what is available and best fits its needs in those areas that satisfy the physiological requirements, and from which it is not driven by competing species.

### SUMMARY

#### *Horned Lark*

1. This species was the most widespread on Bylot Island, and had the largest territories among the passerines.
2. Nearly all singing was in the air and the flight song was identical in form, although different in quality, from that of *praticola*. Song flights took place over the individual's territory.
3. We found a clutch-size of 4-5 eggs and recorded a specific alarm note given by parents with young.
4. (a) "Casual abandonment," (b) very rapid feeding at the nest, and (c) lack of brooding of the young during the day, contributed to effective concealment of nestlings.

#### *Water Pipit*

1. Flight song was regularly two-parted.
2. The trilling song correlated with immediate attack on an intruder.
3. Territories averaged less than 100 yards long and about 200 feet high in the ravines in south-facing bluffs.
4. The single nest found contained five eggs and was excavated into a slight overhang. It was built entirely of grasses.
5. This species is the only clearly Low Arctic representative on Bylot Island. The nest is, we believe, the most northern recorded.

#### *Lapland Longspur*

1. This was the most abundant nesting species: 27 territories in the study area, and at least 60 in the seven square miles between the



Sound and the snout of the Aktineq Glacier on the west bank of the river.

2. When we arrived we found mixed flocks containing many male and a few female longspurs, as well as Snow Buntings and Horned Larks. Males took up territories between 15 June and 25 June.
3. Most songs were given in flight at a height of about 20 feet. Each male had several song perches, and sang repeatedly from the ground. The males had a whispered song given in close company with the female after pairing.
4. Territorial disputes involved flying chases, song duels, and, on the ground, forward postures with a scold note and gaping bill. Rushes were directed at the side of an intruder.
5. Trespassing was tolerated and territorial defense seemed suppressed by the winter flock calls. Song stimulated immediate response in the form of singing and defense of territory.
6. Territories occupied a half acre or less for the twelve most carefully studied pairs. Once a male took up territory, he did not leave it until the end of the breeding cycle except for very brief periods.
7. The first displays to a female resembled hostile displays. In sexual pursuits, one female was pursued by two or three males in succession. When she settled in one territory, she was still pursued by her male, and the pursuit flights still sometimes trespassed. The female incited pursuit in flight and on the ground. At this time the males' displays assumed an upright posture. Song remained vigorous but less frequent than during the pre-pairing period. It occurred on appearance of a neighbor in song or when the female disappeared.
8. Males' pre-copulatory display included carrying dark material, upright posture, and song. This was followed by a crouched, fluffed posture before copulation. The female crept and hopped in a crouched position. After copulation the male returned to the crouching position. The female stood erect, raised her head high and cocked her tail.
9. Nesting sites included a number in which Bell Heather overhung the nest.
10. The nests were constructed entirely by the female, and were made of dead and dry grass, tightly knit and lined with white feathers and often willow cotton. The male constantly accompanied the female while she built, occasionally picking up brown nesting material similar to that she used, only to drop it. The male accompanied her closely until she completed her clutch.
11. Clutches were completed between 22 June and 4 July. Those hatching 3-9 July contained: 4 (6), 1 (5), 1 (4) eggs; and those hatching 10-15 July contained: 2 (5), 5 (4), 2 (3) eggs.
12. The female started to "incubate" sporadically on the second day before the last egg was laid, and incubated most of the day before the last egg was laid in nest No. 6. The day after the last egg was laid, the male stopped his attendance on her and sang actively for three days after that. Then his song diminished until it had effectively

- stopped when the young hatched. The males took no part in incubation, but were constantly alert to trespassing on the territory.
13. During 80 visits to 14 nests, the female was found on the nest on all but 18 visits; two absences for 7-9 visits. The female kept the nest clean of any dirt that fell in among the eggs, and removed broken eggs to such a distance that we did not find any of four we damaged. Removal of eggs during the laying of the clutch and after the clutch was completed had no effect on the number of eggs laid.
  14. Hatching was delayed in nest No. 1 when the eggs were soaked in ice melt-water from the fourth to the sixth day after the clutch was completed, but the embryos were not killed. One malformed nestling (perhaps the result of the chilling) was later ejected by the parents.
  15. Eggs were in the nest from 16 days for the first egg laid in nest No. 6, to a minimum of probably  $10\frac{1}{2}$  days for the fifth egg in the same nest. The usual period for eggs constantly incubated was 11 to 12 days. One egg in each of nests Nos. 2, 7, and 13, and three eggs in nest No. 10 were infertile. These eggs were left in the nest by the parents until the young left.
  16. In some nests all eggs hatched during the same 24-hour period (Nos. 3, 6, 7, and 13), and in others hatching extended over as much as 48 hours (Nos. 1, 11, and 14), or possibly 64 hours (No. 2).
  17. The male took at least as large a part in the feeding of the young as did the female; and in nests Nos. 3, 6, 8, and 12 the male was more active than the female in feeding during the early morning and all evening, when the young were 3-5 and 6-8 days old.
  18. Twenty-two nestlings left the nest after 9 days, 12 left after 10 days, and 3 left after 8 days in the nest. All left 2-3 days before they could fly. Nestlings were essentially silent until the last day in the nest. They had dorsal down on hatching, feathers on their backs at four days (when their eyes opened) and were fully feathered by the seventh to eighth day. Young left the nest from 12-24 July. Our records indicate that the young left within 24 hours of each other in four nests, and within 48 hours of each other in five nests.
  19. Sixty-nine eggs were found, of which 10 were destroyed by us or by a dog with us. Of the remaining 59 eggs, 6 were infertile and 5 abandoned; one young was deformed and pushed out, and three young disappeared. Forty-two young left the nest (we took two specimens). Eight (perhaps 9) of the 15 nests successfully fledged all of the young from the full clutch. Thirteen nests, or 86 percent of the total, hatched one or more eggs. The average number of eggs that hatched in successful nests was four; 75 percent of the eggs produced fledged young.

#### *Snow Bunting*

1. We arrived when birds were paired, but nest-building had not started.
2. Four nests were in holes excavated into loose sand on exposed ridges or vertically-cut banks of the river. One nest was under a boulder.
3. We found 2 (6) and 1 (5) clutches completed 23 June to 3 July.
4. The female at nest No. 3 repeatedly left the nest to feed, but also

begged for food from the male. This same male performed a pre-pairing display to her when there were four eggs in the nest.

5. The young in the nest were as silent as nestling larks and longspurs, but were noisy after they had left the nest. Both parents fed the young.
6. Of five nests found, only two were successful. We found one group of eight young with two sets of parents.

### *Ecology*

1. Except for plovers, only single representatives of a genus were found in our district.
2. We saw no ecological competition among the four passerine species. Territory was largest in Horned Larks ( $\frac{1}{4}$  sq. mile) and smallest in Lapland Longspurs ( $\frac{1}{2}$  acre).
3. We found no special adaptation in Lapland Longspurs (i.e., different from closely related longspurs) which would prepare them to occupy their northern range.
4. All four species walk and have a long hind claw which must be regarded as functional and therefore of no systematic importance.
5. Clutch-sizes show no greater annual productivity in the north than do multiple-brooded, smaller-clutched populations in the south. Adaptation has concentrated the breeding season.
6. No particular time in the breeding cycle is critical with regard to the food supply thereby controlling clutch-size. Food is a critical factor when the species arrives, when there are young in the nest, and especially when the young fledge and the parents molt.
7. An important force selecting annual productivity in arctic breeders is the danger of climatic—non-density dependent—disasters.
8. The advantage of single-broodedness is that recently-fledged but incompetent young are less subject to abandonment than when the female starts a second brood.

### *Behavior*

1. Lapland Longspur behavior is close to published descriptions of Yellowhammer in most of its features, and differs in several details from other longspurs.
2. We found bill-raised run (Andrew) associated with song period, and wing-vibration associated with precopulatory flight. Both drooping wings and upright posture were associated with sexual situations. The precopulatory posture we saw is described under another context by Andrew. Behavior does not yet clarify the taxonomic relationships of Lapland Longspurs within the buntings.
3. We found decrease in aggressiveness of territorial males after pair formation to coincide with intrusion on occupied territories by later males. This allows concentration of the population in the few suitable areas available, and may be an evolutionary mechanism permitting yearlings to establish territories later than adults.
4. In migratory birds, less well-motivated or inexperienced yearlings setting up territories are less subject to discrimination than are yearlings of resident species.

5. Nest site selection by longspurs gave insight into the form of the environment situation which they chose; i.e., sheltering overhang—whether moss hummock, grass tussock, frost-crack, or decumbent growth of Bell Heather.

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- Received January, 1959

## MIST-NETTING BIRDS ON ANDROS ISLAND, BAHAMAS

By LAWRENCE H. and CLARA M. WALKINSHAW

From the 16th to the 26th of March, 1960, we were on Andros Island, Bahamas, making a study of the birds in the area where we stayed. We hoped to capture the long elusive Kirtland's Warbler (*Dendroica kirtlandii*) by the use of mist-nets but failed to even see nor hear the species. However, we did have some luck in capturing other species.

The weather was very good but at times wind bothered. We operated from one to five nets for a total of 305 net-hours. Since the soil is chiefly coral and almost impossible to dig into and the fact that we were unable to get metal poles, we were forced to use long wooden poles improvised in position by ropes, stones, etc. We had much trouble with local wild dogs and at times cats (some of which were also wild). We captured only 105 birds.