Food habits and niche overlap in three alpine passerine birds, South Norway

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The three most common passerine birds in alpine habitats on the Hardangervidda plateau, South Norway, are the Meadow Pipit *Anthus pratensis*, the Wheatear *Oenanthe oenanthe*, and the Snow Bunting *Plectrophenax nivalis*. Analyses of stomach content showed that invertebrates are the main food of these species, but the Wheatear and the Snow Bunting also eat *Empetrum* berries, and the Snow Bunting becomes a seed eater in October when snow has arrived and the two other species have left the area. Seasonal changes in diet were related to phenological changes in the availability of food items. Adult Tipulidae were for instance taken by all species during the swarming period in July. Overlap in food choice was considered medium for all three species combinations. The Snow Bunting overlapped only slightly with the two other species in altitudinal distribution, habitat choice and territory. However, the Meadow Pipit and the Wheatear overlapped strongly in these parameters. Since their reproduction was successful, we assume that these two species can live together with strongly overlapping niches due to a surplus of available invertebrate food. All three species are able to change their food choice rapidly and are thus well adapted to manage unpredictable conditions in a harsh, high altitude ecosystem.

Key words: food habits; niche overlap; Meadow Pipit; Wheatear; Snow Bunting

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INTRODUCTION

In the high mountain habitats of Hardangervidda, South Norway, the three most common passerine birds are the Meadow Pipit *Anthus pratensis*, the Wheatear *Oenanthe oenanthe*, and the Snow Bunting *Plectrophenax nivalis* (Lien *et al*. 1974, Østbye *et al*. 2002). In the course of several years, stomachs were sampled from these species throughout the snow-free season. The stomach content of the Meadow Pipit was analysed by Hågvar & Østbye (1976) on a fresh weight basis. In a master thesis, Glesne (1982) studied the stomach content of Snow Buntings on a dry weight basis. In his calculations, he also introduced correction factors for varying digestion rates of different food items, which had been done by Custer & Pitelka (1975). The stomach content of the Wheatear was earlier poorly known, but has now been analysed in this study. In this publication, we will compare the composition of the stomach content of these three bird species based on common criteria. Adding information on their altitudinal distribution and differences in habitat use (Østbye & Framstad 1987, Lien *et al*. 1974, Østbye *et al*. 2002), we want to discuss niche overlap in these species, according to current knowledge. Alpine ecosystems may be favourable for such studies due to the limited species number of both birds and food items.

Niche overlap in alpine passerine birds has earlier been described mainly on the basis of habitat utilization (e.g. Winding 1990, Landmann & Winding 1993, 1995a,b). Our study also contains detailed information on food choice during the different months they stay in the mountain area.

MATERIAL AND METHODS

Birds were shot on the Hardangervidda mountain plateau between 1968 and 1978, mainly near Finse (60º36'N–7º30'E), but also at Stigstuv (60º18'N–7º45'E). Both sites are approximately 1200 m a.s.l. Snow Buntings were sampled only in the Finse area and mainly at slightly higher altitudes than the two other species (1250-1450 m); including areas close to Hardangerjøkulen glacier. The number of stomachs collected in different months is shown in Table 1. Samples were taken during the first half of the month, except for the «June» and the «July» samples of Snow Buntings, which were made between 25 May and 2 June, and between 20 June and 10 July, respectively. In September, Snow Buntings had started to flock but stayed in their breeding area. Most sampling days were without snow. However, in October, when the two other species had left the area and the ground was snow-covered, Snow Buntings were sampled from larger groups in lower valleys close to Finse.

The stomach content was conserved as soon as possible in 70 % ethanol. For Snow Bunting a 10 % solution of formaldehyde was inserted into the throat immediately after death. Fourteen of the Wheatears were killed in trap lines set for small rodents, which were checked twice a day. Invertebrates from these stomachs did not seem to be digested more than in shot birds.

Within each bird species, there was no significant difference in stomach content between males and females, nor between adults and juveniles after the youngsters had left the nest, therefore, these data were pooled. Stomach content was also studied in nestlings of known age: In six clutches of Snow Bunting, three clutches of Meadow Pipit, and a single nestling of unknown age in Wheatear.

The material consisted of invertebrates and diaspores, often heavily fragmented. Using a magnification up to 100 x, and by making comparisons with an extensive reference material of invertebrates and diaspores from the same area, most fragments were identified. For each stomach, the minimum number of specimens within each taxonomic group was noted by counting the number of wings, heads, legs, pedipalps, jaws or other chitinized fragments. In some cases, the actual species could be identified, in other cases only the genus, family or a higher taxonomic category. Insect larvae could usually be identified to family or order, and were sometimes surprisingly intact.

The total length of each invertebrate specimen was estimated from the size of the fragments, using reference material. Usually, the dry weight could then be estimated, either from our own reference data or from literature (Hofsvang 1973, Hågvar & Østbye 1974, Hågvar 1975). If no

Table 1. Number of stomachs studied from each species in different months. Birds were collected during several years.

Species	Years	Total	June	July	August	September	October
Snow Bunting	1976-78	79	16	10	26	10	17
Wheatear	1968-73	85	3	24	38	20	
Meadow Pipit	1968-71	88	15	25	21	27	

weight data were available, we made estimates from species of similar size. For Lepidoptera identified only by the presence of wing scales, the weight of the apparently most common field species was used as an estimate. The dry weight of diaspores and plant parts were measured from herbarium specimens or estimated by comparison with similar diaspores. When diaspores of *Empetrum hermaphroditum* were recorded, it was assumed that the birds had picked whole berries. The number of berries was estimated based on a mean value of 7.5 small seeds in each berry. Then the mean dry weight of berries was used, and percentages in the tables are based on whole berries.

A general problem with analyses of stomach contents is the different digestive rate of hard and soft components. Custer & Pitelka (1975) measured the residence time of different prey items in the stomach of Snow Buntings and calculated correction factors on the basis of different digestion rates. In their procedure, the digestion rate of seeds was considered to be lowest and given the factor of 1, and the observed quantity of other items was multiplied by their relative disappearance rate in relation to seeds. Glesne (1982) used these correction factors to estimate the real composition of the food intake. We have, however, in the present paper chosen to present the raw data of what was observed in the stomachs. The reasons for this are: 1) Most correction factors used by Custer & Pitelka (1975) were rather similar, varying between 3.9 and 5. Therefore, the corrected composition of invertebrates do not differ very much from the observed relative values in the stomach. 2) Nearly all our invertebrate identifications were made on the basis of resistable chitinous fragments. Due to an extensive reference material, even small fragments could be enough for identification. This means that invertebrate individuals were recognized long after they had been strongly fragmented, in a state which might have been considered «unrecognizable» by Custer & Pitelka (1975). 3) We doubt that diaspores represent the less digestable component, since chitinous fragments of insects are very resistant to digestion. 4) Our main purpose is to demonstrate differences between bird species, as well as seasonal variations. If digestion rates are similar for each food category in the three bird species, the uncorrected data can be used in a relative way. 5) Since caloric values per mg dry weight vary between invertebrate groups, for instance according to the fraction of chitinous parts (which may be high in Coleoptera and low in insect larvae), even correct dry weight relationships are biased in relation to relative energetic content. Therefore, although we acknowledge the uncertainty with uncorrected data, we have not found any better alternative for the present purpose. These raw data may be modified later by others, if good correction factors are developed.

The occurrence of grit, bone fragments or other calciferous material was also noted. In Meadow Pipit and Wheatear, the number of stones and bones larger than about 0.5 mm were counted, and in Meadow Pipit they were also weighed.

Calculations of overlap in stomach contents were based on uncorrected dry weight percentages using the categories in Tables 2-3. In beetles, species level was used when available. If two bird species did not have any taxonomic group in common during a certain month, the overlap was zero. If two bird species had eaten the same taxonomic group, the lowest dry weight percentage was noted, since this represented the overlap. The overlap for all taxa in common were added to give the total overlap for two bird species in a given month (cf. Holmes & Pitelka 1968). An example will illustrate this: Two taxa are in common: Tipulidae and the beetle *Byrrhus* sp. Dry weight percentages for Tipulidae were 10 and 30 % in the two bird species, respectively, showing an overlap of 10 % (the lowest value). Dry weight percentages for *Byrrhus* sp. were 5 and 18 %, so the overlap was 5 %. The total overlap becomes 10+5 = 15 %. Obviously, if two bird species feed on the same taxonomic groups and the dry weight percentages are the same for each group, the overlap will be 100 %. Some collective categories were used in the comparisons: Araneida, Hymenoptera, Tipulidae imagines, larvae of Tipulidae, and larvae of Lepidoptera. However, certain more unprecise categories were not used, as «Coleoptera indet., other Nematocera, insect larvae and insect pupae». Unfortunately, the two earliest Snow Bunting samples (mean dates 29 May and 1 July) were somewhat earlier in time than for the other two species, but will be compared with June and July data sampled approximately one week later.

RESULTS

Stomach content of adults and juveniles

Stomachs of all three bird species contained a high diversity of invertebrates. Also plant diaspores were eaten, with the highest diversity in the Snow Bunting. Tables 2-3 give detailed information on the stomach content of the Wheatear and the Snow Bunting, while the diversity of food components in the Meadow Pipit was described by Hågvar & Østbye (1976). From June to September, invertebrates dominated the dry weight for all species, although the choice varied both during the season and between the species. In early October, when a snow cover usually established and the Meadow Pipit and the Wheatear had left the area, the Snow Bunting remained as a 90 % vegetarian, picking diaspores from available plants.

Figure 1 visualizes the main changes in stomach content during different months for each species, based on uncorrected dry weight data. The Meadow Pipit differed from the two other species by being an almost entirely invertebrate consumer. The highest fraction of diaspores was 3.2 % in September. While the two other birds periodically picked berries of *E. hermaphroditum,* only one single seed of this species was recorded in the Meadow Pipit material (August). A rather stable food element for the Meadow Pipit was Coleoptera, with more than 50 % dry weight in June and a gradually lower amount in later months. Among Coleoptera, the most important species was a ground-living species of Curculionidae, *Otiorhynchus nodosus* (named *Otiorrhynchus dubius* by Hågvar & Østbye 1976). *Helophorus glacialis* (Hydrophilidae) was an important supplement during its swarming period in June, and the rather large ground-living *Byrrhus* sp. (Byrrhidae) in July. Diptera made up about one third of the dry weight during swarming periods in July and September. Tipulidae dominated among Diptera in July, and Bibionidae in September. A feature very typical for the Meadow Pipit was a strong focus on Opiliones (*Mitopus morio*) in August and September, representing about 40 % of the dry weight.

The Wheatear also consumed a lot of Coleoptera from June to August, with 65 % dry weight dominance in July. The same three beetle species which were important for the Meadow Pipit were also relevant for the Wheatear, and in corresponding periods. In July, the food composition of the Wheatear and the Meadow Pipit had much in common, being dominated by beetles and Tipulidae. However, their food composition differed considerably during the other months. In June and August, the Wheatear ate a considerable amount of *Empetrum* berries. While the berries eaten in August had just ripened, berries eaten in June had overwintered. In September, the Wheatear still ate some berries, but the main focus shifted to larvae of Lepidoptera, which represented 70 % of the dry weight. Opiliones, which was very important for the Meadow Pipit in August and September, was eaten only in small amounts by the Wheatear during these months.

The Snow Bunting showed some similarities with the two other birds (Figure 1). Swarming Tipulidae were taken in early July, and Coleoptera (with *O. nodosus* as dominant species) made up one quarter of the dry weight during this period and in early August. The similarity with the Meadow Pipit ceases here, while we find further similarities with the Wheatear. Both the Snow Bunting and the Wheatear ate a certain amount of *Empetrum* berries. These were eaten in all months by the Snow Bunting, representing about 5-20 % of the total dry weight. The

Table 2. Composition of stomach content in adult and juvenile Wheatears from June to September. The contribution of each taxonomic group is given as percentage of dry weight, percentage of the number of food items eaten, and the percentage of stomachs containing this group. The number of Empetrum diaspores is based on whole berries. Values < 0.1 % are indicated by +.

	June			July			August			September		
	% of dry weight	% of number	% stomachs with this group	% of dry weight	% of number	% stomachs with this group	% of dry weight	% of number	% stomachs with this group	% of dry weight	% of number	% stomachs with this group
OPILIONES												
Mitopus morio				1.6	1.7	21	10.5	7.6	55	4.4	4.7	35
ARANEIDA	1.1	2.5	67	1.1	3.2	21	0.7	1.3	26	0.2	0.5	15
HOMOPTERA												
Auchenorrhyncha							+	0.2	3	+	0.7	5
Psylloidea				+	0.4	4						
Coccoidea	0.1	0.9	33							+	0.2	5
Homoptera, indet.										+	0.9	10
HETEROPTERA												
Tingidae							+	0.2	3			
Heteroptera, indet.							+	0.2	3	0.1	1.1	5
PSOCOPTERA							+	0.2	3			
PLECOPTERA				0.1	0.2	4						
DIPTERA												
Tipulidae				14.0	9.8	75	1.6	0.9	18	0.3	0.5	15
Bibionidae				0.1	0.4	4	0.4	1.1	5			
Other Nematocera				0.1	0.4	4	0.1	0.4	5	+	0.2	5
Muscomorpha	3.7	5.9	100	0.6	1.5	17	1.1	1.9	21	0.2	0.7	15
Diptera, indet.							0.1	0.3	5			
LEPIDOPTERA				5.3	3.6	42	4.6	2.7	66	2.7	2.5	45
COLEOPTERA												
Carabidae												
Carabus sp.				0.9	0.2	4						
Patrobus sp.	1.0	0.8	33	2.2	2.3	13	1.2	1.1	16	1.1	1.6	15
Notiophilus aquaticus	0.5	1.7	67	0.1	0.6	8	0.1	0.5	11	0.1	0.7	15
Bembidion sp.				+	0.2	4						
Hydrophilidae												
Helophorus glacialis	7.0	33.1	100	0.1	0.4	8	+	0.1	3	0.1	0.9	20
Staphylinidae	0.5	4.2	33	0.3	3.6	25	0.7	7.6	32	0.4	6.9	20
Byrrhidae												
Byrrhus sp.	5.4	1.7	67	18.1	7.0	71	3.7	1.3	32	0.3	0.2	5
Simplocaria sp.	1.8	1.7	33	0.2	0.2	4						
Scarabidae?				0.2	0.2	4	0.1	0.1	3			
Cantharidae				0.2	0.2	4						
Chrysomelidae												
Chrysomela collaris	3.3	2.5	67	3.1	3.0	17	4.4	3.7	37	0.6	0.7	15
Curculionidae												
Otiorhynchus nodosus	23.2	15.3	100	39.1	31.4	92	20.1	14.1	74	2.0	2.2	35
Rhynchaenus sp. ?							0.2	0.2	3			
Coleoptera, indet.				0.2	0.2	4	0.4	0.8	11	0.1	0.2	5
HYMENOPTERA												
Bombus sp.							1.5	0.4	11			
Parasitica	2.9	6.8	100	3.9	18.4	71	4.3	26.4	92	0.6	4.2	55
Symphyta										0.1	0.2	5
Hymenoptera, indet.										1.4	5.6	15
INSECT LARVAE												
Lepidoptera				1.9	2.8	33	11.9	5.8	32	71.7	52.7	65
Coleoptera	3.0	2.5	33	+	0.2	4				+	0.2	5
Hymenoptera Symphyta				1.3	2.1	13	1.2	0.9	8	2.2	2.9	35
Tipulidae	1.2	1.7	33	0.3	0.2	4	2.4	2.2	8			
Bibionidae?							2.1	3.2	8			
Nematocera, indet.							0.5	2.1	3			
Muscomorpha	2.4	5.1	33	0.9	2.3	4	0.1	0.1	3			
Larvae, indet.	0.6	0.9	33	0.8	2.3	13	2.2	4.0	21	0.6	2.9	25
INSECT PUPAE												
Tipulidae	4.0	0.9	33	3.3	0.8	13						
DIASPORES												
Empetrum hermaphroditum	38.8	11.9	100				23.8	7.8	53	10.5	5.4	35
Other diaspores							+	0.6	5	+	1.3	20
TOTAL DRY WEIGHT (mg)	1009.9			4918.7			8689.9			7966.4		
TOTAL NO. OF ITEMS		118			472			951			552	

Table 3. Composition of stomach content in adult and juvenile Snow Buntings from June to October. The contribution of each taxonomic group is given as percentage of dry weight, percentage of the number of food items eaten, and the percentage of stomachs containing this group. The number of Empetrum diaspores is based on whole berries. Values < 0.1 % are indicated by +.

	June			**July**			**August**			**September**			**October**		
	% of dry weight	**% of number**	**% stomachs with this group**	**% of dry weight**	**% of number**	**% stomachs with this group**	**% of dry weight**	**% of number**	**% stomachs with this group**	**% of dry weight**	**% of number**	**% stomachs with this group**	**% of dry weight**	**%of number**	**% stomachs with this group**
OPILIONES															
Mitopus morio							15.9	0.8	50						
ARANEIDA	0.8	0.7	63	0.1	0.6	10	0.1	0.1	8	0.4	0.6	30	0.1	+	12
HOMOPTERA							+	+	4						
MECOPTERA															
Boreus sp.										0.2	0.2	10			
DIPTERA															
Tipulidae				32.5	18.3	90	5.2	0.2	8						
Diptera, indet.	0.6	0.1	13	5.7	5.5	20	0.6	0.1	15	2.2	0.8	20	7.5	0.6	18
COLEOPTERA															
Carabidae				2.4	1.8	30	0.3	+	4				0.7	+	6
Hydrophilidae															
Helophorus glacialis	0.1	+	6												
Staphylinidae							+	+	4						
Byrrhidae															
Byrrhus sp.	1.0	+	6	4.3	1.2	20	6.8	0.2	23						
Chrysomelidae															
Chrysomela collaris	0.4	+	6				6.2	0.4	35	3.0	0.4	20	1.6	+	12
Gonioctena affinis	1.2	0.1	13	0.9	0.6	10									
Curculionidae															
Otiorhynchus nodosus	3.4	0.2	44	14.3	8.5	60	12.1	0.6	58						
Coleoptera, indet.							0.9	0.1	8	3.0	0.4	20	0.8	+	6
HYMENOPTERA				2.2	14.0	70	1.1	0.6	65						
INSECT LARVAE															
Lepidoptera	43.5	2.0	44	20.5	7.9	30	20.8	0.7	54	73.8	5.4	20			
Coleoptera							0.3	+	4						
Tipulidae	22.5	1.1	81				1.7	0.1	4						
Larvae, indet.							0.5	0.2	4						
INSECT PUPAE	2.8	0.5	19	1.6	3.0	20									
BRYOPHYTA															
Polytrichum, fruit capsules				0.2	2.4	10	1.0	1.0	37	0.3	0.6	20			
Moss fragments	1.4	22.3	44				5.1	53.8	56	2.9	70.0	10	+	+	6
DIASPORES															
Anthoxanthum odoratum	1.0	1.6	31				0.1	0.1	7				14.9	8.1	59
Carex sp.	0.3	0.7	31				1.0	1.8	26	0.9	3.6	30	2.2	1.8	59
Juncus trifidus	1.9	17.9	19										9.7	29.6	41
Luzula spicata	6.5	22.5	75				0.6	1.3	22				0.8	0.9	29
Rumex acetosa	+	+	6										1.1	0.5	12
Polygonum viviparum	0.1	+	6	0.2	0.6	10	0.6	0.1	4	4.6	2.4	10	1.0	0.1	18
Viscaria alpina	1.4	8.6	38							+	0.2	10	14.6	29.6	41
Ranunculus sp.													0.1	0.1	12
Brassicaceae, indet.	0.1	0.4	6												
Saxifragaceae, indet.	0.4	17.7	6				+	0.8	11						
Sibbaldia procumbens	0.1	0.2	13				2.4	2.5	22	1.5	3.6	20	16.4	8.2	47
Rosaceae, indet.							2.4	2.5	7	1.8	4.4	20			
Empetrum hermaphroditum	10.0	0.3	69	15.0	4.3	40	13.5	0.3	37	5.0	0.3	30	18.3	0.2	71
Euphrasia sp.	0.1	0.5	13										9.9	20.1	35
Asteraceae, indet.	0.2	1.9	13				0.5	3.2	7	0.4	7.2	50			
Diaspores, indet.	0.1	0.2	?	0.1	3.0	?	0.5	28.7	?				0.3	0.2	?
Spermatophyta, fragments	+	+	?	0.1	28.0	10									
TOTAL DRY WEIGHT (mg)	2665.1			1269.8			3552.6			731.8			1396.2		
TOTAL NO. OF ITEMS		2853			164			5629			500			4589	

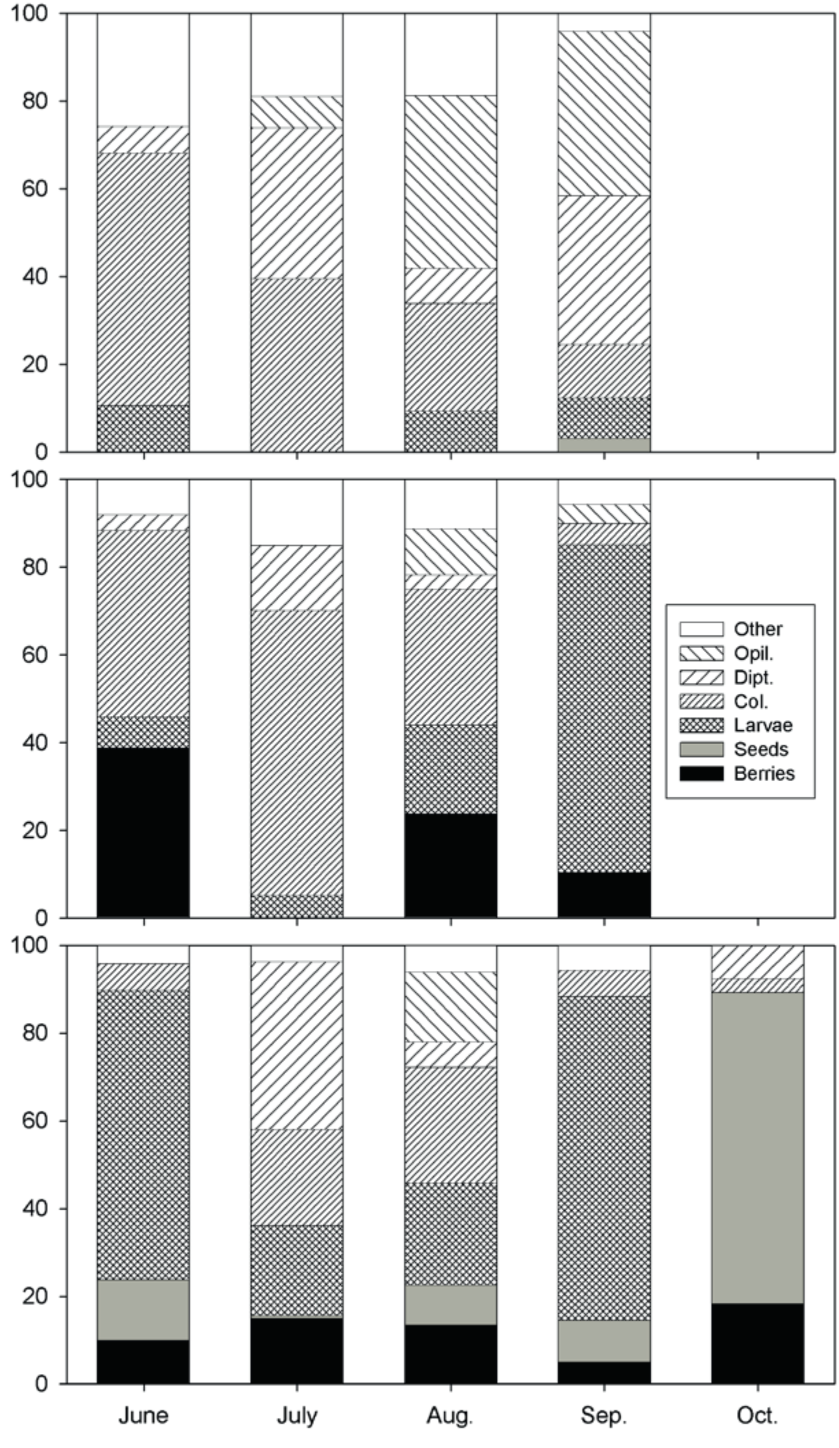

Figure 1. Composition of stomach content (%) in different months, based on uncorrected dry weight data from adults and juveniles. Upper row: Meadow Pipit. Middle row: Wheatear. Lower row: Snow Bunting. Only the main food items are shown: Berries, seeds, insect larvae, Coleoptera, Diptera, Opiliones, and other invertebrates.

Wheatear did not pick berries in July, but in all other months. The small material from the Wheatear in June contained a high amount of *Empetrum* seeds in two of the three stomachs. In August and September, the Snow Bunting and the Wheatear showed several similarities in the food composition, with a mixture of berries, Coleoptera, and Lepidoptera larvae in August, and a high dry weight dominance of Lepidoptera larvae in September. However, while two thirds of the Wheatear stomachs in September contained larvae of Lepidoptera, the apparent dominance of this group in Snow Buntings was mainly due to one stomach with as much as 27 larvae.

Two features separated the food choice of the Snow Bunting from the two other birds: Firstly, the Snow Bunting relied to a considerable degree upon insect larvae during the whole snow-free season. Lepidoptera larvae were continuously eaten, and Tipulidae larvae just after snow melt in June. Secondly, diaspores represented a continuous food element. When snow arrived in October, the Snow Bunting was able to shift to a nearly complete vegetarian diet.

Monthly overlap in stomach content is illustrated in Figure 2. The overlap between Meadow Pipit and Wheatear in June (42 %) was mainly due to a

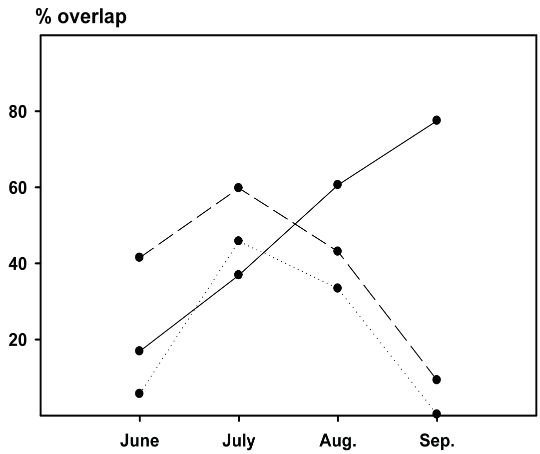

Figure 2. Overlap in food choice between species pairs during different months. Whole line: Wheatear and Snow Bunting. Stippeled line: Wheatear and Meadow Pipit. Dotted line: Meadow Pipit and Snow Bunting.

common interest for *Otiorhynchus*. The relatively high degrees of overlap in July for all species pairs (37-60 %) was due to a common preference for swarming Tipulidae as well as the two beetles *Byrrhus* and *Otiorhynchus*. In August, the Meadow Pipit still overlapped considerably with the two other species (33-43 %), due to a common preference for *Otiorhynchus* and Opiliones. In this month, we observed a still higher overlap (61 %) between Wheatear and Snow Bunting. This was caused by a common mixture of *Empetrum* berries, Lepidoptetra larvae, Opiliones and *Otiorhynchus*. The very high overlap (78 %) between these two birds in September due to Lepidoptera larvae, must be considered artificial since almost all larvae from Snow Buntings were found in one stomach. The two other species pairs showed very low overlap in stomach content during September. Disregarding the artificially high overlap between Wheatear and Snow Bunting in September, we may conclude that the overlap between the three species pairs is lowest early and late in the snow-free season. It is highest in July and August, when the production of invertebrates is highest.

Figure 3 illustrates how numbers per stomach vary throughout the season for separate food items. Evidently, certain invertebrates are in focus rather simultaneously in the three bird species. Correlations with activity peaks in the invertebrates will be discussed later.

Stomach content of nestlings

Stomachs from nestlings also contained a high diversity of invertebrates, but almost no diaspores. The largest material was from Snow Bunting (Table 4), with six clutches and 34 individuals in different age groups. The newly hatched nestlings in clutch 1 received mainly relatively small Diptera, but also a number of other invertebrates including small Hymenoptera. Large Tipulidae were rare, and Coleoptera with hard, chitionus bodies were almost absent. All the other five clutches, with nestlings older than 3 days, were to a high degree fed with rather large Tipulidae, and also the two common beetles *Byr-*

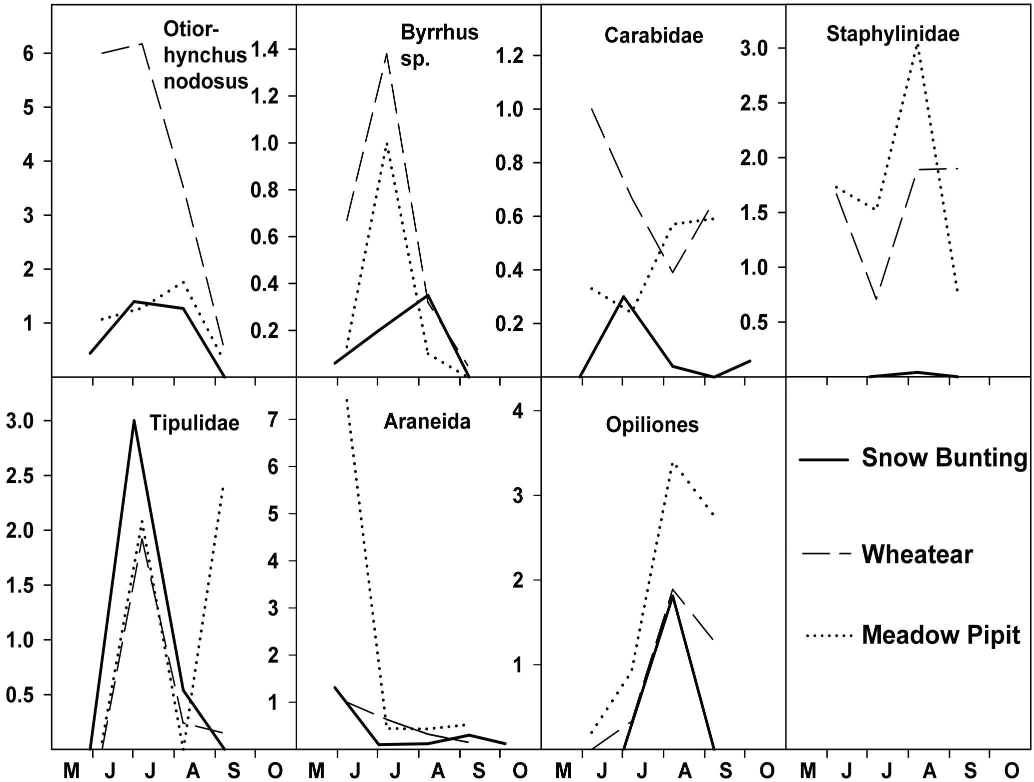

Figure 3. Seasonal variation in mean number per stomach of different prey items for each bird species.

rhus sp. and *O. nodosus*. Even insect larvae represented an important element in some clutches. Hymenoptera were often picked, but represented a low weight. A few *Carex* seeds and *Empetrum* berries were recorded. Some moss fragments may have followed accidentally. The stomach content of adults at the same time differed by having 15 % *Empetrum* berries, but otherwise showed similarities with nestlings through a combination of Tipulidae, Coleoptera and larvae of Lepidoptera.

Also in the two-day old nestlings of Meadow Pipit (clutch 1), large Coleoptera were absent, but such were given to older nestlings (Table 5). Both clutch 1 and the ten days old nestlings in clutch 2 were to a large degree fed with Tipulidae. This was an important food item also for adult Meadow Pipits at this time, in addition to Coleoptera (Figure 1). Clutch 3 with 10-11 days old nestlings were sampled nearly one month later (in early August), when adults to a large degree had shifted to Opiliones (Figure 1). This was also reflected in the nestlings by 26 % dry weight of this group. Bibionidae, which adults usually took in September, were evidently available as nestling food already in August this year. Food composition in Meadow Pipit nestlings in terms of numbers was given by Hågvar and Østbye (1976).

In the stomach of the single Wheatear nestling, the dry weight was dominated by Coleoptera and Hymenoptera (Table 5). About 80 % of the invertebrate numbers were small Hymenoptera and Staphylinidae.

Nestlings of Meadow Pipit and Snow Bunting overlapped 38 % in stomach content. This was mainly due to a common high percent of adult Tipulidae.

Table 4. Composition of stomach content in nestlings of Snow Bunting (six clutches). Percentage of dry weight and numbers are given for each taxonomic group. The number of Empetrum diaspores is based on whole berries. Values < 0.1 % are indicated by +.

Clutch No.	**1**		**2**		**3**		**4**		**5**		**6**	
Date	**22 June 1978**		**20 June 1978**		**5 July 1977**		**5 July 1977**		**10 july 1977**		**3 July 1977**	
Age	**0.5-1.5 days**		**3.5-5.5 days**		**3.5-5.5 days**		**6.5-8.5 days**		**8.5-9.5 days**		**13.5-14.5 days**	
No. of stomachs	**6**		**6**		**6**		**6**		**6**		**4**	
	% of dry weight	**% of number**	**% of dry weight**	**% of number**	**% of dry weight**	**% of number**	**% of dry weight**	**% of number**	**% of dry weight**	**% of number**	**% of dry weight**	**% of number**
OPILIONES												
Mitopus morio	5.4	10.0										
ARANEIDA	1.8	10.0	0.2	3.1	0.2	2.1						
ACARINA	+	1.3										
DIPTERA												
Tipulidae	7.2	2.7	63.8	59.8	57.4	45.8	77.9	80.0	29.3	21.4	60.0	61.1
Diptera, indet.	70.5	48.7										
COLEOPTERA												
Carabidae									3.3	3.6		
Byrrhidae												
Byrrhus sp.			4.0	2.1	28.2	12.5	8.8	5.0			9.8	5.6
Curculionidae												
Otiorhynchus nodosus					6.8	6.3	2.1	2.5	59.3	50.0	14.2	16.7
Coleoptera, indet.	1.3	0.7					1.8	2.5				
HYMENOPTERA	3.5	16.0	0.9	10.3	0.8	8.3	0.4	5.0	1.6	14.3		
INSECT LARVAE												
Lepidoptera	4.8	1.3	30.8	21.7	3.5	2.1			6.5	3.6	14.5	11.1
Tipulidae	2.4	0.7										
Larvae, indet.	1.2	1.3			2.6	6.3						
INSECT PUPAE	1.8	2.0	0.3	1.0							1.5	5.6
BRYOPHYTA												
Polytrichum, fruit capsules			+	1.0								
Moss fragments	+	5.3	+	1.0					+	7.1		
DIASPORES												
Carex sp.					0.5	16.7						
Empetrum hermaphroditum							9.1	5.0				
TOTAL DRY WEIGHT (mg)	828.8		1363.0		574.8		616.4		306.8		275.0	
TOTAL NO. OF ITEMS		150		97		48		40		28		18

The occurrence of small stones, bone fragments and egg shell fragments in stomachs

Small stones (grit) were often present in stomachs of all three bird species, both among adults/juveniles and nestlings. A detailed analysis for the Meadow Pipit (Hågvar & Østbye 1976) showed that 87 % of adults/juveniles contained grit, varying between 67 and 96 % in different months. Most of the grit was hard quartz. The mean number of stones per stomach with stones was 13, and the mean weight of stones was 2.1 mg. A total of 94 % of Meadow Pipit nestlings had stones in their stomachs, and a higher number per stomach than adults (19) but a similar weight per stone. All of the seven youngest nestlings, only two days old, had stones in their stomachs: a mean of 25.

Only 3 of 86 adult/juvenile stomachs from the Meadow Pipit contained bone fragments, and these were in low numbers. However, 7 of the 16 stomachs from nestlings (about 10 days old) contained bone fragments, in the mean 6 fragments weighing 31 mg. Among these was a 6.5 mm long fragment of a small rodent jaw with teeth (Hågvar & Østbye 1976).

Table 5. Composition of stomach content in nestlings of Meadow Pipit (three clutches) and one nestling of Wheatear. The number of Empetrum diaspores is based on whole berries. All data are percent of dry weight. Values < 0.1 % are indicated by +.

	Meadow Pipit			Wheatear
	Clutch 1	Clutch 2	Clutch 3	Clutch 1
Date	14 July	11 July	7 August	18 August
Year	1971	1969	1969	1969
Age	2 days	10 days	10-11 days	?
No. of stomachs	7	4	5	1
OPILIONES				
Mitopus morio	1.8	1.0	25.6	
ARANEIDA	0.7	1.0	0.3	3.2
HEMIPTERA				
Aphidoidea			0.1	
Heteroptera		0.9		
DIPTERA				
Tipulidae	55.7	35.7		4.2
Bibionidae			17.6	
Brachycera		1.3		
Muscomorpha		1.8		
Diptera, indet.	2.9	3.5		
PLECOPTERA	10.6			
TRICHOPTERA		2.6		
LEPIDOPTERA	3.0	16.6	15.1	
COLEOPTERA				
Staphylinidae	+			9.5
Byrrhidae				
Byrrhus sp.		7.0	3.8	28.6
Chrysomelidae				
Chrysomela collaris			7.7	
Indet.			2.3	
Curculionidae				
Otiorhynchus nodosus				13.8
Indet.		4.7		
Coleoptera, indet.				19.1
HYMENOPTERA	5.1	2.0	0.4	21.5
INSECT LARVAE	2.1	1.1	26.7	
INSECT PUPAE	10.7	19.4		
GASTROPODA	3.3	1.4		
DIASPORES				
Empetrum hermaphroditum	4.0			
TOTAL DRY WEIGHT (mg)	699.1	386.6	709.9	94.3
TOTAL NO. OF ITEMS	123	52	55	31

Among adult and juvenile Wheatears, the percentage of birds with grit decreased during the season, from 42 % in July to 24 % in August and 10 % in September. Two of the three individuals from June contained grit. The mean number of stones per stomach with stones was 18 in June, 5 in July, 8 in August, and 2 in September. Figure 4 shows the distribution of stone numbers in different individuals. The stomach from the single nestling contained 22 stones. Stones were not analysed further. Bone fragments were not recorded in Wheatear stomachs.

All adult and juvenile Snow Buntings contained grit but the stones were not counted. Calcium-rich organic material was present in 13 % of the stomachs in June (egg shell fragments), in 40 % of the stomachs in July (30 % with bone fragments and 10 % with egg shell fragments), and in 16 % of the stomachs in August (12 % with bone fragments and 4 % with a body shell from a fish). Also, all of the Snow Bunting nestlings contained grit in their stomach. Egg shell fragments were present in two thirds of nestlings older than 6 days (clutches 4-6), but absent in younger nestlings (clutches 1-3). Bone fragments were found in 80 % of the nestlings within clutches 2-5, but not in the youngest and oldest clutch. Mean number of bone fragments per stomach containing this item was 9, and the maximum number was 30.

DISCUSSION

Seasonal variations in food choice related to phenology of food items

Seasonal variations in the selection of certain food items were illustrated in Figure 3. Pitfall catches from five different habitats in the Finse area during three years (1969-71) allow us to compare the birds' food choice with seasonal variations in surface activity among Coleoptera, Araneida and Opiliones (Hågvar *et al*. 1978, Østbye & Hågvar 1996). We achieved surprisingly high pitfall catches in the pioneer ground, especially of Opiliones and Carabidae. Maximum occurrence of *Otiorhynchus nodosus* in the stomachs of all three bird species in June, July and early August corresponded with rather even, although small pitfall catches in several vegetation types during this period. In September, *O. nodosus* was practically absent from stomachs, and not taken in traps. This beetle is slow-moving and is more abundant than pitfall catches indicate. *Byrrhus* sp. is another large, slow-moving beetle which is eaten by all three birds. On sunny days, it may sit quite exposed on moss, on which it feeds. Small pitfall catches of *Byrrhus fasciatus* were taken in several vegetation types during June and July, in the period when it was eaten most frequently by the Meadow Pipit and the Wheatear. The Snow Bunting took a few specimens in June/July and early August.

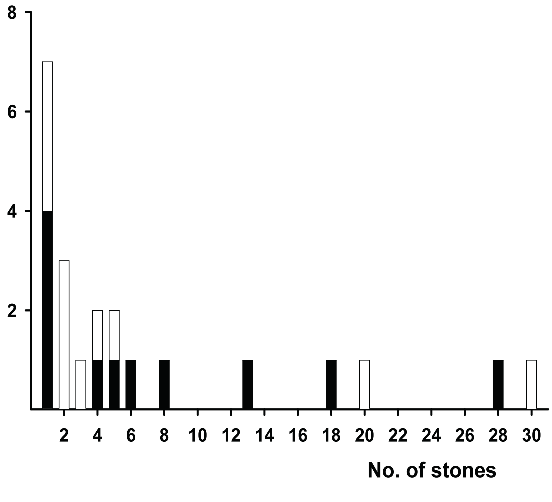

Figure 4. Number of stones in different stomachs of Wheatear. Adults: open columns. Juveniles: dark columns.

Carabid beetles showed a peak in activity in June and July after snow melt. However, most species, including the most abundant one in pitfall traps, *Patrobus septentrionalis*, are nocturnal (Ottesen 1985). This habit seems to be successful in avoiding bird predation, since Carabid beetles were never abundant in stomachs, and the three bird species did not show a common seasonal pattern in picking them (Figure 3). The small, diurnal carabid *Notiophilus aquaticus* was taken in low numbers throughout the season by the Meadow Pipit and the Wheatear. Staphylinidae were taken from June to September by the Meadow Pipit and the Wheatear. In pitfall-traps, maximum catches were usually recorded in July and August. These small beetles were nearly absent from Snow Bunting stomachs. The phenology described for different beetles was confirmed in an extensive pitfall-trapping in many habitats near Finse in 1985 by Ottesen (1996).

Araneida were typically most active in June and September, according to pitfall trapping. All three birds took most spiders in June (Figure 3) but selected other food items during the second spider peak in September.

The relevant species of Opiliones, *M. morio*, has a one-year life cycle in this area. All three birds took a good deal Opiliones in August (Figure 3), when this prey had reached a large size. While the Meadow Pipit and the Wheatear continued to eat adult Opiliones in September, this was not the case for the Snow Bunting. Pitfall catches of Opiliones could be high throughout the snow-free season, but the small individuals in June and July were evidently neglected by all birds. *M. morio* is active during the day and is easy to spot in late summer due to its size.

All three birds ate a considerable amount of adult Tipulidae in early July (Figure 3). This is the swarming period of *Tipula excisa* and *T. subnodicornis* (Hofsvang 1972, 1974, Hofsvang & Hågvar 1976). These large insects are easy to see, they fly slowly and can occur in large numbers. A third species swarming in September, *T. invenusta* (Hofsvang 1974), was taken only by the Meadow Pipit. It is interesting that after snow melt in May/June, the Snow Bunting picks large tipulid larvae, in a phase when these occur close to the soil surface, ready for pupation. Pitfall catches confirm that large tipulid larvae may even be actively moving around on the soil surface, and thus easy to spot by birds (Hågvar, unpubl.).

The beetle *H. glacialis* (Hydrophilidae) was taken by all three bird species during its activity period in June (Table 2-3, Hågvar & Østbye 1976).

These examples illustrate that phenological patterns in the abundance or activity of invertebrates can explain certain common patterns in food choice among the three bird species. We can add that the appearance of ripe *Empetrum* berries in August and September is appreciated by the Snow Bunting and the Wheatear, and even overwintered berries are eaten by the Snow Bunting. The Meadow Pipit, however, ignores these berries and continues to eat large Opiliones in September. It also favours late hatching Bibionidae. The present material therefore shows that not only similarities in food choice, but also differences, can often be explained by phenology of the food items. Availability is always the main point, and all three birds have a great ability to change food items rapidly. The highest degree of flexibility is shown by the Snow Bunting, which stays until October and then becomes a plant feeder (Figure 1), picking diaspores on wind-swept ridges with little or no snow. In spring, this bird arrives when the landscape is still snow-covered (between March and May), also then sitting on wind-swept ridges and evidently relying upon overwintered seeds still present on the plants.

The Wheatear's typical behaviour of flying from one large rock to another might indicate that mobile invertebrates were spotted from these perches. This is sometimes the case, as the bird may show a fly-catching behaviour, returning to the rock. Moving invertebrates on the ground are also evidently identified from such perches. However, apart from the swarming period of Tipulidae, most food items were on the ground and without movements seen from elevated sitting points (berries, and quiet or very slow-moving larvae or beetles). To a large degree, feeding demands a systematic search on the ground. Probably, the flying between large rocks is mainly a territorial behaviour.

The Lapland Longspur *Calcarius lapponicus* is the only major passerine bird on the tundra near Barrow, Alaska. The species also occurs in the Finse area, but in low densities. At Barrow, its diet shifts seasonally from larval to adult arthropods and back to larvae, responding to changes in the abundance of these prey items. In late May and in August, when arthropods are scarce or inaccessible, seeds represent a vital supplementary food (Custer & Pitelka 1978). The success of the Lapland Bunting at Barrow was mainly related to one species of crane fly (*Tipula carinifrons*) which had a substantial dry weight and swarmed in large numbers during June and July. Also four *Calidris* species in the area shifted to adult crane flies during these months (Holmes & Pitelka 1968). The food choice of the Lapland Bunting overlapped strongly with the *Calidris* species also very early in the season, when feeding sites were restricted due to snow and surface water, and the birds were forced to select among a limited number of food items. These five arctic birds on the Alaskan tundra confirm the feeding pattern of the alpine passerines at Finse: All species can change food choice rapidly, and may respond simultaneously when a food source becomes superabundant.

The importance of food size

In all three birds, the major dry weight each month was made up by large food items. The exception is the Snow Bunting in October, when mainly small seeds are available. The frequently eaten beetles *O. nodosus* and *Byrrhus* sp. are among the largest in the area. Adult Tipulidae and Bibionidae represent the largest Diptera at Finse. Opiliones are active throughout the season, but are chosen mainly when they have grown larger in August and September. The dry weight dominance of Lepidoptera larvae in Wheatear stomachs in September was due to 20 mm long larvae (about 20 mg dry weight), of which some were quite intact and could be identified as Pyralidae. These larvae typically occur among moss (Palm 1986), and large catches of adults in water traps during June indicate high populations at Finse (Gjelsvik 1994, Bahus 1995). The Snow Bunting picked large insect larvae (about 20 mg dry weight) throughout the snow-free season, mainly unidentified Lepidoptera larva, but also Tipulidae larvae from the uppermost soil in June. Also *Empetrum* berries represent large units, picked periodically by the Wheatear and the Snow Bunting. Several other studies have demonstrated the preference among birds for big food items when they are abundantly present, for instance in *Tringa totanus* (Goss-Custard 1977) and *Parus major* (Krebs *et al*. 1977). However, large food items may also be preferred although their abundance is relatively low, as shown for nestling diet in prairie passerines in Canada (Maher 1979).

Newly hatched nestlings of Snow Bunting and Meadow Pipit were fed mainly with easily digestable Diptera, and the large, chitinous beetles were avoided. The adults of all three bird species swallow the food unfragmented, as even large food items could be found intact in the stomach. The presence of grit in stomachs of both adults and nestlings shows the necessity of grinding large food items. It also helps to fragment calcium-rich elements such as bones and egg-shells. On Devon Island in the North American Arctic, Hussell (1972) likewise found that nestlings of Snow Bunting were mainly given easily digestible Diptera, small Chironomidae being their major food.

An approach to niche overlap between species

In addition to data on food choice, long-term studies exist on the distribution of these three birds in the alpine landscape on the Hardangervidda. In Table 6, overlap within species pairs have been considered as either low, medium or high for the following parameters: Altitudinal distribution, habitat choice by vegetation type, territory overlap, and food choice. Low overlap in one of these parameters may be sufficient to avoid competition.

Altitudinal distribution. Lien *et al*. (1974) presented bird surveys from Finse and Stigstuv on Hardangervidda through six years (1967-72), from four transects at altitudes between 1200 and 1500 m. The altitudinal distribution of each species varied somewhat between years, probably related to variations in population size and snow cover. However, the Meadow Pipit and the Wheatear showed similar altitudinal distribution in a given year, typically up to about 1350 m in three of the transects and up to 1500 m in a fourth transect. The Snow Bunting preferred higher altitudes, mainly above 1300 m in the three first transects, and above 1450 m in the fourth. After 19 years the surveys to a large degree confirmed this view, except that the Snow Bunting and Wheatear to a certain degree occurred together in the higher parts of the transects (Østbye *et al*. 2002, Østbye unpubl.). In alpine habitats at Nedal in Central Norway, Moksnes (1973) found a similar altitudinal distribution between the three species. In Table 6 we conclude that altitudinal overlap is high between Meadow Pipit and Wheatear, low/medium between the Snow Bunting and Wheatear, but low between the Meadow Pipit and the Snow Bunting.

Habitat choice. On the Hardangervidda plateau, long-term bird censuses have been made in several transects containing a mosaic of different vegetation types, as described by Lien *et al*. (1974). In the Finse area, where most of the present material was collected, the mean density during 19 years was 22 territories per km^2 of Meadow Pipit, 13 of Wheatear and 8 of Snow Bunting (Østbye *et al*. 2002). Østbye & Framstad (1987) showed that all three bird species had preferences for certain

Table 6. Degree of overlap in various niche parameters within three species pairs.

Niche parameter	Meadow Pipit/ Wheatear	Meadow Pipit/ Snow Bunting	Wheatear/ Snow Bunting
Altitudinal distribution	High	Low	Low/medium
Habitat choice	High	Low	Low
Territory overlap	High	Low	Low/medium
Food choice	Medium	Medium	Medium

vegetation types, and also that their preferences were significantly different. Most obvious was the preference of the Snow Bunting for pioneer ground with or without vegetation, which contained nearly half of the territories. In contrast, only 5 % of the Meadow Pipit territories and 11 % of the Wheatear territories were situated here. Although there were significantly different preferences for certain vegetation types between Meadow Pipit and Wheatear, both occurred together in a number of vegetation types. The two most common vegetation types, which were equally abundant and together covered 56 % of the ground, contained 50 % of the Meadow Pipit population and 61 % of the Wheatear population. One was Arctostaphyleto-Cetrarion nivalis Dahl 1956, an oligotrophic community on windswept ridges. Typical vascular plants are *Carex bigelowii, Empetrum hermaphroditum, Festuca ovina, Juncus trifidus*, and *Luzula spicata*. Typical lichens are various *Cetraria* and *Cladonia* species, and the habitat is often called a «lichen heath». The other common vegetation type was Cassiopeto-Salicion herbaceae Nordhagen 1936, usually called «snow bed» since it has a prolonged snow cover. The dominant plant is the tiny willow species *Salix herbacea*, growing on unstable, oligotrophic ground, mixed with the moss *Kiaeria starkei* (Lien *et al*. 1974). In Table 6, we conclude that habitat overlap is high between Meadow Pipit and Wheatear, but low between Snow Bunting and the other two.

Territorial overlap. Gjelsvik (1994) and Bahus (1995) showed that Wheatear territories at Finse were about ten times larger than Meadow Pipit terrirories (0.65-4.5 ha, and 0.1-0.4 ha, respectively). The smallest territories were situated in the most insect-rich sites. The Meadow Pipit territories lay for a large part within Wheatear territories, thus total overlap was rather the rule than the exception. In Table 6, territorial overlap between these species is noted as high. The Snow Bunting had very large territories, with an estimated mean of 11 ha in 1977 (Glesne 1982), and to a certain degree overlapping with the Wheatear in the higher parts of the landscape (overlap indicated as low/medium). In the early part of the breeding season in 1977, Snow Bunting was observed to chase away Wheatear in three cases, and the opposite in one case (Glesne, unpubl.), indicating some conflicts. Territories of Snow Bunting and Meadow Pipit almost never overlapped.

Food choice. Figure 2 shows that overlap in food choice varied significantly from June to September. In July and August, all species pairs showed an overlap in the area of 30-60 %, which can be considered as medium. From June to July, the overlap increased among all species. After this, the overlap between the Meadow Pipit and the two other species decreased. Contrary to this, the overlap between Wheatear and Snow Bunting continued to increase. As explained above, the high overlap in September is, however, uncertain. In Table 6, food choice overlap between all three species pairs has been considered medium, based on the entire season. This study illustrates well that food overlap between species may change considerably from month to month, and that food choice studies must cover the whole period when the birds are present.

Conclusion. While the Snow Bunting differs from the two other species in habitat choice, and from the Meadow Pipit in altitudinal distribution, the Meadow Pipit and the Wheatear overlap strongly in these parameters, and even in territories and food choice. How can these two birds occur together in such apparently similar niches? We assume that the answer is a surplus availability of food in periods with high overlap in food choice. If food resources had been a limiting factor, we assume that the territories of these two bird species would not have overlapped so strongly as they do. The period of highest dietary overlap, July, is when Tipulidae swarm in great numbers. Both species also find considerable amounts of the beetles *O. nodosus* and *Byrrhus* sp., which are surface active at this time. In June and August, the Wheatear takes a considerable amount of *Empetrum* berries, while the Meadow Pipit stays on invertebrates and takes a lot of large Opiliones in August. In September, the diet of the two species was very different, as the Wheatear relied heavily on larvae of Lepidoptera.

Competition between species demands that one or more resources are limiting. We have not been able to show any such limitations. As pointed out by Colwell and Futuyma (1971), dietary overlap is a potential evidence for competition, but it can also be taken as evidence against competition depending on availability of foods. The reproduction success of all three species is high at Finse, and often higher than other populations, indicating that food is in excess (Glesne 1982, Gjelsvik 1994, Bahus 1995). Perhaps food resources in principle could carry a much higher population of these mountain birds. However, because years can be variable and unpredictable with respect to hatching times of insects, weather conditions or the length of the snow-free season, periodically reduced availability of large invertebrates is possible. Therefore, the ability to change food habits rapidly, focusing on what may be available at any time, indicates good adaptations to harsh alpine conditions and could reduce possible competition in unpredictable, adverse situations.

Niche overlap and possible competition in arctic/alpine birds.

The identification of possible competition can be a difficult task. Competition can be time-limited, for instance occurring only very early in the season, or competition may occur for resources which are not measured, for instance suitable nesting places. In reality, the density, behaviour, habitat and food choice of the different species may be the result of earlier competition, having shaped the species to coexist.

When several coexisting bird species successfully raise most of their clutches, interspecific competition has not been a problem during the breeding period. In our case, a surplus of food seems to explain why the Meadow Pipit and the Wheatear can coexist despite overlapping considerable in food choice, sharing the same altitudinal gradient and even overlapping in territories. Clearly, a high niche overlap may exist without triggering competition, as long as food is superabundant and the bird densities are limited. Alpine and arctic environments often produce various groups of Diptera in huge amounts, for instance during swarming periods of Chironomidae or Tipulidae. Just as in our case, swarming Tipulidae periodically represent a superabundant food source in arctic Alaska, allowing four *Calidris* species and the Lapland Longspur to overlap strongly in food choice (Holmes & Pitelka 1968, MacLean 1969, Custer & Pitelka 1978). The *Calidris* species even overlapped strongly in habitat. Maher (1979) likewise observed a strong overlap in nestling diets of several praire passerine birds in Canada, and assumed that the availability of food was superabundant.

Several studies on arctic and alpine bird communities have demonstrated clear niche separation between species, either in food, habitat or both parameters. Finches and turdid birds on Himalaya are well distributed along the altitudinal gradient. Decreasing height, density and cover of vegetation with increasing altitude characterized the niche axis along which species were arranged. The two bird groups showed convergent evolution, with the heaviest and best flyers at the highest and windiest sites (Landmann & Winding 1993, 1995a,b). In North American alpine habitats, clear differences between bird species were found in habitat choice, but considerable overlap in food choice (Fleming 1973, Hoffman 1974, Conry 1978, Cody 1985). Conry (1978) concluded that these birds were typically generalists and opportunists, and that the only time when competition might take place would be in early spring with limited snow-free areas. The opposite situation was found by Fleming (1973) in a tropical alpine community in South America: The bird species overlapped strongly in macrohabitat, but differed in food choice. The fourth possible combination of habitat and food overlap, namely both different habitats and different food choice, was demonstrated between five passerine bird species in the high altitude Alps of Austria (Winding 1990).

Any study showing great niche overlap should be followed up by analysing whether any of the overlapping resources are limiting. One limiting factor may be sufficient to trigger competition, for instance the availability of nesting places. On the other hand, superabundance of a single parameter, for instance food, may be sufficient to avoid competition.

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SAMMENDRAG

Næringsvalg og nisjeoverlapp hos tre spurvefuglarter i sørnorske høyfjell

De tre vanligste spurvefuglene på Hardangervidda er heipiplerke *Anthus pratensis*, steinskvett *Oenanthe oenanthe* og snøspurv *Plectrophenax nivalis*. Analyser av mageinnhold viste at evertebrater er hovedføden hos alle tre artene, men steinskvett og snøspurv spiser også bær av krekling, og snøspurven blir en ren frøspiser i oktober når det er kommet snø og de to andre artene har forlatt vidda. Forandringer i føden fra måned til måned kunne i stor grad forklares ut fra vekslende tilgjengelighet. Voksne stankelbein (Tipulidae) ble for eksempel tatt av alle artene under svermeperioden i juli. Overlapp i næringsvalg ble ansett å være middels stor for alle tre artskombinasjonene. Snøspurven overlappet lite med de to andre når det gjaldt høydefordeling i terrenget, habitatvalg og territorium. Imidlertid overlappet heipiplerke og steinskvett sterkt med hensyn på disse faktorene. Siden begge artene hadde god hekkesuksess, antar vi at de kan leve sammen med sterkt overlappende nisjer fordi det er overskudd av evertebrat-næring. Alle tre fugleartene har stor evne til å endre næringsvalget hurtig og er derfor godt tilpasset til å klare seg under uforutsigbare betingelser i et barskt høyfjells-økosystem.

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