

# Diet of three sympatric species of granivorous songbirds in a Norwegian high mountain area during the early breeding season

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**Abstract.** Stomach samples of Lapland Longspur *Calcarius lapponicus*, Snow Bunting *Plectrophenax nivalis*, and Horned Lark *Eremophila alpestris* were collected at Hardangervidda in an early phase of the breeding season (during egg-laying and onset of incubation) in 1974. Our analyses of diet composition found that plant material, mainly seeds, made up 90, 95 and 97% by number of items, and 49, 66 and 83% by dry mass, in the diets of Lapland Longspur, Horned Lark, and Snow Bunting, respectively. Seeds of *Potentilla*, *Luzula*, different Caryophyllaceae, and *Omalotheca* were important foods for all three species. Seeds of *Empetrum* were only found in longspurs and buntings, and fragments of Bryophyta were abundant only in the Horned Larks. Arthropoda were dominated by adult Coleoptera (in particular *Patrobus* spp., *Helophorus glacialis*, and *Otiorrhynchus dubius*) and Diptera larvae (notably Tipulidae), and were taken by all three species in small quantities by number of items but made up 51, 34 and 17% by dry mass in the diets of Lapland Longspur, Horned Lark, and Snow Bunting. Food overlap compared asymmetrically between the species ranged from 0.49 to 0.74 by number of items and from 0.43 to 0.74 by dry mass (scale from 0 to 1.0). Recent population declines in Lapland Longspur and Snow Bunting but increases in Horned Larks may have affected interspecific food competition among the three species early in the breeding season. The food overlap has presumably increased over the last decades due to a longer-lasting snow cover over the nesting habitats of longspurs and buntings which has been a result of increased precipitation due to climate change.

**Keywords:** climate change, diet composition, interspecific competition, mountain birds, niche overlap

## INTRODUCTION

Five species typically comprise the majority of the breeding passerines in mountain areas above tree line in southern Norway: Meadow Pipit *Anthus pratensis*, Wheatear *Oenanthe oenanthe*, Horned Lark *Eremophila alpestris*, Lapland Longspur *Calcarius lapponicus*, and Snow Bunting *Plectrophenax nivalis* (Lien et al. 1974). Whilst Meadow Pipits are entirely insectivorous and Wheatears primarily so although they do ingest berries, the three other species are mainly granivorous during the non-breeding season but switch more or less to insectivory in the breeding season (Custer & Pitelka 1978, Cramp 1988, Cramp & Perrins 1994, Dierschke 2002, Hågvar et al. 2009).

Passerines arrive in the last days of April and early May at the Hardangervidda mountain plateau in southern Norway. At that time, snow cover is substantial, with limited patches of bare ground found only on hilltops and ridges (Figure 1). Snow-free areas often constitute less than 10% of the ground (Byrkjedal 1980a). Although the five species of songbirds are to some extent segregated by habitat and altitude, they also exhibit a large degree of habitat overlap (Østbye & Framstad 1987). Horned Larks are the first of the five

species to establish breeding territories, which they hold on the small snow-free patches on dry hilltops. Here the vegetation is dominated by lichens, *Juncus trifidus*, *Empetrum nigrum* and similarly low vegetation which is their favoured nesting habitat (Haftorn 1971, Østbye & Framstad 1987). Lapland Longspurs and Snow Buntings frequent open patches for feeding while waiting for their preferred nesting habitats to thaw out from the snow. Lapland Longspurs nest in areas with *Salix* or *Betula nana* shrubs growing in landscape depressions, whereas Snow Buntings typically nest in talus slopes or in boulder fields (e.g., Cramp 1988, Cramp & Perrins 1994, Fjeldheim et al. *manuscript*). Depressions in the landscape accumulate substantial snow depth over the winter. Stony ground can be wind-swept for snow, but snow and ice often remain among the stones, blocking entrances to potential nesting sites and may hence postpone the onset of breeding.

A similar food ecology of the Horned Larks, Lapland Longspurs, and Snow Buntings could make them competitors for food resources, as pointed out by Tisell & Berglund (1992). These authors dismissed food competition as significant, however, due to the different breeding habitats of the species. However, snow cover early in the season may force the three



Figure 1. View of the collection site on 2 June 2019, showing the snow conditions at the time when the first Horned Larks have nests and Lapland Longspurs and Snow Buntings wait to establish territories. The snow-free ground consists primarily of the *Juncus trifidus*-lichen community, the most frequently used nesting habitat of Horned Larks. Nesting habitat of Lapland Longspur is mainly in depressions and leeward slopes, here covered by snow.

species to feed in the same snow-free habitat, which is a limited resource with a restricted distribution. Thus, interspecific competition during the early stages of the breeding season might be substantial and according to our own observations, could also last for 2–3 weeks.

In 1974, Lapland Longspurs, Snow Buntings, and Horned Larks were collected for scientific purposes at the beginning of the breeding season by researchers affiliated with the Museum of Zoology, University of Bergen. The stomachs of these birds were preserved and kept at the museum, and were made available to us for a comparison of the early season diet of the three species. Facilitating a comparison of dietary overlap, all birds had been collected in the same general area at Hardangervidda in southern Norway. Here, we describe the stomach contents of the collected specimens and then discuss possible competitive relationships among the three species.

## MATERIAL AND METHODS

The birds were collected under license during the 9-day period of 5–13 June 1974, and the sample was comprised of 39 Lapland Longspurs (23 males, 15 females, 1 unsexed), 14 Snow Buntings (10 males, 4 females), and 7 Horned Larks (3 males, 4 females). A majority of the birds were collected on 5 June (median dates 6 June for Lapland Longspurs, 5 June for Snow Buntings, and 8 June for Horned Larks). From nests found by IB in the late 1970s and the 1980s in and near the area where the birds had been collected,

Horned Larks were the first of the three species to start breeding, and Snow Buntings were the last. Dates of completed egg-laying were estimated by counting back from hatching dates and nest-leaving dates of young (IB unpubl. data). Laying interval between eggs is 24 h in all three species and duration of incubation is 10–11 days in Horned Larks, 11–13 days in Lapland Longspurs and 12–13 days in Snow Buntings. Young depart the nest after 8–12 days in Horned Larks, 11–13 days in Lapland Longspurs, and 12–14 days in Snow Buntings (Haftorn 1971, Cramp 1988, Cramp & Perrins 1994). The earliest Horned Lark nest was estimated to have completed egg laying by 15 May (median: 4 June; inter-quartile range: 29 May–10 June;  $n = 11$  nests). For Lapland Longspurs, the corresponding date was 30 May (median: 10 June; inter-quartile range: 7–12 June,  $n = 27$ ), and in Snow Buntings 15 June (median: 19 June; inter-quartile range: 18–20 June;  $n = 8$ ). According to the species' differences in phenology, the Horned Larks and Lapland Longspurs were likely collected at the time of egg laying or early incubation phase, while the Snow Buntings probably had not yet started to lay eggs.

All birds were collected at Hardangervidda at an elevation between 1000 and 1150 m a.s.l., at two sites near Dyranut and Halne (c. 60° 21' N, 7° 33' E; Figure 2). The sampling sites lie above the tree line, with habitat characterized by prostrate bush vegetation, bogs, and heaths with primarily sedges and lichens. For more details on habitat of the general area, see Byrkjedal (1989) and Erikstad et al. (1989).

The birds were transferred to a storage box

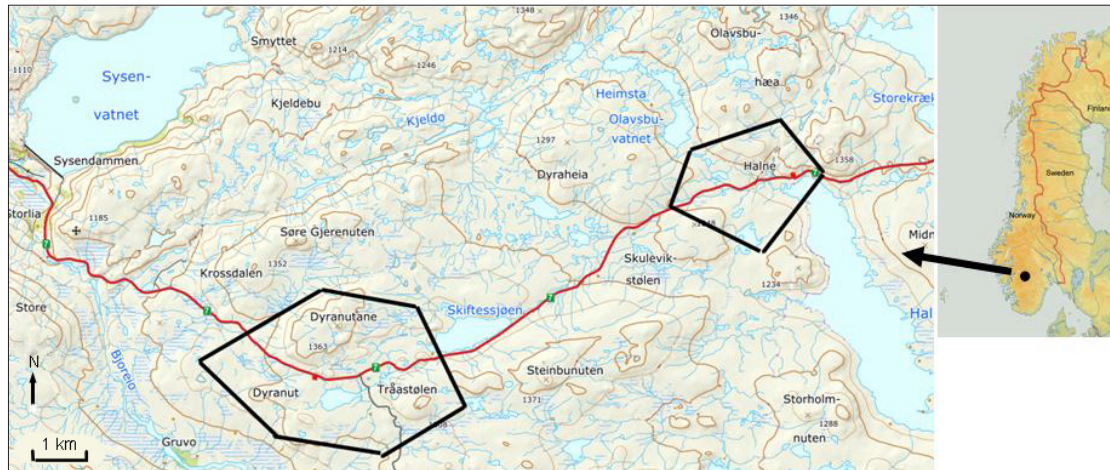


Figure 2. Collection sites at Hardangervidda, Norway, 5–13 June 1974. The birds were collected within the marked polygons.

containing dry ice (sublimation temperature  $-78.5^{\circ}\text{C}$ ) after being shot, but the handling time was not recorded. The birds were then stored in a deep freezer at the museum until they were skinned or prepared as skeletal specimens. During preparation, the birds' stomachs were removed and transferred to 70% ethanol for long-term storage. The thawing process added to the time the stomach contents were exposed to postmortal digestion.

Stomach contents were analysed more than forty years after their initial collection and preservation. The contents of each stomach were spread over a millimetre grid in a vial and examined under a binocular dissection microscope with a 6.4–40X magnification. Food items were identified to the lowest possible taxon, arthropods by comparison with a reference collection at the University of Bergen (UoB) and plant material by use of detailed descriptions of alpine flora (Lid 1963, Mossberg & Stenberg 2015) and by comparison to a reference collection of seeds at UoB. Quantification of items was completed separately for each stomach. Number of whole seeds were counted, while arthropods usually had to be counted from fragments, such as elytrae corners, insect heads, insect mouthparts, insect legs, or spiracle openings. The number of items of each taxon should be regarded as minimum numbers. For example, fragments of three anterior elytrae of a particular Coleoptera species were counted as two individuals if two were from left hand elytrae and the third one from a right hand elytra. Spiracle openings of Diptera larvae were divided by two to obtain a minimum number of individual larvae in a stomach sample. Dry weights (mg) from Byrkjedal (1980b) were used when estimating biomass of different diet items.

We compared food overlap by the MacArthur and Levins' Measure (MacArthur & Levins 1967, Krebs 1989):

$$M_{jk} = \sum^n p_{ij} p_{ik} / \sum p_{ij}^2$$

Here,  $M_{jk}$  is food overlap by species  $j$  on species  $k$ ,  $p_{ij}$  and  $p_{ik}$  proportion that food category  $i$  is of the total food categories used by species  $j$  and species  $k$ , and  $n$  total number of food categories. The index measures the food overlap of species  $j$  on species  $k$  and vice versa, instead of estimating a symmetrical overlap between species. The range of the measure was bounded from 0 (no overlap) to 1 (complete overlap).

## RESULTS

### Diet composition

The total number of food items (including seeds, moss bits, arthropod individuals) found in the stomach samples was 2469 for Lapland Longspurs, 1772 for Snow Buntings and 982 for Horned Larks (Table 1). Not included in analyses, number of gastroliths are given for completeness in Appendix 1. Based on the number of items (Table 1 and Figure 3), granivory was the main feeding mode for all three species early in the season. Plant remains comprised 89.2% of the diet items in Lapland Longspurs, 94.5% in Horned Larks, and 96.9% in Snow Buntings. The proportion of plant material was lower if calculated from estimated dry weights, viz. 49.3%, 65.9% and 83.3%. All the Lapland Longspur individuals had eaten both plant material and arthropods. All of the Snow Buntings had eaten plant material, but two individuals (14.3%) had not eaten arthropods. In contrast, all of the Horned Lark individuals that we examined had eaten arthropods, but one bird (14.3%) had no plant material in its stomach.

*Potentilla* was the most frequently recorded taxon of plants in all three bird species, with seeds found in 79–93% of the stomachs and constituted 26–33% of



Table 1. Diet composition of three mountain birds listed by lowest identified taxonomic levels.

Taxon	Lapland Longspur			Snow Bunting			Horned Lark		
	% of stomachs	% by items	% by dry mass	% of stomachs	% by items	% by dry mass	% of stomachs	% by items	% by dry mass
Bryophyta indet.	0.0	0.0	0.0	21.4	0.6	0.5	71.4	22.3	15.5
Selaginellaceae									
<i>Selaginella selaginoides</i>	10.3	18.8	10.4	14.3	6.9	5.9	0.0	0.0	0.0
Salicaceae									
<i>Salix</i> sp.	0.0	0.0	0.0	14.3	0.1	0.1	0.0	0.0	0.0
Betulaceae									
<i>Betula nana</i>	7.7	0.6	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Polygonaceae									
<i>Bistorta vivipara</i>	2.6	0.04	0.02	14.3	0.9	0.7	14.3	0.2	0.1
Caryophyllaceae									
<i>Stellaria cf. media</i>	0.0	0.0	0.0	7.1	0.3	0.3	14.3	12.0	8.4
<i>Stellaria longifolia</i>	7.7	1.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Cerastium</i> sp.	2.6	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sagina nivalis</i>	0.0	0.0	0.0	14.3	8.5	7.4	14.3	19.5	13.6
Ranunculaceae									
<i>Ranunculus</i> sp.	2.6	0.04	0.02	0.0	0.0	0.0	0.0	0.0	0.0
indet.	18.0	1.2	0.7	7.1	0.2	0.2	28.6	0.4	0.3
Saxifragaceae									
<i>Saxifraga stellaris</i>	0.0	0.0	0.0	7.1	0.7	0.6	0.0	0.0	0.0
Rosaceae									
<i>Potentilla</i> sp.	79.5	25.8	14.3	92.9	26.2	22.4	85.7	32.8	22.8
<i>Alchemilla</i> sp.	2.6	0.5	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Violaceae									
<i>Viola</i> sp.	2.6	0.04	0.02	0.0	0.0	0.0	0.0	0.0	0.0
Ericaceae									
<i>Empetrum nigrum</i>	43.6	4.2	2.3	57.1	6.0	5.2	0.0	0.0	0.0
Asteraceae									
<i>Omalotheca</i> sp.	15.4	5.3	2.9	42.9	36.5	31.5	14.3	0.3	0.2
Juncaceae									
<i>Juncus trifidus</i>	12.8	1.7	0.9	42.9	4.9	4.2	14.3	0.6	0.4
<i>Luzula</i> sp.	56.4	19.2	10.6	28.6	4.3	3.7	42.9	6.3	4.4

Cyperaceae	10.3	0.5	0.3	7.1	0.3	0.3	0.0	0.0	0.0	0.0	0.0
<i>Eriophorum angustifolium</i>											
<i>Carex bigelowii</i>	7.7	0.7	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Carex nigra</i>	2.6	0.5	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Carex cf. brunnescens</i>	51.3	6.3	3.5	21.4	0.2	0.2	14.3	0.1	0.1	0.1	0.1
<i>Carex</i> sp.	23.1	2.5	1.4	7.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera: Carabidae											
<i>Amara praetermissa</i>	2.6	0.04	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Calathus melanocephalus</i>	2.6	0.04	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Notiphilus aquaticus</i>	12.8	0.2	0.2	21.4	0.2	0.2	28.6	0.3	0.3	0.4	0.4
<i>Patrobis assimilis</i>	15.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Patrobis septentrionis</i>	7.7	0.1	0.8	7.1	0.1	0.7	28.6	0.3	0.3	3.0	3.0
<i>Patrobis</i> sp.	46.2	1.4	11.0	42.9	0.3	4.1	28.6	1.0	1.0	9.9	9.9
Coleoptera: Hydrophilidae											
<i>Helophorus glacialis</i>	20.5	0.5	0.2	0.0	0.0	0.0	14.3	0.2	0.2	0.1	0.1
Coleoptera: Staphylinidae											
<i>Arpedium cf. brachypterum</i>	5.1	0.1	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Arpedium</i> sp.	7.7	0.1	0.04	0.0	0.0	0.0	14.3	0.1	0.1	0.03	0.03
<i>Tachinus cf. elongatus</i>	2.6	0.04	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera: Scarabaeidae											
<i>Aphodius lapponum</i>	2.6	0.04	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera: Chrysomelidae											
<i>Phytodecta pallidus</i>	2.6	0.02	0.04	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera: Curculionidae											
<i>Othiorhynchus dubius</i>	71.8	3.4	24.3	21.4	0.2	2.5	71.4	1.7	1.7	15.7	15.7
Coleoptera indet.	25.6	0.3	0.2	0.0	0.0	0.0	28.6	0.4	0.4	0.3	0.3
Hymenoptera indet.	2.6	0.04	0.03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Insecta inagines indet.	2.6	0.04	0.04	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera larvae indet.	7.7	0.2	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidoptera larvae indet.	5.1	0.1	0.3	0.0	0.0	0.0	57.1	0.5	0.5	1.6	1.6
Diptera: Tipulidae larvae indet.	61.5	3.2	8.7	78.6	2.1	9.0	57.1	0.8	0.8	2.8	2.8
Diptera: Muscidae larvae indet	2.6	0.04	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera larvae indet.	5.1	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Insecta larvae indet.	7.7	0.1	0.3	0.0	0.0	0.0	14.3	0.1	0.1	0.3	0.3
Araneae indet	12.8	0.2	0.1	28.6	0.2	0.2	0.0	0.0	0.0	0.0	0.0
Opiliones											
<i>Mitopus morio</i>	5.1	0.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sample size	39 birds	2381 items	4462.9 mg	14 birds	1678 items	2054.4 mg	7 birds	983 items	1410.4 mg		

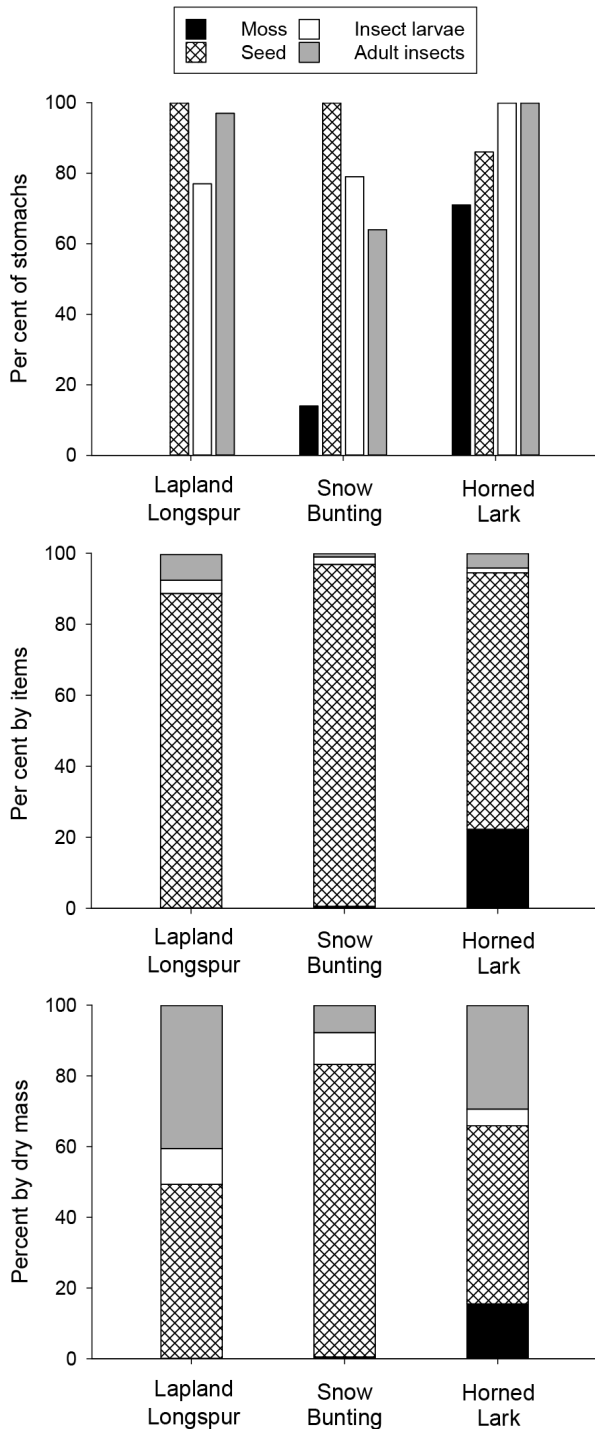


Figure 3. Stomach contents of three mountain birds in Hardangervidda, Norway, 1974. The category “Adult insects” includes Arachnida (Araneae and Opiliones).

the food items (Table 1). *Potentilla* is usually found on the dry hilltops with little snow cover. Other plant taxa found in all bird species included *Luzula* and *Juncus*, both plants mostly found on dry hilltops. Seeds of *Luzula* were found in 43–64% of the stomachs and constituted 19% of the food items in Lapland Longspurs, but only 6% and 4% in Snow Buntings and Horned Larks respectively. Seeds of *Omalotheca*,

which mainly grows in early snowbeds, were also found in stomach samples from all three bird species. All three bird species, but fewer of the individuals (10–21%), had eaten seeds of Caryophyllaceae (represented by *Stellaria*, *Cerastium*, and *Sagina*). In Horned Lark, seeds of *Sagina nivalis* and *Stellaria cf. media* (both mostly found in snowbeds) made up 32% of the food items. Seeds of *Carex* were found in many of the stomachs but constituted only traces in the number of items. *Carex* is comprised mainly of dry hilltop taxa, but also early–wet snowbed plants.

Seeds of *Empetrum* were found in the stomachs of 44% of Lapland Longspurs and 57% of Snow Buntings but in both species constituted <10% of the food items.

Fragments of mosses (Bryophyta) were abundant in the samples from Horned Larks. Mosses were present in 71% of the stomachs and made up 22% of the diet items found in Horned Larks. Three Snow Buntings contained moss fragments, but they made up only a trace of the Snow Buntings’ food items. No Lapland Longspur stomachs contained parts of mosses.

Coleoptera were numerically the most important of arthropod taxa, occurring in 64% of the Snow Bunting stomachs (1% of diet items), in 86% of Horned Lark stomachs (4% of diet items), and in 95% of Lapland Longspur stomachs (7% of diet items). The second most important group of arthropod taxa in numbers was Diptera larvae, recorded in 86% of the Horned Larks (0.8% of diet items), 79% of Snow Buntings (2% of diet items), and 67% of Lapland Longspurs (3% of diet items). When diet composition was compared by estimated dry weight, the relative importance of invertebrates increased in relation to seeds for all three species of birds (Figure 3).

#### Dietary similarity and interspecific overlap

When comparing the food items consumed by the three species, the similarity among species was more striking than the differences. Food overlap (Figure 4) calculated from the taxonomic levels used in Table 1, ranged from 0.49 (overlap of Snow Bunting by Horned Lark) up to 0.74 (overlap of Lapland Longspur by Snow Bunting) if based on number of food items, and from 0.41 (Snow Bunting by Horned Lark) up to 0.71 (Lapland Longspur by Horned Lark) if based on dry mass. Degree of overlap based on number of items versus dry mass showed similar patterns. A fairly symmetrical overlap was found between Lapland Longspur and Horned Lark and between Horned Lark and Snow Bunting, while Lapland Longspurs were overlapped more by the Snow Bunting than buntings by longspurs. The highest food overlap values were found between Lapland Longspur and Horned Lark, and in the Lapland Longspur’s overlap by the Snow Bunting (0.65–0.74 by items and 0.57–0.71 by dry

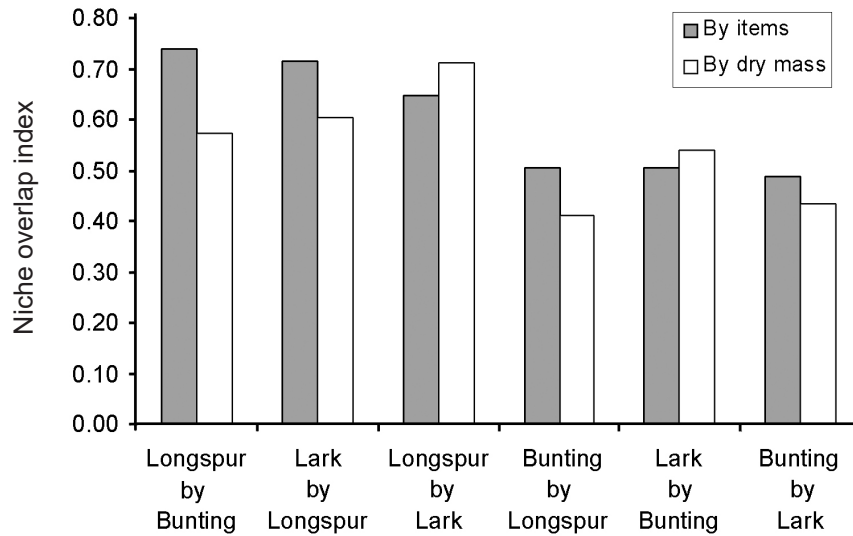


Figure 4. Food overlap (MacArthur and Levins' Measure) of species  $j$  by species  $k$  and of species  $k$  by species  $j$ , expressed by number of food items and by dry mass, calculated from taxonomic levels as given in Table 1. The species' names are given in an abbreviated form on the X-axis to improve diagram clarity.

mass), while overlap values of Horned Lark vs. Snow Bunting, and of Snow Bunting by Lapland Longspur were slightly lower (0.49–0.51 by items and 0.41–0.54 by dry mass).

## DISCUSSION

Analyses of stomach contents confirmed that Horned Larks, Lapland Longspurs, and Snow Buntings are mainly granivorous at the beginning of their breeding season, as they are during the non-breeding season, although they are known to change into feeding largely on arthropods during the summer (Cramp 1988, Cramp & Perrins 1994). The plant species composition of seeds, which all were produced during the previous growing season, was similar to previous reports summarized by Cramp (1988) and Cramp & Perrins (1994).

Horned Larks were found to ingest bits of moss in addition to seeds, as did a few individuals among the Snow Buntings. We have not found previous reports of either of these species feeding on moss, but Horned Larks are known to include shoots of *Carex* and buds of *Salix* in their diet early in the breeding season at Yamal, Siberia (Danilov et al. 1984) and bits of leaves are a regular part of the winter diet of Skylarks *Alauda arvensis* (Green 1978). Green vegetation eaten as additional food may be commonplace for larks in general (de Juana et al. 2004). Mosses are generally not eaten by herbivores presumably due to low digestibility and low energy returns (Prins 1982). However, mosses are found in the diet of some species of waterfowl and grouse (Anatidae and Tetraonidae) as well as some mammalian species living in cold environments,

and a possible reason is the mosses' high content of arachidonic acid, a polyunsaturated acid, which could contribute to improved cold tolerance (Prins 1982).

Seeds of *Empetrum* were found only in stomachs of the longspurs and buntings. However, Horned Larks have been reported to feed on *Empetrum* berries from the previous year during the early breeding season in Siberia (Danilov et al. 1984). Berries of *Empetrum* from the previous year's crop (still attached to the plant) emerging as the snow retreats have been found to be important in the diet of some shorebirds just after their arrival to their breeding grounds at Hardangervidda (Byrkjedal 1980b, 1989). Berries of *Empetrum* have been found in the diet of Lapland Longspurs and Snow Buntings in other studies (Cramp & Perrins 1984). However, whether the buntings had eaten whole berries or just extracted the seeds, as is the case with berry-eating Fringillidae, remains unknown. Almost half of the examined Lapland Longspurs and more than half of the Snow Buntings had *Empetrum* seeds in their stomachs.

The insects consumed by the birds were most frequently adult ground-living Coleoptera, which can occur abundantly in the area during the early part of the season (Erikstad et al. 1989), and larvae of Tipulidae, which live in the near-surface soil layer and in moss (Hofsvang 1972). These insect taxa and stages would be easily available to the birds while they are foraging on the previous year's seeds lying on the ground.

The relative proportions of food items changed to some extent when compared by dry weight rather than by number of items. Insects made up a somewhat larger proportion compared to plant material. Larvae of Tipulidae and some species of Coleoptera can have a dry weight more than ten times that of small seeds (cf.

Byrkjedal 1980b). However, in most of the insects here found, mainly Coleoptera imagines, the exoskeleton, which is indigestible to the birds, makes up a dominant contribution to the dry weight. To a varying degree, the inedible fraction also applies to husks of seed. Thus, dry weight of the food items recorded in this study may not reflect their nutritional value to the birds more accurately than number of items.

Overall, our study shows a similar early season diet among the three study species. The high dietary overlap clearly makes the three species potential competitors for food resources at the beginning of the breeding season when they must feed in the limited areas of snow-free patches. In the last few decades, breeding populations of Lapland Longspurs and Snow Buntings have declined severely in Norway, whereas Horned Larks have had a favourable population trend (Byrkjedal & Kålås 2012, Lehtikoinen et al. 2014, Byrkjedal & Högstedt 2022). Climate change has led to a general increase in precipitation, including greater snowfall at high elevations (Dyrrdal et al. 2013), and has increased snow depth in spring during the last few decades in the Norwegian mountains. The resulting late spring thaw may be a possible environmental cause for declines of longspurs and buntings. The two species have their nesting grounds covered by snow longer and are thus most likely forced to delayed breeding with possible lower reproductive outcome (cf. Gierow & Gierow 1991, Boelman et al. 2017), and in some places or years the seasonal delays may prevent individuals from breeding. Horned Larks may be less affected since the species is primarily found nesting on the snow-free windswept summits. Population increases among Horned Larks could largely be an effect of restoration of habitat in the major wintering grounds in the Wadden Sea area since the 1990s (Dierschke & Bairlein 2002, Byrkjedal & Högstedt 2022). Climate-related change in breeding habitat are probably the most important factor behind population trends in Lapland Longspurs and Snow Buntings, whereas changes in winter habitat are most important for the trend for Horned Larks. Nevertheless, interspecific competition might affect the changes in numbers of the three species under the following two scenarios.

First, if the gradual declines of both longspurs and buntings are due to snow cover, the Horned Larks may have become increasingly released from competition with these species, possibly with a positive effect on Horned Lark numbers. Alternatively, if the increase in numbers of Horned Larks is due to improved wintering survival, increased competition during the breeding season may have had negative effects on the longspurs and buntings. Being the largest bodied of the three bird species (mass of males; Haftorn 1971, Cramp & Perrins 1994), Horned Larks (males 32.5–46 g) might be physically dominant over Lapland Longspurs (22–27.8 g) and perhaps also Snow Buntings (28.4–42.5 g). Size-

based dominance fits with our observations of Horned Larks chasing Lapland Longspurs. The following two cases were specifically noted: (a) on 19 June 1977, a male Horned Lark chased after a Lapland Longspur male in Steinbuheii, (b) on 8 July 1977, a female Horned Lark attacked and chased a male Lapland Longspur. No skirmishes between Snow Buntings and Horned Larks or Lapland Longspurs were seen. Moreover, Horned Larks starting their breeding earlier than the others and occupying territories on the habitat used by all three species for early season feeding, provides an incentive for larks to be the most aggressive species. A combination of these two scenarios may act on the coexistence of the three species, strengthening their population trends seen over the last decades.

However, Lapland Longspurs have been far more numerous than Snow Buntings and until recently also far more numerous than Horned Larks in the region of Hardangervidda where the samples were collected. In the 8-year period of 1978–1985, territorial Snow Buntings and Horned Larks were recorded in the 7 km<sup>2</sup> Steinbuheii study area used for shorebird studies, and on average there were 4.8 territories of Horned Lark (3–7, Byrkjedal & Högstedt 2022) and 3.8 territories of Snow Buntings, giving 0.8 Snow Bunting territories per Horned Lark territory. A line transect census in the same general area in 1980 gave 124 territories of Lapland Longspurs versus 2 of Horned Lark (Byrkjedal & Kålås 2012), i.e., 62 Lapland Longspur territories per Horned Lark territory. No Snow Bunting territories were recorded on the line transect census, but the ratios from the line transect census applied to the 7 km<sup>2</sup> study area would indicate 78 Lapland Longspur territories per territory of Snow Bunting. Thus, Lapland Longspur would range far above the other two species in competitive potential from numbers alone, and the strong regional declines in numbers of Lapland Longspur since the 1980s may have benefitted Horned Larks, rather than an increasing number of Horned Larks having negative effect on numbers of Lapland Longspurs.

Our evaluations of competition rely on the assumption that the early season food of the three species is sampled representatively by the study. The number of stomachs sampled were relatively low for Horned Lark ( $n = 7$ ) and Snow Bunting ( $n = 14$ ). Moreover, the discussion also assumes that the availability of the insects and plants preyed upon in the actual area has not changed notably over the last decades. In this time span, not only the depth but the duration of snow cover in sheltered places have increased. The cover of lichens has increased noticeably, possibly due to reduced grazing pressure from a declining population of reindeer *Rangifer tarandus* and from less trampling damage to lichens from reductions in the grazing stock of domestic sheep (Strand et al. 2005, Byrkjedal & Kålås 2012). Possible effects on plant and



invertebrate communities by changes in snow cover, lichen cover, and mammalian herbivore populations could have impacted the ecology of terrestrial birds at Hardangervidda and would be worth future study. Effects of delayed thaw due to increasing precipitation falling as snow are expected still to continue. In the future, gradual rises in temperatures from climate change could shift spring precipitation from snowfall to rain, and the effect of delayed thaw could be reversed. However, in the long term increase rainfall would facilitate an uphill climb of bushes and trees (Myers-Smith et al. 2011), altering montane habitats profoundly.

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Appendix 1. Number of gastroliths (grit). All examined stomachs contained gastroliths, size ca. 1–2 mm across.

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	Average number of gastroliths per stomach	SD
Lapland Longspur (n = 39)	95.8	55.53
Snow Bunting (n = 14)	331.5	75.38
Horned Lark (n = 7)	176.6	131.56

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