Small Mamals
Wash

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Lemming Predators on the Siberian Tundra

In the Eurasian Arctic, the most common lemming species are the Siberian lemming (*Lemmus sibiricus*) and the collared lemming (*Dicrostonyx torquatus*). Lemmings constitute the main food item for 5 common predators in the area: arctic fox; snowy owl; rough-legged buzzard; long-tailed skua; and pomarine skua. Hence, these predators form a foraging guild. We have studied factors influencing the structure of this guild. When comparing co-occurrence of the predators between 17 sites across Siberia, there were positive associations between the snowy owl and the two skuas, and a negative association between snowy owl and rough-legged buzzard. There was also a large variation in local population density among the predators, conceivably, due to the risk of intra-guild predation as well as the variation in food supply. There were significant relationships between lemming abundance and the abundance of each predator. An analysis of the predatory response by the arctic fox indicated a response pattern similar to that of a delayed numerical response to lemming abundance. For this and other reasons, we propose that the arctic fox is a resident specialist predator on microtine rodents. Further, the birds appeared to be nomadic specialist predators with, perhaps, one exception, the rough-legged buzzard.

INTRODUCTION

The very large fluctuations in numbers of microtine rodents are, perhaps, the most fascinating trait of arctic and subarctic ecosystems. For example, the variation in densities of lemmings (*Lemmus* and *Dicrostonyx* spp.), the prey species of this study, could be 200–fold, sometimes even 1000–fold (1). This variation in density has attracted the interest of a wide range of naturalists for centuries. However, it was first after the discovery of a pattern of regularity in these fluctuations, that there was a large increase in the number of studies aiming to explain the cyclicity of voles and lemmings. In arctic and subarctic areas, microtine rodent populations often reach peak numbers every 3 to 5 years (2, 3). The many hypotheses that have been put forward to explain these population cycles can be grouped into one of three categories of hypotheses relating the population cycles to *a)* food; *b)* predation; and *c)* intrinsic factors (4–13).

Recently, the predation hypothesis has received some support (9, 14–21). This hypothesis suggests that predators cause the cyclic behavior of microtine rodent populations. For example, studies made in the taiga zone have proposed that small mustelids play a key role in driving microtine rodent populations to an extreme low (9). Such a simple mechanism, including only small mustelids as predators, is unlikely for the population dynamics of lemmings on the Arctic tundra, for several reasons. Small mustelids are absent in some Arctic areas, e.g. Wrangel Island (22), where numbers of lemmings fluctuate in a pronounced cyclic pattern (23, 24). Moreover, the tundra ecosystem harbors several species that, for successful reproduction, are dependent on lemmings (22, 25–32). Although, these facts do not exclude the possibility that the predation hypothesis may apply also to lemmings on the tundra, they suggest that the relationships between lemmings and various predators on the tundra are complex. A better understanding of the tundra ecosystem requires studies on both lemmings and their predators, that are geared to examine factors that limit the population size of each species and that permit co-occurrence of two and more species.

The animals in focus of this report are some well-known microtine rodent predators: long-tailed skua *Stercorarius longicaudus*, pomarine skua *S. pomarinus*, arctic skua *S. parasiticus*, snowy owl *Nyctea scandiaca,* rough-legged buzzard *Buteo lagopus* and arctic fox *Alopex lagopus*. It is inevitable that these species form a foraging guild, i.e. they exploit the same food resource in the same way (25–28, 30–32). They are functionally diurnal as there is continuous daylight on the tundra during the breeding season. Moreover, earlier studies suggest that offspring production of each species is related to microtine rodent abundance, particularly the abundance of lemmings (22, 23, 25–29). Which factors influence the co-occurrence of species in this guild? Does local population size of the predators depend on similar factors? Community ecology theory suggests that inter-specific competition, predation and recruitment processes determine the guild structure (33–40). However, since competitive interactions may have little effect on population dynamics and on long-term community attributes (38, 39), inter-specific competition may be less important in structuring guilds. This was also corroborated in studies of foraging and foraging behavior among raptors and owls (41, 42). Hence, strong evidence for competition-structured guilds is lacking. In contrast, recent studies suggest that predation could affect the spatiotemporal distribution of species and thus organize assemblages of species (40, 43–45).

This report summarizes the results of studies of predators on the Siberian tundra. The most important results have been published elsewhere (31, 32, 46). Here, we include only a few, simple calculations to make clear the variation in distribution and density among the different species. Our studies show that the combination of studies on the community and the population levels can provide results that lead to a better understanding of the tundra ecosystem. Moreover, it is shown that large sample sizes, i.e. many study areas, are required to obtain some of these results. One important lemming predator, the stoat *Mustela erminea*, was not included in our study due to lack of resources. We believe, however, that the main conclusions of our studies are robust and do not critically depend on the lack of data on mustelids. In addition, the largest carnivores in northern Siberia, the polar bear *Ursus maritimus* and the wolf *Canis lupus*, were not considered in this study.

THE SPECIES

Arctic Fox

The arctic fox is a circumpolar canid with opportunistic feeding habits, but in most inland areas it is dependent on lemming population peaks for successful reproduction. During such years there can be up to 18 cubs in a single litter (47). Although arctic foxes are territorial in the breeding season, they are nomadic during winter, being capable of migrations of more than 1000 km in one season and up to 2300 km in total, also across pack ice. They spend the winter on the tundra or on sea ice.

In most continental areas, rodents are the main food for arctic foxes during the summer season. In Scandinavia, the Norwegian lemming *Lemmus lemmus* constituted 47–91% of the summer diet each year (48). The importance of lemmings has also been clearly demonstrated in North America (49) and Siberia (32). Other important types of food in summer are reindeer *Rangifer tarandus* carcasses, voles Arvicolinae, hares *Lepus timidus, L. arcticus*, ptarmigan *Lagopus mutus*, willow grouse

L. lagopus, and other birds (mainly Passeriformes). In winter, the most important food resources are reindeer carcasses, ptarmigans and grouse (49, 50).

The Rough-legged Buzzard

The rough-legged buzzard is a migratory bird with northern, circumpolar distribution. Each year rough-legged buzzards arrive at the breeding areas from mid-April to early May. Breeding occurs if food abundance is high, i.e. the number of breeding rough-legged buzzards is often related to microtine rodent abundance. In years with poor food abundance many buzzards abandon the breeding areas already in early June. The diet of breeding birds varies from 6 to 95% microtine rodents (lemmings and voles such as *Microtus* and *Clethrionomys* species) with grouse species as alternative prey. Clutch size varies from 2–7 eggs, conditioned upon foraging success. In August–October, the birds commence autumn migration to the south. Birds start to breed at an age of 2–3 years. Life-span, breeding intervals, lifetime reproductive success, adult and natal dispersal and fidelity to breeding areas are unknown.

The Snowy Owl

The snowy owl has a circumpolar distribution in the high north. It has a wide distribution in arctic habitats, from arctic deserts, rolling tundra in America and Siberia, and alpine tundra in Fennoscandia. Many pairs breed successfully during microtine rodent peaks, while only a few pairs may raise chicks in years when the microtine rodent population crash occurs early in the breeding season. Clutch size varies between 3 and 12 eggs, conditioned upon food availability. Analyses of owl pellets from rodent peak years show that microtine rodents make up 95% of the owls' diet by numbers, but snowy owls can also feed on prey such as geese, raptor chicks, and passerines. Autumn migration takes the owls to areas south of the breeding areas. Recoveries of dead birds indicate that juvenile birds move further to the south than adult birds and that males do not move as far south as females do. Recent studies at the center of the snowy owl's range have found no evidence for sudden irruptions in numbers. Many life history characteristics such as life span, lifetime reproductive success, breeding intervals, adult and natal dispersal and fidelity to breeding areas are unknown.

The Long-tailed and the Pomarine Skuas

This study deals with 2 of the 3 *Stercorarius* species; the long-tailed skua and the pomarine skua. The long-tailed skua, the smaller species, is circumpolar in northern areas with the exception of Iceland where it is missing. It appears to have high fidelity to breeding territories, often returning to the same territory from one year to another. The breeding range of the larger pomarine skua covers tundra areas from the Kanin peninsula in Russia to eastern Canada. Birds arrive at the breeding grounds in late May/mid-June and may not commence laying until early July. Nonbreeders and failed breeders leave the tundra already in July. Both species often nest in the same area of the tundra. The pomarine skua is generally found breeding in areas with high soil humidity, while such a clear preference has not been found in the long-tailed skua.

The pomarine skua generally has a more vagrant behavior than the long-tailed skua, but little is known about dispersal behavior among breeders in this species. In both species, successful pair formation and breeding require high numbers of microtine rodents, mainly lemmings. The summer diet of the long-tailed skua is 50–99% rodents, especially *Lemmus* species. During summers of low rodent availability, also passerine birds, insects and berries can be important. Apparently, the pomarine skua is more or less totally dependent on high numbers of lemmings for breeding. They breed in high densities in areas where lemmings are abundant. Intra- and interspecific aggression is common among breeding skuas, which defend mutually exclusive territories in the breeding season.

The skuas are determinate layers and lay a clutch of two eggs in a scratched hollow in the ground, a nest without insulation. Skuas put the eggs between their feet and body during incubation. Both species are long-distance migrants, spending the winter pelagically on the southern oceans. The pomarine skua generally winters furthest to the north and is regularly recorded in the northern Atlantic during the winter.

These reviews of the birds' biology are based on references 25–31, 46, 51–55.

Lemmings and Voles

In most of the Arctic, lemmings of the genus *Lemmus* coexist with *Dicrostonyx.* These differ in habitat preference and in diet. *Lemmus* prefer wet grasslands and feed mainly on sedges, grasses and moss (56). *Dicrostonyx* prefer drier areas and feed primarily on dicotelydones such as *Salix* spp. and *Dryas* spp. (56). It has been proposed that co-existing microtine rodents are exposed to similar variations in predation pressure, and, moreover, the population fluctuations appear to be synchronous among several species (57, 58).

We follow Jarrell and Fredga (59) and regard all collared lemmings in the Eurasian Arctic as one species, *Dicrostonyx torquatus*. The Siberian lemming *Lemmus sibiricus* is the main *Lemmus* species in the Russian Arctic except on the Kola Peninsula, where it is replaced by the Norwegian lemming *L. lemmus*, and east of the Kolyma River where it is replaced by the brown lemming *L. trimucronatus*. When discussing the genera separately, we use the terms "*Lemmus*" and "*Dicrostonyx*", respectively, while the term "lemmings" refers to both genera combined. A number of vole species also occur in northern Siberia: *Microtus oeconomus* and *Clethrionomys rufocanus* in western Siberia, and *M. gregalis* and *C. rutilus* in western and central Siberia (60).

MATERIAL AND METHODS

Field Methods

The studies of avian and mammalian lemming predators were performed during a ship-based expedition along the north coast of Siberia in 1994 (43), from the Kola Peninsula in the west, 67°23'N, to Wrangel Island in the east, 71°18' N (Table 1). The censuses of arctic foxes and birds were made during one or two days at each study site. The data used in the analyses were obtained between mid-June and mid-August, i.e. within the breeding period of all species (27, 28, 30–32, 51–53). The study areas varied in size, from 6 to 160 km^2, depending on the time available for field studies at each study site, and whether it was a study area for birds or arctic foxes. The study areas for arctic foxes were larger than those used for bird censuses (31, 32). In 19 different study areas, we collected data on birds attempting to breed while data on arctic foxes were obtained from 17 study areas. At each of 15 of these sites, microtine rodents were trapped according to the small quadrat method (61, 62).

The arctic fox dens are often made in areas with characteristic landforms. Moreover, they are easy to spot due to their lush vegetation compared with that of the surrounding area. These features simplified the surveys for breeding arctic foxes, which could thus be made over large areas comprising a total of 1464 km^2. In total, 142 dens were recorded. A single visit at a den was considered to be sufficient to detect if young were present or not. Three adults were recorded at only one out of the 85 dens with young (32). The number of breeding foxes was, therefore, estimated by multiplying the number of dens with litters by two. The values obtained by this calculation were then used as an index of arctic fox breeding density (63). Some of the western sites were visited twice, and the data collected during the first and

Table 1. Microtine rodent indices and local population densities of the different predators are shown for each study area on the Siberian tundra. The densities of the various predators are number of individuals per 100 km^2. For the calculations of the various microtine indices see the Data analysis section. Sites where counts and trapping were not made are indicated.

Site	Densities of predators					Microtine rodent index			
	Rough-legged buzzard	Snowy owl	Long-tailed skua	Pomarine skua	Arctic fox	Bird study	*Lemmus*	*Dicrostonyx*	Total
1	17.2	0.0	6.9	0.0	3.7	2.5	0.0	–	0.89
2	11.1	0.0	5.5	0.0	2.5	3.0	0.0	0.0	0.0
3	10.0	0.0	0.0	0.0	5.7	–	–	–	–
4	0.0	0.0	0.0	0.0	7.1	–	–	4.8	4.8
5	52.8	0.0	3.8	0.0	10.8	10.0	10.0	16.5	29.2
5b	160.0	0.0	0.0	0.0	–	–	–	–	–
6	33.3	38.9	22.2	11.1	5.1	2.5	0.0	8.7	8.7
8	0.0	2.9	37.1	342.9	10.1	10.0	10.0	4.6	40.9
9	0.0	13.0	34.8	0.0	6.2	13.7	11.7	48.9	78.5
9b	0.0	66.7	133.3	16.7	–	2.5	0.0	–	–
10	0.0	2.2	35.6	64.4	9.6	10.0	9.6	2.4	25.9
11	0.0	0.0	0.0	1.8	2.2	0.0	0.0	0.5	2.6
12	6.9	43.1	27.6	0.0	26.9	14.1	12.9	9.1	24.0
13a	0.0	57.8	60.0	151.1	28.0	28.7	28.8	–	51.8
13b	0.0	61.9	111.9	69.1	28.6	21.7	21.7	0.0	40.3
14	0.0	34.7	43.1	31.9	24.6	6.2	6.3	0.6	14.9
15	30.3	9.1	18.2	0.0	5.5	8.8	8.3	11.0	47.0
16	0.0	2.0	2.0	0.0	8.0	–	2.0	0.0	1.2
17	0.0	51.6	24.6	99.2	12.5	27.9	27.5	24.0	57.0

second visit were pooled before calculations and analyses were made (sites 1–5 and 8–10; Table 1).

Bird censuses were made in study areas adjacent to or overlapping those used for the arctic fox studies. Each bird study area was censused for avian lemming predators, using binoculars to spot birds and nests. Records were then taken on number of birds, number of pairs of mated birds, and number of nests. Birds that displayed territorial and/or breeding behavior were classified as mated birds. The nest positions were recorded using a GPS-system, which calculates coordinates using up to 6 satellites.

A standardized trapping program, the small quadrat method, was applied to estimate the density of microtine rodents in each of 15 study areas. In this program, 20 quadrats, each 15 m x 15 m, were randomly located at each study site. Three snap-traps were set within 3 m of each corner of the quadrat (61). The traps were checked every 8 hrs for 24 hrs. Further details of this trapping program are given by Erlinge et al. (61).

Data Analysis

Due to the tight time schedule of this expedition, the time needed in the field for finding all birds' nests was not available. In particular, we missed nests of the skuas, which are cryptic and difficult to find. Therefore, for each bird species, we examined data for a relationship between number of birds that were mated and number of individuals that were recorded. These relationships were:

no. of rough-legged buzzard pairs = 0.45 x (no. of buzzards counted) + 0.04

no. of snowy owl pairs = 0.46 x (no. of owls counted) – 0.65

no. of long-tailed skua pairs = 0.25 x (no. of long-tailed skuas counted) + 0.69

no. of pomarine skua pairs = 0.28 x (no. of pomarine skuas counted) – 0.94.

Since these relationships were significant ($P < 0.001$, for all regressions), and the amount of variance explained by each model was high ($r^2 = 0.81$ and higher), the most complete data set, number of birds recorded, was used in the analyses (see also 31).

The analysis of the distribution of species is problematic. Firstly, it is necessary to demonstrate that a set of observations from discrete localities represents a nonrandom distribution of the species, and, secondly, there may be interactions between different species. Recently, a new method was developed for the analysis of interactions between species using data on species occurrences on islands (64). This method was further developed to apply in a broader context, namely to discrete localities in general including islands as well as discrete localities distributed over large geographical areas (31). The method compares the statistics found for a real set of occurrences with the statistics obtained by a randomization process, a generalized Monte Carlo test (for further details of the method see 31, 64, 65). In the analysis of the distribution of birds, a Markov chain of 10 000 reconstructed data sets was used to obtain the test statistic S (31). This test statistic was also used to calculate, $n_{(i)}$, a measure of the extent to which the number of co-occurrences of different species differed from expectation (64, 65). The multiple testing of 4 species required an adjustment of the significance level to 0.05/6 to reduce the probability of committing a Type I error (31).

In addition, the analyses run in the bird study used data only from the standardized trapping program for microtine rodents. An index for microtine rodent abundance was then calculated as number of individuals trapped per 100 trap-days (61). This index includes, all microtine rodents, both lemmings and voles, which were trapped in the program.

The arctic fox study used 3 different indices for microtine rodent abundance. Two are based on the standardized trapping program. The *Lemmus* index was calculated as the number of *Lemmus* captured per 100 trap-nights and used as an estimate of the *Lemmus* population density. This particular *Lemmus* index was created because it was thought that the number of small quadrats was underrepresented in the *Dicrostonyx* habitat (66), although individuals of this species were trapped within the standardized trapping program at several study sites. An additional study site, site 16, was also included. At this site the trapping program was run for only 50 trap-nights (Table 2).

Moreover, a second index, called *Dicrostonyx* index, was based on the standardized trapping program as well as a study directed to trap as many *Dicrostonyx* as possible, for later analyses of the genetics and the taxonomy of this species (60). In the *Dicrostonyx* trapping scheme, a constant number of 200 Sherman live traps and 50 snap-traps were set selectively at active *Dicrostonyx* burrows at each site (V. Fedorov, pers. comm.). The *Dicrostonyx* index was calculated as the total number of *Dicrostonyx* trapped per 24 hrs including data from both trapping programs.

The third index uses the results of 3 different trapping programs: the standardized trapping program, the selective trapping program for *Dicrostonyx* and a third program developed for selective captures of *Lemmus* (61). In the latter program, 50 traps were set at sites with signs of recent lemming activity (61). This "total lemming index" was calculated as the total number of lemmings trapped per 24 hrs. Different methods and scales have been used to calculate the *Lemmus* and *Dicrostonyx* indices and, therefore, the total lemming index may suffer from some uncertainties.

RESULTS

Variation in Occurrences of Species

Individuals of all 5 species were recorded only at study site 6, and 4 species were represented at 8 other study sites (Table 1). Only one study site seemed to have no more than one of the 5 species (Table 1). It is notable that breeding arctic foxes were recorded at all study sites (Table 1) while the occurrences of different birds varied much more. For example, rough-legged buzzards and pomarine skuas occurred in 8 and 9, respectively, of the19 study areas. Snowy owls and long-tailed skuas were slightly more common occurring in more than 50% of the study areas. There was a nonrandom distribution of the birds (31), permitting further analyses of factors that could influence the distribution and local population density of the birds.

It appears that there is a negative association between rough-legged buzzards and snowy owls while there are positive associations between snowy owls and long-tailed skuas as well as pomarine skuas (Table 2). The arctic fox was not included in this analysis. Assume, however, that the bird and the arctic fox study areas were representative of a wider area at each study site. Thus, the fact that arctic foxes were recorded in all the surveyed study areas suggests that each one of the bird species may co-occur with arctic foxes (Table 1).

Variation in Local Population Density

Besides this variation in species occurrences, there was a large variation in local population density of predators (Table 1). This variation also seemed to differ much between the 5 species of our study. Thus, the mean densities of breeding individuals of the arctic fox and the snowy owl were 11.6 ± 9.3 (mean ± SD) individuals per 100 km^2, and 20.2 ± 25.1, respectively (Table 1). Among the skuas, the densities of birds attempting to breed were for the long-tailed skua 50.2 ± 99.4 and for the pomarine skua 34.1 ± 80.2 (Table 1). The figures for the rough-legged buzzard, 29.2 ± 46.5 also suggest a fairly large variation in breeding density between study areas. Note, that the calculations made for the rough-legged buzzard did not include records from some study areas (sites 8, 9, 9b, 10, 11, 13a, 13b and 17). In this study, no breeding rough-legged buzzards were observed north of 73°31'N. One, probably not mated, individual was recorded north of 75° (31).

Since the means differed among species, coefficients of variation, CV = (100 x SD)/mean, were calculated for comparisons of the variation in local population density among species. The coefficient of variation was for the arctic fox 80.2, the snowy owl 124.3, the rough-legged buzzard 159.3, the long-tailed skua 198.0, and for the pomarine skua 235.2. These figures suggest that the arctic foxes were more evenly spaced out over the 17 study sites than the birds were, and that the skuas, particularly the pomarine skua, either occurred with high densities in the study areas or were not present (see also Table 1). In the case of the rough-legged buzzard, the figures are influenced by the observations made in study area 5b, which comprised only 10 km^2. Excluding the data from this area in the calculations changed the mean and SD to 16.2 ± 17.5. Consequently, the CV also changed, to 108.0. This CV suggests a more even distribution of rough-legged buzzards among study areas compared with that of the skuas.

The densities of all 5 predators appeared to be related to the abundance of microtine rodents, mainly lemmings (Table 1). For example, numbers of snowy owls, long-tailed skuas and pomarine skuas were positively correlated with the lemming-index used in the bird study (31). There was no simple relationship between number of rough-legged buzzards and microtine rodent abundance, however. Therefore, we ran a multiple regression analysis including snowy owl density and lemming abundance as independent variables from study areas within the assumed breeding range of the rough-legged buzzard (31). This analysis showed a significantly negative effect of snowy owl density and, a significantly positive effect of lemming abundance on the density of rough-legged buzzard, respectively (31).

Table 2. The calculated values of $n_{(ij)}$. It is a measure of co-occurrences of species, which here indicates pair-wise interactions among the 4 avian lemming predators on the Siberian tundra (from ref. 31).
*** indicates a significant (P < 0.05) positive (+) or negative (–) interaction.**

	Rough-legged buzzard	Long-tailed skua	Pomarine skua
Snowy owl	–2.11*	2.27*	2.44*
Rough-legged buzzard		0.13	–2.91
Long-tailed skua			0.20

The data on arctic fox density indicated a comparatively low density of breeding foxes in some of the study areas, at sites 1, 2, 6, 11, 16 (Table 1). In study areas at sites 5, 8, 9, 10 and 15, both the arctic fox density and the *Lemmus*-index were classified to be of medium size. Moreover, the arctic fox density and the *Lemmus*-index were considered to be high at sites 13a, 13b and 17 (Table 1). In two arctic fox areas, at 12 and 14, the arctic fox densities were considered to be high and the *Lemmus*-index fairly low (Table 1; 32). In contrast, there was no relationship between the density of arctic foxes and the *Dicrostonyx*-index (Fig. 4b in 32). Hence, our studies on the Siberian tundra showed that microtine rodent abundance is one important factor determining local population densities of these 5 predators, which is in line with the results of other similar studies. A new result was that one species influenced the abundance of another species, even the occurrence of that species (31).

Diets of Arctic Foxes, Rough-legged Buzzards and Snowy Owls

Diet analyses were based on the contents of arctic fox scats and pellets from the rough-legged buzzard and the snowy owl. The arctic fox scats, collected near dens, were of 2 categories, old and fresh (32). The bird pellets, which were collected in and near nests, were regarded to be fresh, i.e. pellets likely to have been cast in 1994 were chosen (31).

Lemmings were the main prey of arctic foxes with 83% in fresh scats and 74% in old scats (32). There were more than 50% *Lemmus* in both fresh and old scats while the proportion of *Dicrostonyx* were 24% and 21% in fresh and old scats, respectively (Table 3, details are given in Angerbjörn et al. (32)). The scat analysis also showed that arctic foxes preyed on birds. Thus, various bird species occurred with 8 and 16% in fresh and old scats, respectively (Table 3).

Similarly, lemmings were the main prey items of the birds with 68.6% in the rough-legged buzzard and 98.6% in the snowy owl (Table 3, details are given in Wiklund et al. (31)). The frequency of other microtine rodents was significantly higher in pellets of the rough-legged buzzard, 26.1%, than in those of the snowy owl, 0.6% (Table 3). Moreover, the pellets of the snowy owl contained proportionally more *Lemmus* than the pellets of the rough-legged buzzard (Table 3; 31). However, the analysis of fresh prey items, prey that were counted in or near nests, showed that the rough-legged buzzard as well as the snowy owl preyed on both lemming species (31). Therefore, taken together the analyses of fresh prey items and the pellets, did not indicate a preference for any of the 2 lemming species, neither in the snowy owl nor in the rough-legged buzzard (31). These results agree with the results of other similar studies (51, 52) and, thus, support the conclusions that both the rough-legged buzzard and the snowy owl are opportunistic in their prey choice feeding on the most abundant microtine rodents.

DISCUSSION

This study of lemming predators was a longitudinal transect along the Siberian coast with the westerly situated sites visited several weeks earlier than the sites in the far east. In the study areas where the final censuses were made, e.g. sites 5b and 6, there was no evidence of complete breeding failure, such as previously occupied, but empty dens and nests. In at least one of these sites, all species included in the study tended large young during the censuses. Hence, the frequency of breeding failure

Table 3. Prey items of microtine rodent predators on the Siberian tundra. Percentages of different prey items found in pellets of the rough-legged buzzard and the snowy owl and in scats of the arctic fox. There are 2 categories of prey items for the arctic fox, prey items found in fresh scats and in old scats, respectively. (Details of handling of pellets and scats and of the analyses are given in 31, 32).

Type of prey	Rough-legged buzzard	Snowy owl	Arctic fox	
			Fresh	Old
Lemmus	31.8	71.8	59	54
Dicrostonyx	36.8	26.8	24	21
Voles	26.1	0.5	4	1
Other mammals	0	0.3	–	–
Birds	5.3	0.6	8	16

and subsequent emigration of individuals from study areas may not have been higher in areas that were visited later in the season. We believe, therefore, that there were species-specific differences in the spatial distribution of the predators.

Over large areas where lemmings are abundant, many individuals of the predators bred highly successfully (22, 25–30). Also, there were significant relationships between lemming abundance and the abundance of the birds, and such a relationship could be inferred from data on arctic fox and *Lemmus* abundance (31, 32). For the rough-legged buzzard, this relationship did not appear until the effect of snowy owl abundance was removed. Similarly, in another study area on the Siberian tundra the density of rough-legged buzzards seemed to be lower than expected due to the presence of snowy owls (30). Although, that result was obtained from a single study area, it was in line with the result of our study. Hence, both studies agree in that there is a negative effect of snowy owls on the distribution of rough-legged buzzards.

There are important differences between the rough-legged buzzard and the snowy owl as well as the two skuas. Nests of the rough-legged buzzard are large and bulky, also on the Siberian tundra where the majority of nests are on the ground (30, 31). The chicks are conspicuous due to loud begging calls, movements, and apparent plumage coloration. In contrast, nests of snowy owls and skuas are cryptic, their young are cryptically colored and, shortly after hatching, they leave the nest and scramble over the territory (67—70). Moreover, the snowy owl is a dietary opportunist, preying on animals other than lemmings, e.g. several species of large birds and even snowy owl chicks before they reach fledging size (references in 31). Therefore, Wiklund et al. (31) proposed that the risk of nest predation is one reason for the spatial separation of rough-legged buzzards and snowy owls. There is evidence that predation is a major cause of chick loss among buzzards breeding on the tundra (30).

One consequence of the spatial separation between species would be reduced competition. Interestingly, comprehensive reviews (41, 42) have given no support for competition-structured assemblages of raptors and owls. Rather, these studies suggest that raptors and owls are opportunistic feeders that move to areas with plenty of food (41, 42), as the birds of our study do (25–30, 35, 36, 51–53). Similarly, it is less likely that reduced competition is the cause of the spatial separation between rough-legged buzzards and snowy owls. Rough-legged buzzards commence breeding before skuas arrive at the breeding areas (25–28, 30, 51–54), and, hence, there would have been breeding sites available in several sites where long-tailed skuas, but not the rough-legged buzzards, bred.

Our studies clearly showed that local population density varied among study sites. There were also large interspecific differences in the variation in local population density. Andersson and Erlinge (71) pointed out that it may be important to distinguish between different types of predators such as resident and nomadic specialists. The snowy owl and the skuas have more vagrant behavior than the arctic fox. The arctic fox could therefore be classified as a resident specialist, although individuals of this species sometimes move long distances (32). It is more difficult to classify the rough-legged buzzard because it seems to return to the same breeding sites in a succession of breeding seasons even when rodent numbers are low (Wiklund, unpubl. data). In contrast, the pomarine skua strongly depends on lemmings for breeding, abandoning areas with low lemming density (26, 27, 53, 54). Similarly, large numbers of long-tailed skuas regularly breed when lemmings are abundant, although breeding occurs also in years with lower lemming abundance (26–28, 53, 54). Snowy owls have a more diversified diet than the pomarine skua and may therefore breed at lower densities of lemmings than the pomarine skua does (26, 27, 29, 52, 53). The pomarine skua is thus expected to breed only in areas with lemming peaks, while long-tailed skuas and snowy owls as well as rough-legged buzzards may breed also in areas where lemmings are increasing (25–28, 30, 51–54). A common response of the arctic fox is to vary offspring production in accordance with lemming density while long-distance movements may be rare (32). Hence, these differences between the species as well as the risk of intra-guild predation could explain, at least, some of the species-specific variation in local population density that we recorded.

The Arctic Fox Response to Lemmings

Angerbjörn et al. (32) made a detailed analysis of the relationship between the arctic fox and the lemmings. In their study (32), the numerical response of the arctic fox seemed to vary with prey species, *Lemmus* and *Dicrostonyx*, respectively. The conclusion of the analysis was that there is a delayed numerical response in the arctic fox to *Lemmus* with a time lag of about 1 year (32). Similarly, a delayed numerical response has been proposed for mustelids (9, 18), but not yet for any avian predator on microtine rodents. Delayed numerical responses may be more common in mammals than in birds because birds generally respond directly to variations in food abundance. They stay and breed or move elsewhere within a couple of days, e.g. the pomarine skua, or weeks, e.g. the long-tailed skua and the rough-legged buzzard (25–28, 30, 51–53).

Moreover, the functional response of the arctic fox was examined. In this analysis, Angerbjörn et al. (32) tested Holling's type II and type III predator response functions on lemming abundance. Due to much variation in data there was a lack of statistical significance. Arguments were presented, however, for a type of functional response to *Lemmus* that would correspond to a Holling's type II function (32). Interestingly, when the total lemming index was used in the analysis, it indicated a response that significantly agreed with both Holling's type II and type III. After examination of the slopes and the intercepts of the 2 different functions, it was concluded that the response of the arctic fox to total lemming density, i.e. total lemming index, also should be a Holling's type II (32), the type of functional response expected for specialist predators.

A time lag in the numerical response is expected to generate cyclicity in a predator-prey system (9, 18, 21, 71). There are also other reasons that suggest that the arctic fox is a resident specialist predator on lemmings. Hence, the arctic fox is an important member of the microtine rodent predator guild on the tundra, and there are reasons to believe that it, at least, contributes to the limitation, perhaps the regulation, of lemming populations.

CONCLUSION

There were large variations in species occurrences as well as local population density among the microtine rodent predators on the Siberian tundra, most likely due to variance in predation risk and food supply. It appeared that the variation in density was highest in the 3 species that for a long time have been considered as nomadic lemming specialists: the pomarine skua, the long-tailed skua and the snowy owl. In contrast, this variation was markedly lower particularly in the arctic fox, which for several reasons can be classified as a resident microtine rodent specialist. In addition, a time lag of about 1 year was proposed for the numerical response of the arctic fox. Such a time lag in the numerical response of mustelids has been considered important for the regulation of microtine rodents in boreal areas (9, 18).

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