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SEASONAL TRENDS IN SUMMER DIET OF THE LAPLAND LONGSPUR NEAR BARROW, ALASKA

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The Lapland Longspur (*Calcarius lapponicus*), near Barrow, Alaska, is the only major passerine in a terrestrial insectivorous guild which mainly consists of shorebirds. The guild includes four sandpipers of the genus *Calidris* (*alpina*, *melanotos*, *pusilla*, and *bairdii*), the American Golden Plover (*Pluvialis dominica*), the Ruddy Turnstone (*Arenaria interpres*), and the Red Phalarope (*Phalaropus fulicarius*). Other species that rely on arthropods but are irregularly or only locally present include the Snow Bunting (*Plectrophenax nivalis*) and eight additional shorebird species (Pitelka 1974). Jaegers, gulls, and waterfowl consume arthropods but their total impact is much less than the other species (MacLean 1969).

The diversity of potential habitats and prey for insectivores is extremely limited at Barrow (Holmes 1966). The terrain is a mosaic of poorly drained lowland and variably drained upland tundra broken by small ponds, lakes and streams. The predominant vegetation is grasses and prostrate sedges underlain with mosses and lichens (Britton 1957, Wiggins and Thomas 1962). Two families of Diptera (Chironomidae and Tipulidae) account for more than 80% of the insect biomass (Holmes 1966). The most conspicuous feature of the insect fauna near Barrow is the abundance of adult dipterans during July. Members of this order overwinter as larvae and, at least in the larger species, this stage lasts several years (MacLean 1973). Those that pupate in a given year emerge within a two-week period in early July (MacLean and Pitelka 1971). A detailed list of the arthropods at Barrow is provided by Hurd (1958).

Two studies concerning the shorebird community at Barrow demonstrate that four major *Calidris* species are strikingly similar in diet (Holmes and Pitelka 1968) and overlap widely in habitat usage (MacLean 1969). Competition among coexisting sandpipers is suggested by differences in bill lengths and other features of bill structure and by the observation that there are only four consistently abundant *Calidris* species at Barrow.

The main objective of this study was to provide dietary information on the Lapland Longspur that could be used in an energetic model to calculate number of prey items required per day to sustain existence (Custer 1974). Here we examine seasonal trends in the diet and then compare them with existing data from other members of the avian tundra community. Information on breeding density, reproductive success, and adult survival for longspurs at Barrow is presented elsewhere (Custer and Pitelka 1977).

METHODS

Information on longspur diet was obtained in two ways between 28 May and 20 August from years 1969, 1971, 1972, and 1973. First, male, female, and juvenile longspurs were collected within 10 km of the Naval Arctic Research Laboratory, Barrow, Alaska, and as soon as possible (usually within 5 min) a solution of 10% formaldehyde was injected into the stomach using a syringe inserted into the throat. The stomachs and esophagi of these birds were then removed and examined in the laboratory. Second, specimens of longspurs were obtained from lemming snap-trap lines (see Pitelka 1973). Due to postmortem decomposition of stomach contents in the snap-trap specimens, only food items in the esophagi were removed and examined.

The categories of prey identified in the food samples are listed in Table 1. The number of each prey type was determined either from whole individuals or the number of specific parts present in each stomach. The lengths of larvae were measured when possible.

Freshly collected living specimens of arthropods were frozen immediately and shipped frozen to Berkeley, California, for analysis. The specimens were dried in an oven at 70°C for 48 h and then weighed on a Mettler balance to the nearest 0.01 mg (Table 1). The mean weight of a crane fly (*Tipula carinifrons*) and of chironomid larvae, large numbers of which are eaten by longspurs, was estimated by using available length-weight regressions and averaging the weights for the lengths actually taken by longspurs.

Samples of adult and juvenile longspurs were pooled in the analysis of diet. This was necessary because of small sample size and missing age information for several samples. Combining age groups does not appear to bias the data since juveniles were not collected prior to 1 July, and comparisons between adult and juvenile longspurs for the periods 1–10 July and 11–20 July indicate that the diets are similar. Most of the samples from 1–10 August were of unknown age composition and all samples from 11–20 August consisted only of juveniles.

The dietary information is presented in two ways: (1) percent of diet by number of all food items present in all stomachs and esophagi (enumeration meth-

TABLE 1. Mean weight and correction factor for prey items taken by the Lapland Longspur.

Prey item	Mean dry weight (mg)	Correction factor
Collembola	0.06	5.0
Saldidae (immature)	1.57[a]	5.0[b]
Saldidae (adult)	3.05	3.9[b]
Carabidae (larvae)	2.60	5.0
Carabidae (adult)	5.90	3.9
Staphylinidae (adult)	1.20[a]	6.0
Chrysomelidae (larvae)	9.38	5.0[b]
Chrysomelidae (adult)	8.70	3.9[b]
Tipula (larvae)	10.66[c]	5.0
Male *Tipula* (adult)	7.39	4.3
Female *Tipula* (adult)	21.63	4.3
Pedicia (adult)	1.00[a]	6.5
Chironomidae (larvae)	0.17[d]	7.5
Other large Nematocera (adult)	0.93	5.0[b]
Small Nematocera (adult)	0.20	5.0[b]
Muscidae (larvae)	1.82	5.0
Muscidae (pupae)	1.90	5.0[b]
Large Brachycera (adult)	3.28	5.0
Small Brachycera (adult)	0.23	5.0
Tenthredinidae (larvae)	6.05	5.0[b]
Hymenoptera (adult)	0.20	5.0[b]
Arachnida	1.41	8.3
Nematoda	0.20[e]	7.5[b]
Luzula confusum (seed)	0.28	1.0[b]
Cerastium sp. (seed)	0.26	1.0[b]
Calamagrostris or *Luzula* (seed)	0.16	1.0[b]
Unidentified seed	0.20[e]	1.0[b]
Moss capsule	0.32	1.0[b]

[a] Data from Holmes (1966).
[b] Estimated using similar species.
[c] Data provided by L. Clement (pers. comm.).
[d] Data provided by D. Bierle (pers. comm.).
[e] Estimate used in calculation.

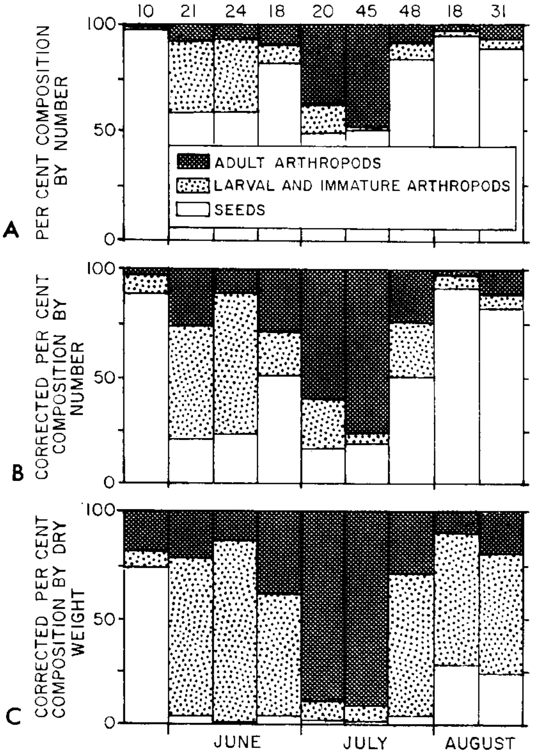

FIGURE 1. Diet of the Lapland Longspur in four summers (1969, 1971, 1972, and 1973) at Barrow, expressed in: (A) percent by number; (B) corrected percent by number; and (C) corrected percent by dry weight. Numbers above bars refer to the total stomachs and esophagi examined from successive time intervals.

od of Hartley 1948); and (2) percent of diet by dry weight, calculated by multiplying the number of items of each prey category by its respective dry weight (Table 1) and then expressing these values as a percent of total dry weight.

The stomach samples were corrected for differential digestion of prey items following the procedure of Custer and Pitelka (1975). In this procedure, seeds are held constant and other prey items are multiplied by their relative disappearance time in relation to seeds. The correction factor used for each food item is listed in Table 1. Esophageal samples were not corrected for differential digestion.

Diets of longspurs can be compared with those of shorebirds only on the basis of numbers of items present. Because shorebirds do not eat seeds and because Holmes and Pitelka (1968) did not correct for differential digestion, we adjusted the longspur data to make them comparable with the shorebird information. A single correction factor of 5.0 was used, as an average of the ratio of time over which seeds versus arthropods persist in the stomach (Custer and Pitelka 1975). Thus, values for seeds from longspur stomachs were divided by five and percent representations were newly obtained. Then, overlaps with the shorebird diets were calculated. In this way, the arthropod fraction of the longspur diet was adjusted to bring the numerical intakes of the two kinds of birds onto a comparable basis. The number of prey categories used to calculate overlap between longspurs and shorebirds included five immature categories (*Tipula* larvae, chironomid larvae, muscid larvae, muscid pupae, and coleopterous larvae) and seven adult categories (*Tipula*, other Diptera, Hymenoptera, Carabidae, Staphylinidae, Arachnida, and Collembola).

Percent overlap between longspurs and shorebirds was calculated by following the method of Holmes and Pitelka (1968), in which the minimal percent of each food resource shared by two species is summed. Thus, two species with identical resource usage would have an overlap of 100 and two with completely different resource usage would have an overlap of zero.

RESULTS

A total of 8,849 prey items were identified from 174 stomachs and 61 esophagi of longspurs. Figure 1A illustrates the percent composition by number of prey items divided into three basic categories (seeds, immature arthropods, and adult arthropods) in successive 10-day intervals of the summer.

When percent composition of the diet is corrected for differential digestion rates of various prey types, the significance of seeds drops (Fig. 1B). Percent composition by dry

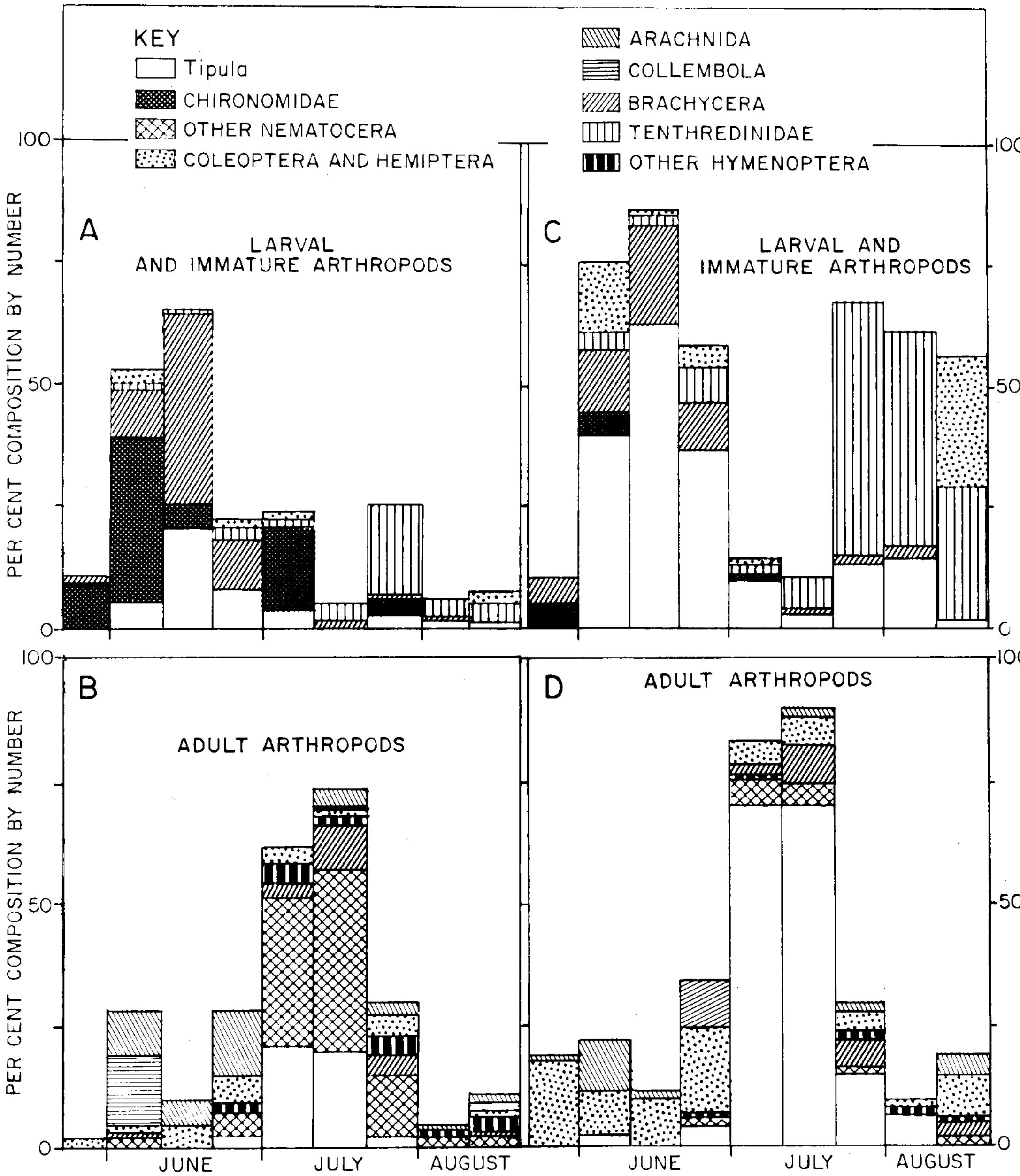

FIGURE 2. Corrected percent composition by number and by dry weight of the arthropod portion of the Lapland Longspur diet divided into major categories of adult and immature arthropods.

weight (Fig. 1C) further de-emphasizes the role of seeds in the diet. Seeds comprise a large part (70%) of the diet in late May when longspurs are just arriving at Barrow, and a moderate part (24–30%) in mid- and late August, but in June and July their contribution is slight (less than 6%).

Seasonal shifts in pattern of food consumption by longspurs are strong. As just shown, early and late in the season, seeds dominate the diet. Within the arthropod fraction, the birds shift in the intermediate time period (June and July) from larvae to adults, and then back to larvae (Fig. 2). The peak consumption of adult arthropods occurs during early and mid-July, a period that corresponds to the peak of insect emergence (Holmes 1966, MacLean and Pitelka 1971). Dipterous larvae dominate the arthropod portion from the beginning of the season until the end of June; dipterous adults dominate during early and mid-July; and hymenopterous larvae and adults dominate during late July and August. Certain other arthropod groups comprise considerable portions of the diet during particular periods. For example, spiders are important

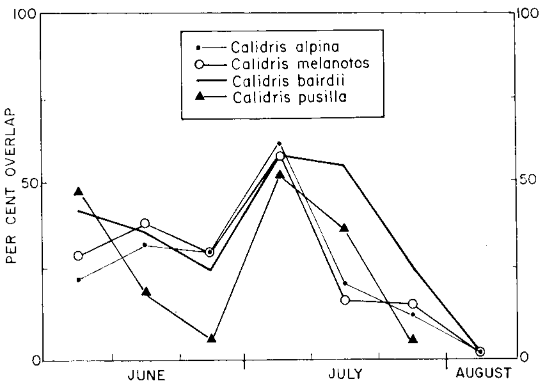

FIGURE 3. Percent overlap in diets (by number) of the Lapland Longspur with four sympatric sandpipers (*Calidris*).

during June. Additionally, collembola are taken in considerable numbers during the first part of June.

The seasonal shift just considered is even more strongly evident when the data are cast as percent dry weight (Fig. 2). During June, late July, and August more than half of the dry weight of the diet is composed of larval forms. In the intermediate period (1–20 July) more than 80% of the dry weight is adult arthropods. Most of the arthropod dry weight consists of dipterans and hymenopterans: from 1 June until 20 July, over 60% are Diptera; Hymenoptera predominate from 21 July until the end of the season.

On a dry weight basis, *Tipula carinifrons*, larvae and adults combined, is the single most important prey species during June and July (Fig. 2). During successive 10-day periods in these months, total percent dry weight of *Tipula* varied from 27.5 to 71.9 (mean 54.3).

Overlap of longspur diet with that of the four shorebirds on the basis of numbers of items is highest in early June and in the first three weeks of July (Fig. 3). Between 53 and 63% of the longspur diet is similar to that of all four shorebird species during 1–10 July, and 43 to 57% is identical to diets of the two smallest species (*C. bairdii* and *pusilla*) during 1–10 June and to *bairdii* during 11–20 July. In all other periods, overlap falls below 40%.

In the period of high dietary overlap, food items of several different types account for most of the similarity. During 1–10 June, chironomid larvae accounted for 28.8% of the overlap between longspurs and *bairdii*, and also between longspurs and *pusilla*. For the period 1–10 July, small adult dipterans, adult tipulids, and larval chironomids together represented 56.6, 56.8, 53.6, and 46.5% of the overlap between longspurs and *C. alpina*, *melanotos*, *bairdii*, and *pusilla*, respectively. During 11–20 July, small adult dipterans and adult tipulids accounted for 56.9% of the overlap between longspurs and *bairdii*.

DISCUSSION

We (Custer and Pitelka 1975) discussed the assumptions required to determine the correction factors used to adjust for differential digestion. In the current analysis, we further assume that the correction factors derived for the Snow Bunting can be used for the Lapland Longspur. For Barrow, this assumption seems to be reasonable because these closely related emberizine finches are relatively catholic in their diet and commonly feed in the same habitats. This is probably true of other locations where they exist together. For example, the major prey item fed to young longspurs and buntings on Devon Island was chironomid adults (Hussell 1972).

The seasonal shift in longspur diet is correlated with availability of food resources. Seeds appear to be the major item in the diet when the ground is largely covered by snow, at least locally shallow, and the temperatures are extremely low. Under these conditions, which occur during early and late summer, longspurs commonly feed off culms of exposed grasses. Low temperatures may inhibit arthropod movement, and under such circumstances, longspurs may shift from arthropods to seeds (Custer 1974). The ability of arctic insectivores to readily switch diet has been discussed by Williamson (1968) and Holmes (1966).

Though seeds are important early and late in the season, they are secondary to animal items in the overall summer diet of the longspur. This is perhaps a necessary consequence of the low energy value of the typically small seeds of arctic herbs. For example, more than 35 seeds are needed to equal the dry weight of one average-sized *Tipula* larvae (Table 1). Additionally, seeds are digested more slowly than arthropods (Custer and Pitelka 1975), and digestive efficiency for seeds may be lower than that for animal items (Bliss et al. 1973).

Of the animal items in the diet, larval dipterans predominate early and late, while adult dipterans predominate in July, reflecting the seasonal succession in availability (Holmes 1966). The biomass of adult insects on the tundra never reaches half that of larval insects even during peak of insect emergence (Holmes 1966). Nevertheless, longspurs and all four shorebirds heavily consume adult insects during this period.

The occurrence of *Tipula carinifrons* may be important in contributing to the success of longspurs at Barrow. This species is both abundant and heavy. Adults and larvae combined contributed 40 to 80% of the dry weight of longspur diet during June and July. In addition, *Tipula* occurs in upland sites (Holmes 1966, MacLean and Pitelka 1971), and its high positioning in the soil (1–2 cm from surface, Holmes 1966) from mid-June on makes it an easy prey for longspurs and other insectivorous birds.

Longspurs generally forage in upland, more or less dry sites (Drury 1961, Williamson 1968), whereas shorebirds generally forage in wet or soggy sites (MacLean 1966). This broad difference probably relates to their bill structures. With elongated bills, shorebirds can easily penetrate moist earth while longspurs, with a conical fringillid bill, must rely on surface food. But there is more overlap in diet between longspurs and shorebirds than these remarks would suggest and, during most of the summer, longspurs select kinds of food also used by the four shorebirds considered.

Early and late in the season longspurs rely on seeds, and in late July and August, they rely heavily on sawfly larvae (Tenthredinidae), which are not eaten by the shorebirds. Near Barrow, sawflies become active earlier (mid- to late June) than other Hymenoptera, and their larvae forage on prostrate willows (*Salix* spp.) chiefly on upland sites during late July and August (Holmes 1966). Large size and surface location makes them easy prey for longspurs. In contrast, late in the summer, shorebirds rely chiefly on chironomid larvae taken on mud flats and along pond margins (Holmes 1968, MacLean 1969).

Longspurs have a similar diet to some or all of the calidridines during two periods. In early June, their diet is much like that of the two smallest species (*bairdii* and *pusilla*) and only slightly like that of the two largest (*alpina* and *melanotos*). Similarity is not surprising at this time because snow cover limits the number of available feeding sites. Both the longspur and the two smallest shorebirds consume many chironomid larvae in early June. In contrast, the larger species take tipulid larvae. It appears that earlier in the season tipulid larvae are deep in the soil and only the longer-billed species are able to capture them.

In early July longspurs overlap more than 50% with all four *Calidris* species, as all rely heavily on the synchronous emergence of adult Diptera (Holmes 1966, MacLean and Pitelka 1971). Dietary divergence increases in mid-July, when longspurs still overlap extensively with *bairdii*, but only slightly with the remaining three species. During this period, longspurs along with *bairdii* and *pusilla* continue taking mainly adult Diptera, whereas, *alpina* and *melanotos* are taking mainly chironomid larvae.

We regard dietary overlap as potential evidence of competition, but it can also be taken as evidence against competition depending on availability of foods (Colwell and Futuyma 1971). To be meaningful in terms of competition, overlap values should take into account abundance of the avian species involved, their habitat separation, the energy requirements of each, and the relative abundance of the prey items comprising their diets. These cautions, however, do not preclude interpretation, albeit tentative and incomplete.

Comparisons of levels of overlap among these four shorebird species (see Fig. 5 in Holmes and Pitelka 1968) with those among longspurs and the same shorebird species (Fig. 3 here) reveal that the former vary between 40–90% whereas the latter vary between almost 0 and 57%. The shorebirds, with their graded bill sizes, will be considered elsewhere; here we comment only on the longspur's overlap with them.

Within the observed overall range of similarity (Fig. 3), values are intermediate early in the season when snow cover is still extensive and limited habitat is available. Such overlap as occurs results from common use of chironomids at pond margins and small arthropods on snow and exposed upland. Dietary similarity is low by late June when most habitats become available and species-specific separations with regard to food-type and feeding site are maximal. When adult Diptera emerge, surface food is so abundant that overlap peaks. Subsequently, it declines for the same reason as in late June (i.e., maximal diversity and availability of habitat sites), but falls yet lower in August as habitat and/or food become less available. Longspurs then turn to seeds and also eat insects in uplands, which are not used by shorebirds.

Although the overlap values may not directly reflect competition, and our present analysis is incomplete, we consider that competition for food is possible. This could most likely occur in early and middle June, and late July and August. The overlap values are lower than those among sandpipers (Holmes and Pitelka 1968), but they represent averages over time and thus do not reflect conditions of markedly variable weather which can modify and restrict the accessibility of foraging areas. Any adverse conditions triggering competition would be temporary and would most probably cause longspurs to interact with the two small calidridine sandpipers (*bairdii* and *pusilla*). Do competitive interactions occur frequently enough to affect densities reciprocally? If longspurs were absent, would the small sandpipers be more numerous? These questions cannot be answered now. The high values of overlap in early July simply reflect opportunistic convergence on an abundant food supply and cannot be regarded as evidence of significant competition.

These considerations of dietary overlap help to explain the presence and success of longspurs as the single abundant passerine in the avifauna near Barrow. Longspurs are the major seed-eaters on the open tundra. They also feed in relatively dry uplands, where they find a major prey item, *Tipula carinifrons*. (Shorebirds also forage in uplands and consume many of these insects, but as a group they forage more in lower, wetter areas.) Furthermore, in August longspurs feed on tenthredinid larvae, an upland resource not shared with any shorebird. Whether their food is insects or seeds, their small size and squat body enable comparatively easy maneuvering and searching in the low vegetation.

These factors favor longspurs, but do not explain why there is only one passerine. The explanation probably lies in the uniformity and simple structure of the flat, wet Barrow environment. Barrow is limited to a fraction of the overall range of habitats occupied by arctic passerines. A passerine in the Barrow area has to be a granivore-insectivore to cope with early and late season unpredictability in food. Near Barrow the habitat is a locally complex but repeated mosaic of variably wet microhabitats. Longspurs occur mainly in the "upland," better drained end of this habitat gradient. The habitat needs of other seed-eating passerines are not met either for the locally occurring Snow Bunting or for other species occurring as breeders 25 km or more inland (see Pitelka 1973 for candidates). Furthermore, it seems unlikely that the Barrow longspur habitat could regularly accommodate more than one fringillid species. First, the physical variety of sites from which longspurs glean seeds or insects is limited; second, the size range of available seeds and surface insects is fully used by longspurs; and third, the interdigitation of habitats occupied by longspurs is small-scale, tight, and repetitive, hindering the spatial subdivision usually seen when similar species co-occur. The presence of shorebirds in upland tundra may also act against subdivision of longspur habitat.

SUMMARY

Contents of Lapland Longspur stomachs and esophagi were sampled near Barrow, Alaska, from May to August, in 1969, 1971, 1972, and 1973. Data from stomach contents were corrected for differential digestion of prey items.

Longspurs shift seasonally from larval to adult arthropods and back to larvae, responding to changes in the abundance of these prey items. Seeds are a vital supplementary food in late May and August, when arthropods are scarce or inaccessible.

One species of crane fly is the major dietary component for longspurs during June and July. Its high abundance and substantial dry weight per individual may contribute to the success of longspurs at Barrow.

The diets of longspurs and four common shorebirds (*Calidris* spp.) at Barrow are similar in the range of prey items taken except for seeds and tenthredinid larvae. Their diets overlap closely when feeding sites are restricted because of snow and surface water (chiefly at the beginning of the season) and when prey is abundant in early and mid-July. Competition is possible early in the season but unlikely in July when surface insects are superabundant. In addition to exclusive fractions of diet, habitat separation and the advantages of fringillid form apparently contribute to the success of longspurs in a tundra community of insectivores dominated by shorebirds.

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