Journal of Animal Ecology 1999, **68**, 34–49

Predator–prey relationships: arctic foxes and lemmings

ANDERS ANGERBJÖRN*, MAGNUS TANNERFELDT* and SAM ERLINGE

**Department of Zoology, Stockholm University, S–106 91 Stockholm, Sweden; and Department of Ecology, Lund University, S–223 62 Lund, Sweden*

Summary

1. The number of breeding dens and litter sizes of arctic foxes *Alopex lagopus* were recorded and the diet of the foxes was analysed during a ship-based expedition to 17 sites along the Siberian north coast. At the same time the cyclic dynamics of co-existing lemming species were examined.

2. The diet of arctic foxes was dominated by the Siberian lemming *Lemmus sibiricus* (on one site the Norwegian lemming *L. lemmus*), followed by the collared lemming *Dicrostonyx torquatus*.

3. The examined *Lemmus sibiricus* populations were in different phases of the lemming cycle as determined by age profiles and population densities.

4. The numerical response of arctic foxes to varying densities of *Lemmus* had a time lag of 1 year, producing a pattern of limit cycles in lemming–arctic fox interactions. Arctic fox litter sizes showed no time lag, but a linear relation to *Lemmus* densities. We found no evidence for a numerical response to population density changes in *Dicrostonyx*.

5. The functional or dietary response of arctic foxes followed a type II curve for *Lemmus*, but a type III response curve for *Dicrostonyx*.

6. Arctic foxes act as resident specialist for *Lemmus* and may increase the amplitude and period of their population cycles. For *Dicrostonyx*, on the other hand, arctic foxes act as generalists which suggests a capacity to dampen oscillations.

Key-words: Arctic, cycles, functional response, numerical response, tundra.

Journal of Animal Ecology (1999) **68,** 34–49

Introduction

The Arctic tundra communities may appear simple due to low diversity and relatively uncomplicated food webs. Nevertheless, the population dynamics of many tundra species and interactions between their determinants are intriguingly complex. One of the major features of these systems are drastic fluctuations of some herbivore populations, which in turn influence a majority of the mammalian and avian species in the community. In boreal forests in North America, snowshoe hares *Lepus americanus* Erxleben are the pivot of these fluctuations, with a period of roughly 10 years (Elton & Nicholson 1942; Sinclair *et al.* 1993; Boutin *et al.* 1995). In Eurasia, the pattern is governed by 3–5 years fluctuations of lemmings (*Lemmus* and *Dicrostonyx* spp.) and voles (*Clethrionomys* and *Microtus* spp.) (Collett 1911–12; Hansson & Henttonen 1985; Stenseth & Ims 1993). The fluctuations are referred to as cycles, although they may, in fact, be chaotic with a strong periodic element (Oksanen & Oksanen 1992; Hanski *et al.* 1993). The cause of these hare and lemming cycles are not yet fully understood, but a number of recent studies have suggested that predators play a critical role (e.g. Erlinge *et al.* 1983, 1984; Erlinge 1987; Tostel *et al.* 1987; Korpimäki & Norrdahl 1989; Korpimäki, Norrdahl & Rinta-Jaskari 1991; Hanski *et al.* 1993; Hanski & Henttonen 1994; Hanski & Korpimäki 1995; Krebs *et al.* 1995). Small mustelids are suggested as the most influential predators 'in the north' (Hanski *et al.* 1993). In models of this predator–prey complex, the least weasel (*Mustela nivalis* L.) and *Microtus* voles are the presumed key species (Korpimäki *et al.* 1991; Hanski & Korpimäki 1995). Most of these studies have concentrated on the boreal taiga zone. On the Arctic tundra, however, the dominant rodents are lemmings and it has not been shown that small mustelids here play the

Correspondence: A. Angerbjörn, Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden. Fax: +46-8-16 77 15. E-mail: tanner@zoologi.su.se

© 1999 British Ecological Society

suggested key role. In some areas, as on the Wrangel Island, where lemming numbers fluctuate in a pronounced cyclic pattern (Chernyavskii & Tkachev 1982; Ovsyanikov 1993), small mustelids are absent (Dorogoi 1987). If the suggested predator-generated fluctuations are valid also for lemming cycles, there may be other predators on the tundra that assume a role similar to that of weasels.

Nomadic avian lemming predators can be abundant on the tundra, especially during summers with rodent peaks (Potapov 1997; Wiklund, Kjellén & Isaksson 1997). The most important of these are long-tailed, pomarine and arctic skuas (*Stercorarius longicaudus* Vieillot, *S. pomarinus* Temminck, *S. parasiticus* L.), snowy owls *Nyctea scandiaca* (L.) and rough-legged buzzards *Buteo lagopus* Pontoppidan. However, these species lack a number of traits which have been assumed for the dominant predator in the models mentioned above. First, avian predators are not present during the winter season, which means that rodents have a complete refuge from these predators for three-quarters of the year. Secondly, they usually give up breeding and move elsewhere during rodent lows, and hence do not deepen and prolong rodent population crashes in the way mustelids are suggested to do (Hanski & Korpimäki 1995; Potapov 1997). Thirdly, the numerical response of avian lemming predators shows no time lag (Potapov 1997; Wiklund *et al.* 1997). This is because many have a generalist diet or migrate when food abundance decreases.

Instead, the arctic fox *Alopex lagopus* (L.) is a strong candidate for being a most influential lemming predator. Due to its habit of food caching and a slightly less specialized diet, adult mortality is not so strongly influenced by rodent crashes as in mustelids (Hiruki & Stirling 1989; Tannerfeldt & Angerbjörn 1996). Also, arctic foxes have the capacity to migrate over vast distances. Arctic fox breeding success and population dynamics are nonetheless strongly influenced by lemming populations in areas where the species co-exist (Macpherson 1969; Ovsyanikov 1993; Angerbjörn *et al.* 1995; Kaikusalo & Angerbjörn 1995; Tannerfeldt & Angerbjörn 1998). Furthermore, arctic foxes are present on the tundra also in winter and they often stay in an area once they have established a territory (Tannerfeldt & Angerbjörn 1996). All these features are characteristic of the modelled predators. Further investigations of the role of arctic foxes in lemming dynamics are thus warranted. The interaction has so far only been examined from the viewpoint that lemmings govern fox populations.

The role of predation in intraguild relationships between prey species is little known, but has gained recent attention (Boutin 1995; Schmitz 1995; Abrams & Matsuda 1996; Hanski & Henttonen 1996). In most of the Arctic, lemmings of the genus *Lemmus* co-exist with *Dicrostonyx*. These differ in habitat preference and in diet. *Lemmus* occur preferably in wet grasslands and feed mainly on sedges, grasses and moss (Batzli 1993). *Dicrostonyx* prefer dry sandy areas and feed primarily on dicotelydones, such as *Salix* spp. and *Dryas* spp. (Batzli 1993). Co-existing microtines are exposed to similar variations in predation pressure and their dynamics seem to be linked (Henttonen *et al.* 1987; but see Pitelka & Batzli 1993).

Arctic fox predation patterns are also interesting in themselves. The foxes show a large intraspecific variation in diet and with this follow striking differences in life history traits and population dynamics (Hersteinsson 1990; Tannerfeldt & Angerbjörn 1998). Furthermore, the arctic fox is a species of significant economic value to the human inhabitants of the Arctic. If we are to evaluate the role of the arctic fox in the tundra community, we must understand its predation patterns. In this study, we examine the predatory relationship, in terms of functional and numerical response, of arctic foxes in relation to changes in lemming densities on the Siberian tundra.

Materials and methods

The study was performed during a ship-based expedition along the north coast of Siberia in the summer of 1994 where we visited 17 sites, from the Kola Peninsula in the west to Wrangel Island in the east (Fig. 1). The sites were not situated in coastal habitat. At each site, Erlinge and co-workers censused lemming populations, focusing on the Siberian lemming *Lemmus sibiricus* (Kerr) (Erlinge *et al.* 1995), whereas Angerbjörn and Tannerfeldt surveyed arctic fox dens and collected scats for diet analysis (Angerbjörn & Tannerfeldt 1995). Some of the western sites were visited twice (sites 1–5 and 8–10). For arctic foxes, data collected during the second visit have been pooled with data from the first visit (Table 1). During the 3-month expedition, we covered 1464 km^2 and inspected 142 arctic fox dens. Normally, the predatory response to prey population fluctuations are discussed for one population along a time scale. We instead use each population as a data point and construct response curves along a gradient of prey densities.

CENSUSING ARCTIC FOXES

Arctic fox dens are usually situated in characteristic landforms and have lush vegetation, making them relatively easy to locate (e.g. Smits *et al.* 1989; Prestrud 1992a; Smith *et al.* 1992). A single visit at a den was sufficient to detect if it was occupied with a litter or not. We are convinced that we found a similar proportion of dens in all inventoried areas and that this was a majority of all breeding dens in the area. A longer stay was needed at each den to observe the number of adult foxes and to estimate litter size. Litter size estimates were made between June 25 and August 26, i.e. when the cubs were between 3 and 12 weeks old. These estimates must be regarded as minimum numbers (Garrott, Eberhardt & Hanson 1984;

© 1999 British Ecological Society

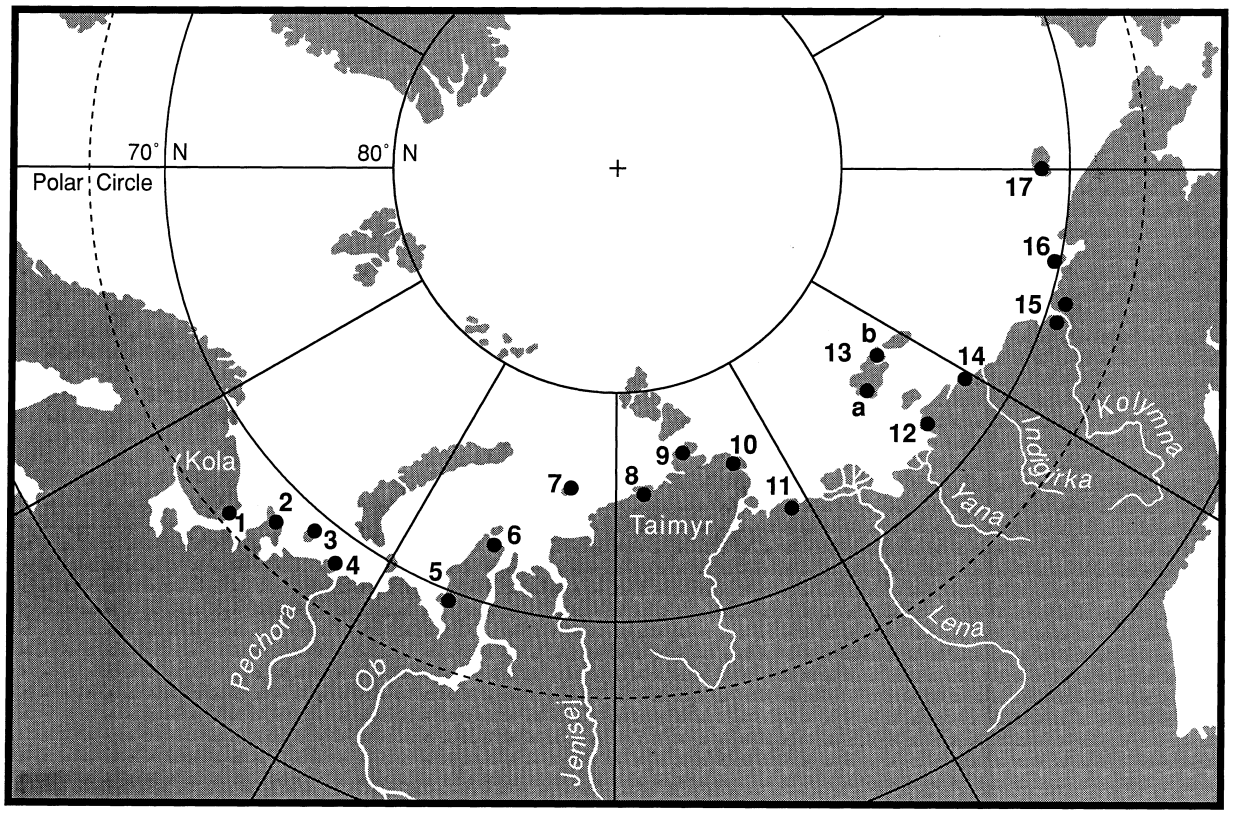

Fig. 1. Map of northern Siberia with study site numbers as in Table 1.

Table 1. Summary of arctic fox inventories. Site numbers and names follow Hedberg (1995). Asterisk (*) denotes data that were excluded from calculations; at site 3 due to absence of rodents, at other sites due to small sample sizes. The summation 'Total' is only of scats included in the analyses

Site no.	Site name	Inv. area (km^2)	Fox dens per 100 km^2	Breeding foxes per 100 km^2	Fox litter size means ± SD	No. fresh fox scats	No. old fox scats
1	Kola Peninsula	109	2·50	3·67		48	2*
2	Kanin Peninsula	79	1·67	2·53		2*	40
3	Kolguyev Island	70	4·44	5·71		19*	22*
4	Pechora Bay	84	3·33	7·14	2·50 ± 0·71	62	20
5	W Yamal Peninsula	93	3·63	10·75	2·50 ± 2·12	166	30
6	N Yamal Peninsula	39	2·56	5·13	1·00 ± 0·00	50	0
8	NW Taymyr Peninsula	79	6·67	10·13	2·50 ± 0·71	35	25
9	Chelyuskin Peninsula	65	4·00	6·15		25	25
10	NE Taymyr Peninsula	104	10·00	9·62		35	15
11	Olenëkskiy Bay	90	1·11	2·22		30	20
12	Yana Delta	67	13·43	26·87	4·70 ± 2·56	50	20
13a	N.S.I. Faadeyevskiy	100	14·00	28·00	3·12 ± 1·55	75	20
13b	N.S.I. Kotel'nyy	35	14·29	28·57		40	30
14	Indigirka/Lopatka	130	12·31	24·62	3·19 ± 1·52	50	10
15	Kolyma Delta	110	2·73	5·45		10	0
16	Ayon Island	50	4·00	8·00	2·00 ± 0·00	30	30
17	Wrangel Island	160	6·25	12·50	4·00 ± 2·24	45	35
Total		1464	5·00	11·59	3·54 ± 2·01	751	320

N.S.I. = New Siberian Islands.

© 1999 British Ecological Society

Tannerfeldt & Angerbjörn 1998). It should also be noted that the long time span make litter size comparisons between populations uncertain. We have assumed that each breeding den was occupied by two adult foxes. In a total of 85 breeding dens, there was only one observation of three adults at the same den.

The number of occupied dens multiplied by two was used as an index of density of breeding arctic foxes (Angerbjörn *et al.* 1995). The area inventoried at each site varied from 35 to 160 km^2 (Table 1), mostly dependent on the number of hours spent at each site.

EXAMINING LEMMING POPULATIONS

We follow Jarrell & Fredga (1993) and regard collared lemmings from all visited sites as one species, *Dicrostonyx torquatus* (Pallas). The Siberian lemming *Lemmus sibiricus* is the only *Lemmus* at all sites except no. 1, the Kola Peninsula, where it is replaced by the Norwegian lemming *L. lemmus* (L.). The brown lemming *L. trimucronatus* Davis has been reported from site 16, Ayon Island, but is now considered a synonym to *L. sibiricus* (Corbett & Hill 1991; Wilson & Reeder 1993). When discussing the genera separately, we use the terms '*Lemmus*' and '*Dicrostonyx*', respectively, while the term 'lemmings' refers to both genera combined.

The population densities of lemmings were estimated by trapping. We concentrated our trapping effort on the Siberian lemming. Relative density estimates of Siberian lemmings were obtained according to a standardized grid snap-trapping program, the 'small quadrate method' (Myllimäki *et al.* 1971). On each locality generally 20 quadrates (15 × 15 m) were set out, each with 12 traps (three in each corner of the quadrate). The site of a trap was carefully chosen and if possible the traps were set at the entrance of a nest or across a lemming runway. We placed the quadrates about 50 m apart on representative and suitable habitat for the Siberian lemming (wet grasslands). The traps were checked every 8 h and trapping was carried out for 24 h on each locality. Site 16 was an exception with only 50 trap-nights (Table 2). In this trapping programme, the number of captured *Lemmus* per 100 trap-nights was used as an index of their population density. To obtain further information on the demography of Siberian lemming populations we placed additional traps at selected places where there were signs of recent lemming activity.

Body weight and sex of captured Siberian lemmings were determined. We removed eye-lenses to be used for age determination according to Hagen *et al.* (1980). The weight of eye-lenses made it possible to separate five cohorts: juveniles and sub-adults (less than 2 and 4 months old, respectively), and three categories of adults, adult 1 (4–8 months and born in preceding winter), adult 2 (9–14 months and born in previous summer), and adult 3 (more than 14 months old). The detailed data on age determination will be published separately (Sam Erlinge *et al.* unpublished data). The data on Siberian lemmings permitted us to determine in which phase the examined population was. In doing so, we used information on present and previous densities together with information on the age profile of the population. Estimates on previous densities were based on the amount and frequency of old lemming faeces and earlier used runways in typical Siberian lemming habitats. A population in the increase phase is expected to have medium present density and indications of low past density; typically, the age profile should be dominated by younger age categories. A population in the peak phase, on the other hand, is expected to have a high density, both in the preceding and present season. Furthermore, the population should have a relatively high frequency of older individuals. A population in the decline phase should have a moderate present density and high past density, and an age profile dominated by older cohorts. The low phase is characterized by very low present density and indications of higher previous density.

As discussed earlier, *Lemmus* and *Dicrostonyx* have different habitat preferences (Rodgers & Lewis 1986; Batzli 1993). The grids were set to trap *Lemmus*, but *Dicrostonyx* were also trapped to some extent. However, we do not consider this trapping efficient for estimates on *Dicrostonyx* density. Other scientists on the expedition trapped lemmings, especially *Dicrostonyx*, for genetic and taxonomic analyses (Fredga *et al.* 1995). They used a constant number of 200 Sherman live traps and 50 snap-traps, set selectively at active *Dicrostonyx* holes at each site (Vadim Fedorov, personal communication). We have used the number of *Dicrostonyx* trapped by Fredga and co-workers divided by the time the 250 traps were active, i.e. number of trapped animals per 24 h (per 250 traps). We call this estimate '*Dicrostonyx* index' (Table 2). It is important to note that this index has a different scale than the number of *Lemmus* per 100 trap-nights. For an estimate on both species together, we have therefore calculated a 'total lemming index'. It is derived in the same way as the *Dicrostonyx* index, but also includes total captures of *Lemmus* by selective and grid trapping, again per 24 h (Table 2). We have used the most reliable index type for each category of lemmings and the indices cannot be compared directly. However, testing for *Lemmus*, the two types of trapping indices were highly correlated ($r = 0{\cdot}85$, $P = 0{\cdot}0001$, $n = 15$).

ANALYSIS OF ARCTIC FOX SCATS

We collected arctic fox scats at occupied dens. Fresh scats, from the summer of 1994, were separated from older scats by appearance. Older scats are dry and weathered or overgrown by recent vegetation. Fresh and old scats contained similar proportion of migrating birds, indicating that scats on the dens were from summers only, making age separation easier. We ignored scats that were 2 years or older, as determined by extensive weathering, generally being white and brittle, or overgrowth of vegetation from previous seasons. Scats were dried at 90°C and prey remains

© 1999 British Ecological Society

© 1999 British Ecological Society
Journal of Animal Ecology, **68**, 34–49

Table 2. Relative density of *Lemmus* spp. and *Dicrostonyx torquatus* populations, with age profile and phase of examined *Lemmus sibiricus* populations. Density of *Lemmus* is measured as number of animals captured per 100 trap-nights with the small quadrate method, whereas for *Dicrostonyx* and total lemming density it is number of animals captured per 24 h with selectively set traps (see text for details). *n* is the number of examined *L. sibiricus* for age and phase determination. Age profile is based on weight of eye-lenses; the figures are the average of the lens-weights of each population. Note that the lens-weights are not comparable for mainland and island populations (lemmings on islands were about 40% heavier). Phase determination is based on information on age profile of the population, captures and estimated density during previous season (indicated by the frequency of old lemming faeces, winter nests and lemming runways). During the second visit to some sites (2^{nd}), additional captures were made of *L. sibiricus* for population phase analyses. Lemming trapping at site 4 was insufficient for analysis. Asterisk (*) denotes *Lemmus* indices not used in comparisons with arctic fox data

Site number	*Lemmus* captures (per 100 trap-nights)	*Dicrostonyx* captures (per 24 h)	Total lemming captures (per 24 h)	Time at site (h)	No. trap-nights for *Lemmus*	*Lemmus sibiricus* Sampling date	*n*	Lens weight (g) +/− SE	Population phase
1	0		0.89	27	240	10 June	0		Low
2	0	0	0	31	240	12 June	0		Low
5	10.0	16.47	29.18	51	120	18 June	27	34.92 ± 3.40	Increase/peak
6	0	8.73	8.73	22	120	20 Aug			
8	10.0	4.60	40.85	47	420	24 June	82	31.91 ± 1.35	Increase/peak
8 (2nd)	7.5*				240	15 Aug	17		
9	11.7	48.92	78.46	26	120	27 June	25	37.16 ± 2.70	Peak/decline
9 (2nd)	0*				120	13 Aug	0		
10	9.6	2.40	25.92	50	240	30 June	61	33.89 ± 1.59	Increase/peak
10 (2nd)	10.8*				240	10 Aug	24		
11	0	0.51	2.55	47	240	6 July	0		Low
12	12.9	9.12	24.00	50	240	4 Aug	31		Increase
13a	28.8		51.77	51	240	10 July	112	49.58 ± 1.13	Peak
13b	21.7	0	40.26	31	240	31 July	62	52.20 ± 11.52	Peak
14	6.3	0.57	14.86	42	240	15 July	25	41.55 ± 2.51	Decline
15	8.3	11.00	47.00	24	240	18 July	39	33.73 ± 1.94	Increase
16	2.0	0	1.20	20	50	20 July			Low
17	27.5	24.00	57.00	48	240	24 July	102	55.49 ± 1.18	Peak

were identified using reference material. In the analysis of scats we identified rodent species, reindeer *Rangifer tarandus* (L.), mountain hare *Lepus timidus* L., bird groups (ducks and geese, ptarmigan and grouse, waders, passerines), insects and plant material, as far as possible. At site 3, Kolguyev Island, we found rodent remains in one of the arctic fox scats ($n = 41$). This is the first report of rodents from the island, but the remains were only 20% by volume in the single scat and we were unable to determine the species. Since the amount was negligible, we excluded data from this site from all analyses of predatory response to rodents. The remains of *Lemmus* in the scats followed known distributions, with the Norwegian lemming *Lemmus lemmus* only on site 1, the Kola Peninsula, and the Siberian lemming *L. sibiricus* on all other sites. The collared lemming *Dicrostonyx torquatus* is not known for sites 1 and 13a (Faadeyevskiy Island). We found remains of *Dicrostonyx* in five out of 40 arctic fox scats from site 13b (Kotel'nyy Island), where the species previously was unknown.

We used a modified frequency of occurrence measure to estimate the amount of each prey category. When there were remains from more than one species in a single scat, we took into account the proportion of each prey species by dry volume. For example, one scat with 40% *Lemmus* and 60% *Dicrostonyx* plus another scat with 60% *Lemmus* and 40% *Dicrostonyx*, were considered to be equivalent to one scat with 100% *Lemmus* and one with 100% *Dicrostonyx*. We call this semi-quantitative measure 'percentage whole scat equivalents' (% WSE). Sample sizes remain the same as for frequency of occurrence. The advantage of this measure is that the relative amount of each prey category in the faeces is taken into account. This is especially important for prey items such as insects, which occur in small quantities in each scat. With a strict frequency of occurrence measure, these will be over-estimated. Very small or broken scats were joined with others from the same sample to form a scat of normal size.

We could not classify all prey items to species level. In some cases, lemming remains could be identified, but not as species (14% WSE in fresh, 9% in old scats). That class of remains was for each site divided into the *Lemmus* and *Dicrostonyx* classes, respectively, in the same proportion as the remains identified to species level. We have no reason to believe that there was a bias towards one species in the unidentified lemming class. In the same way we divided the class of unidentified rodents (22% WSE in fresh and 13% in old scats) among all rodents species found at each site. Beside *Lemmus* and *Dicrostonyx*, these were *Microtus* spp. and *Clethrionomys* spp. We did not identify these voles to species level, but trapped species were *M. oeconomus* (Pallas) (sites 1, 2, 4), *M. gregalis* (Pallas) (sites 5, 15), *Clethrionomys rufocanus* (Sundevall) (site 1) and *C. rutilus* (Pallas) (site 5) (Fredga *et al.* 1995).

Results

ARCTIC FOX DIET

We collected a total of 751 fresh and 320 old arctic fox scats at dens, excluding those at site 3 due to absence of rodents, and at a few other sites due to very low sample sizes (Table 1). In the following, percentage WSE will be given for fresh scats (with old in parentheses). The diet of arctic foxes in Siberia, as revealed from analyses of scats, was dominated by *Lemmus* (on most sites the Siberian lemming *L. sibiricus*) 59% (54%), followed by the collared lemming *Dicrostonyx torquatus* 24% (21%) (Fig. 2). Altogether, both species of lemmings constituted 83% (74%) and together with *Microtus*, *Clethrionomys* and unidentified rodents, arctic foxes included 87% (76%) of small rodents in their diet. In addition, birds were important, forming 8% (16%) of the diet. A similar distribution of prey items appeared in fresh and old scats (Fig. 2). The proportion of migrating birds (all

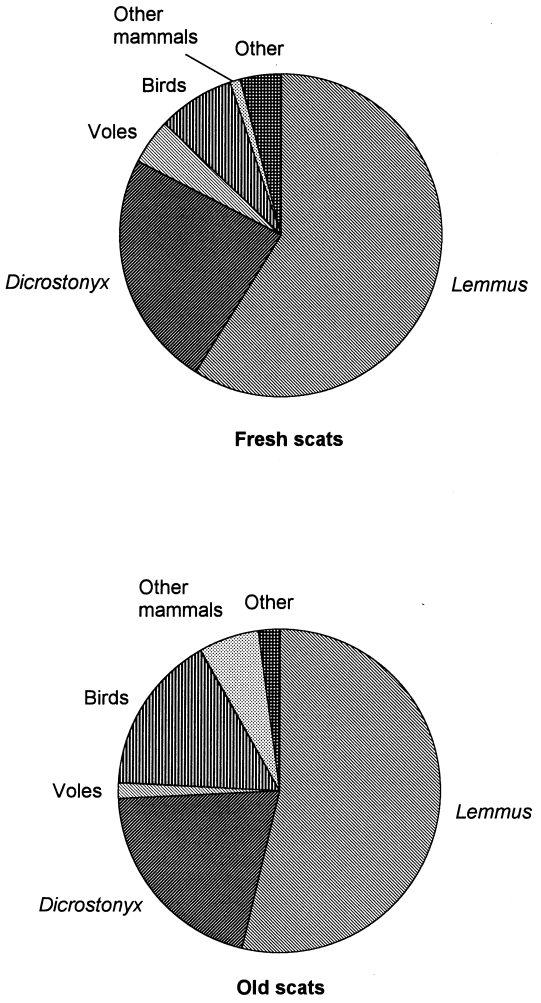

Fig. 2. Diet of arctic foxes as measured from (a) fresh and (b) old scats. Shown is the percentage of whole scat equivalents (WSE) for all sites combined. The measure WSE is a modified frequency of occurrence measure that takes into account the proportion of each prey species by dry volume.

© 1999 British Ecological Society

bird species except ptarmigan and grouse) was relatively high in both old (14%) and fresh scats (7%).

LEMMING DENSITIES AND THE PHASE OF THE CYCLE

The number of Siberian lemmings obtained in the grid trapping (small quadrate method), varied from 0 to 29 captured animals per 100 trap-nights. Information on densities and age profiles showed that the populations were in different phases of the lemming cycle (Table 2). On the islands in the east (sites 13a, 13b and 17), densities were very high and the age profile had a dominance of older individuals. Frequent old lemming faeces and runways indicated that densities had been high also during previous winter. These data strongly suggest that the populations were in the peak phase. We did not catch any *Lemmus* in the grid trapping at site 11, but there were indications of a recent crash. The density had been high during the past winter; at suitable wintering sites the ground was covered by lemming faeces. Also at site 1, no *Lemmus* were caught in the grid trapping, but here there were few signs of past activity. The population at site 9 crashed during the summer. In June, the density was intermediate and the age profile was dominated by older individuals. Upon our return in August, no *Lemmus* were caught. The population at site 14 showed strong indications to be in the decline phase. The age profile had a predominance of older individuals and present density was rather low. Frequent old lemming faeces and runways also suggested that past density had been high. The *Lemmus* populations on sites 5, 8, 10 and 15 had medium densities and age profiles dominated by young individuals. On the later visit in August, densities at sites 8 and 10 were similar to those obtained in June. Signs (faeces and runways) from previous season indicated a considerable lemming presence. At site 15, on the other hand, the few signs of lemming activity indicated low previous density. Altogether, these observations suggest that the *Lemmus* population at site 15 was in an early increase phase, whereas the populations at sites 5, 8 and 10 were in the late increase or peak phase. Eye-lenses of the individuals at site 12 were lost during transport, but body weight could be used to separate younger age categories (juveniles and sub-adults) from adults. The majority of captured Siberian lemmings on this locality belonged to the younger age category (17 out of 31, i.e. 55%). The age profile dominated by younger individuals, medium present density and signs suggesting low previous density, point at a population in the increase phase (Table 2).

Also collared lemming populations densities differed between sites, with an index ranging from 0 to 49 (Fig. 3). From the population density estimates, there was no evident synchrony between *Lemmus* and *Dicrostonyx* populations (Table 2, Fig. 3). At a few sites there were signs of correlated densities. Sites 2, 6 and 11 had low densities of both species. The *Dicrostonyx* population density was highest at site 9, where *Lemmus* reached an intermediate peak during the summer. At site 17, with the highest *Lemmus* density, there was also a high *Dicrostonyx* density (Fig. 3). We lack data on population phases for *Dicrostonyx* and can therefore not analyse the relation of population dynamics between lemming species in detail.

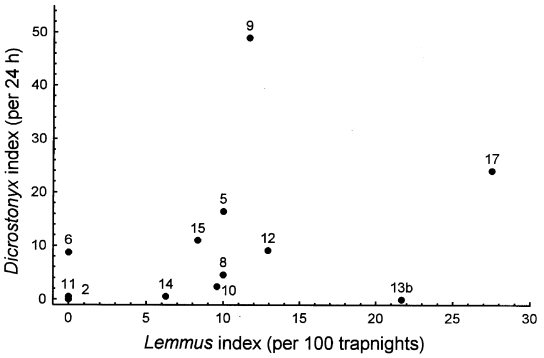

Fig. 3. The relation between *Dicrostonyx* and *Lemmus* trap indices at each study site; note that the scales of the two indices are not the same. Study site numbers as in Table 1.

NUMERICAL RESPONSE

The density of breeding arctic foxes varied between sites from 2 to 29 per 100 km^2, a ratio of over 1:14 (Table 1). When plotting the numerical response of arctic foxes preying on *Lemmus* (Fig. 4a), there was one group of sites with low density of both *Lemmus* and arctic foxes (sites 1, 2, 6, 11, 16). Another group had medium density of *Lemmus*, but low to medium density of foxes (sites 5, 8, 9, 10, 15). A third group had a high density of *Lemmus* and medium or high density of foxes (sites 13a, 13b, 17). Sites 12 and 14 had low to medium *Lemmus* density, but high fox density. The numerical response of arctic foxes preying on *Dicrostonyx* showed a different pattern (Fig. 4b). No site had high density of both arctic foxes and *Dicrostonyx*. When we combined all lemmings in the analysis, the pattern resembled that for *Lemmus* (Fig. 4c).

We have also compared how the proportion (% WSE) of lemmings, in fresh and old scats, respectively, could predict the number of breeding arctic foxes. In a linear regression, there was no significant relationship between the estimated number of breeding foxes and *Dicrostonyx*, neither for fresh ($P = 0{\cdot}68$, $t_{11} = -0{\cdot}43$) nor old scats ($P = 0{\cdot}20$; $t_{11} = -1{\cdot}35$). The same was true for all lemmings combined (fresh: $P = 0{\cdot}18$, $t_{13} = 1{\cdot}42$; old: $P = 0{\cdot}12$, $t_{11} = 1{\cdot}67$). However, the proportion of *Lemmus* in fresh scats tended to be positively correlated with the number of breeding foxes ($P = 0{\cdot}061$, $b = 0{\cdot}196$, $t_{13} = 2{\cdot}05$) and for one-year-old scats the relationship was significant ($P = 0{\cdot}011$, $b = 0{\cdot}190$, $t_{11} = 3{\cdot}03$; Fig. 5).

© 1999 British Ecological Society

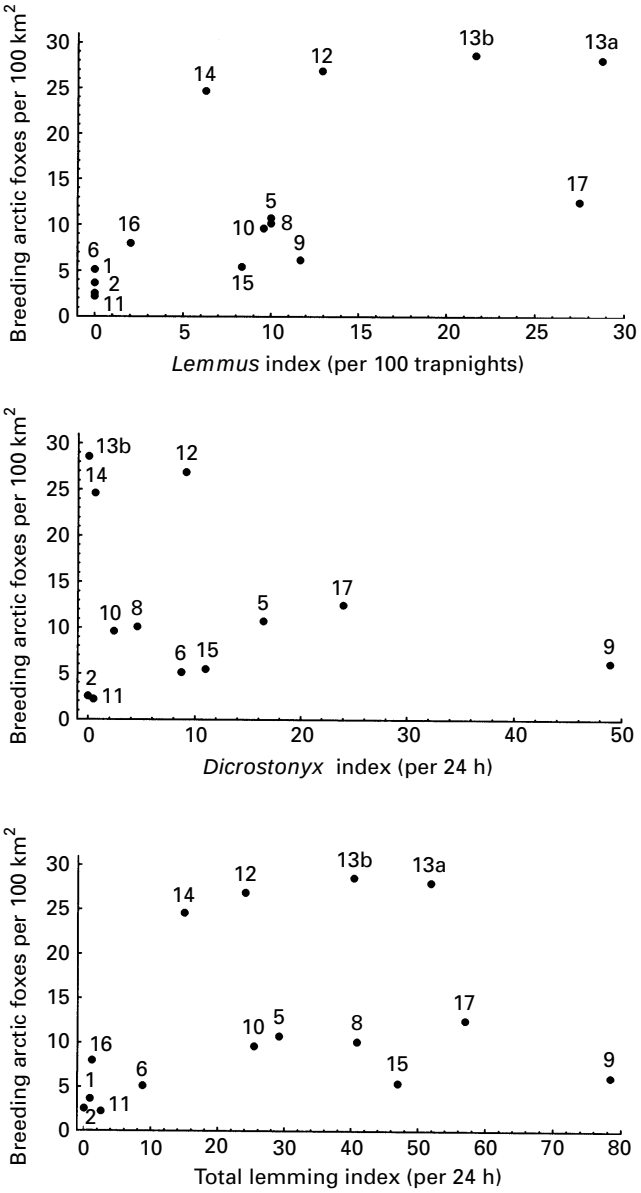

Fig. 4. Numerical response of arctic foxes to different population densities of (a) *Lemmus*, (b) *Dicrostonyx* and (c) all lemmings combined. Fox density is measured as number of breeding adults per 100 km^2. Lemming trap indices are explained in the text. Study site numbers as in Table 1.

In total, we counted 191 cubs in 54 dens at eight sites (mean = 3·54, SD = 2·01, Table 1). Mean litter size at each site was not related to total lemming density (Spearman $r_s = 0{\cdot}52$, $P = 0{\cdot}19$, $t_6 = 1{\cdot}47$) nor to *Dicrostonyx* density ($r_s = 0{\cdot}45$, $P = 0{\cdot}31$, $t_5 = 1{\cdot}13$), but there was a positive correlation with *Lemmus* density ($r_s = 0{\cdot}71$, $P = 0{\cdot}048$, $t_6 = 2{\cdot}48$; Fig. 6). No time lag could be detected for this parameter. Thus, arctic foxes responded to high *Lemmus* abundance with large litter sizes the same season.

FUNCTIONAL RESPONSE

Information on fox diet and lemming density at different sites made it possible to analyse how arctic foxes utilized prey in relation to prey abundance, i.e. the functional response. In the following, we only use data from fresh scats. When we plotted the proportion of *Lemmus* in fresh scats against the relative densities of *Lemmus*, a Holling's type II curve could be fitted when capture values of zero were excluded ($y = 63{\cdot}3x/(x + 0{\cdot}37)$; $R^2 = 0{\cdot}01$, $P = 0{\cdot}71$; Fig. 7a). This curve fit was not significant; neither was a type III functional response curve fit ($y = 61{\cdot}9 \times {}^2/(x^2 + 0{\cdot}74)$; $R^2 = 0{\cdot}02$, $P = 0{\cdot}68$). However, at densities so low that we were unable to trap *Lemmus*, they constituted 26–89% of the arctic foxes' diet. This indicates that arctic foxes showed a functional response to *Lemmus* which corresponds to a Holling's type II curve. The functional response of foxes to different densities of

© 1999 British Ecological Society

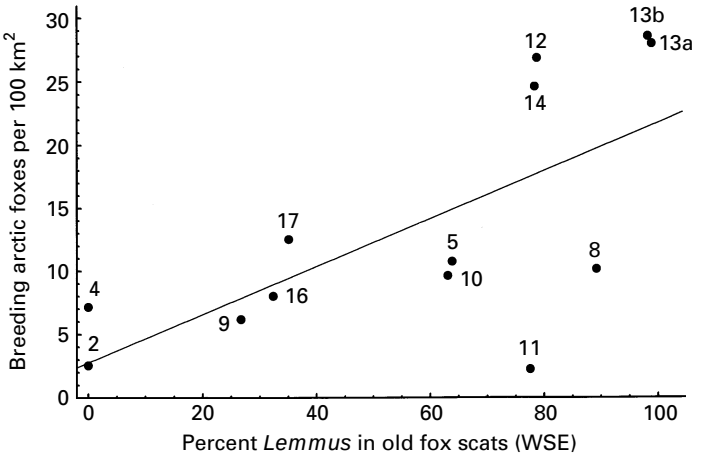

Fig. 5. The relationship between the density of breeding arctic foxes and the percentage of whole scat equivalents (WSE) of *Lemmus* in 1-year-old scats (only *L. sibiricus* is present at these sites). The line fit was significant ($P = 0{\cdot}011$, $b = 0{\cdot}190$, $t_{11} = 3{\cdot}03$) indicating that the numerical response of arctic foxes to changes in *L. sibiricus* population density had a time lag of approximately one year. Study site numbers as in Table 1.

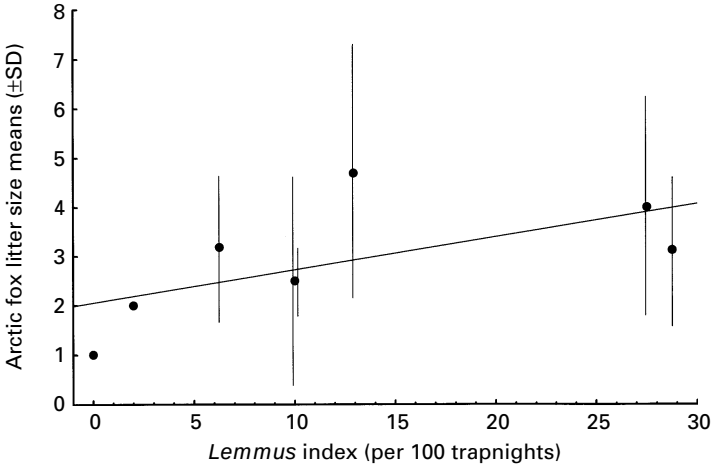

Fig. 6. Arctic fox litter size means (± SD) against *Lemmus* trap index for eight sites. There was a correlation between litter size means and *Lemmus* density ($r_s = 0{\cdot}71$, $P = 0{\cdot}048$, $t_6 = 2{\cdot}48$). Litter size estimates are minimum numbers for cubs at 3–12 weeks of age.

Dicrostonyx could be fit to a type III response curve ($y = 70{\cdot}6 \times 2/(x^2 + 165{\cdot}5$; $R^2 = 0{\cdot}45$, $P = 0{\cdot}024$; Fig. 7b). There was no significant fit to a type II functional response curve for the *Dicrostonyx* data ($y = 97{\cdot}1x/(x + 22{\cdot}8)$; $R^2 = 0{\cdot}18$, $P = 0{\cdot}19$). However, the coefficient of determination for the type III function was not significantly higher than for the type II ($P = 0{\cdot}23$). For both *Lemmus* and *Dicrostonyx* there was a considerable variance in the foxes' response at all prey densities. This variance disappeared when we analysed the functional response to total lemming densities (Fig. 7c). Here, data could be significantly explained both by a type II ($y = 94{\cdot}9x/(x + 0{\cdot}57)$; $R^2 = 0{\cdot}42$, $P = 0{\cdot}012$) and a type III functional response curve ($y = 93{\cdot}2 \times 2/(x^2 + 0{\cdot}68)$; $R^2 = 0{\cdot}55$, $P = 0{\cdot}003$). Pech *et al.* (1992) described a line test to discriminate between type II and III functions. In this test a linear regression is fitted and successively the data points with the highest x-values are deleted until $n = 5$. In short, if the slope of the new fitted line gets steeper and the intercept is positive and approaches zero when n decreases, a type II function can be inferred. If the slope approaches zero and the intercept goes from positive to negative values as n decreases, a type III function is suggested. In this test for all lemmings the slope increased while the intercept decreased, indicating a type II function (Fig. 7c). Arctic foxes responded very quickly to an increase in lemming abundance and used these species close to 100% already at moderate lemming densities. Although data was scarce for low lemming densities, we therefore conclude that the response to all lemmings combined was of type II.

To investigate a possible preference for *Lemmus* relative to *Dicrostonyx*, we plotted the proportion of *Lemmus* to all lemmings eaten by arctic foxes (from

© 1999 British Ecological Society

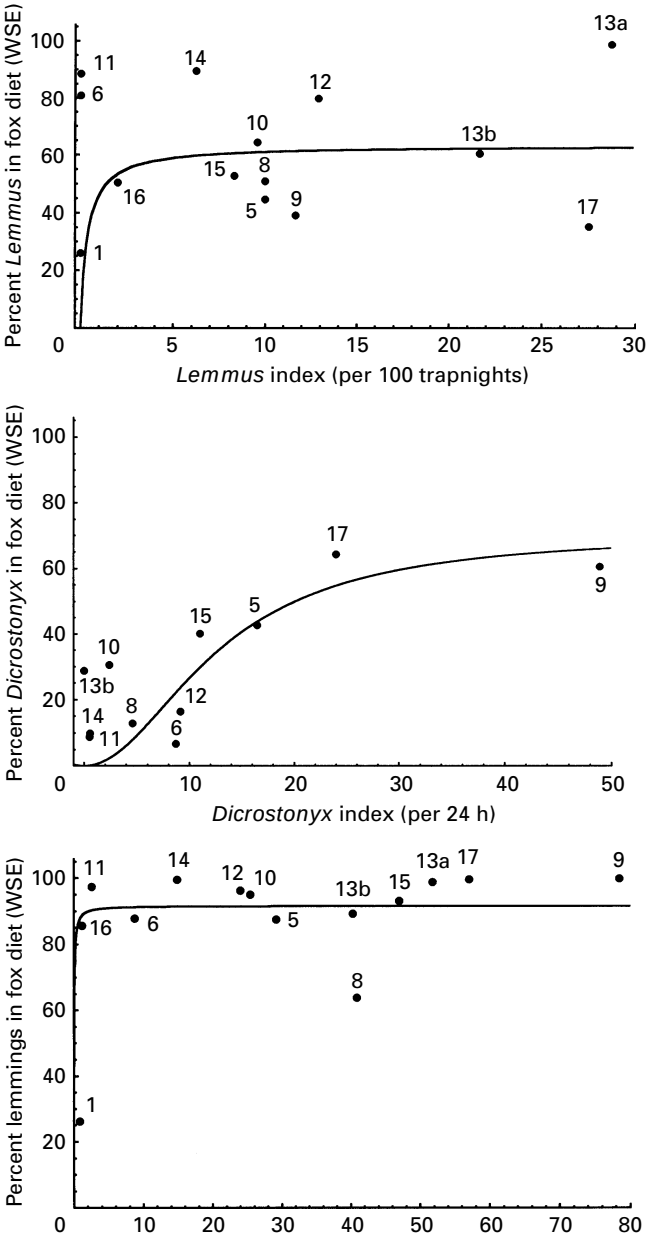

Fig. 7. Functional response of arctic foxes to different population densities of (a) *Lemmus*, (b) *Dicrostonyx* and (c) all lemmings combined. Fitted are curves of type II for (a) and (c) and type III for (b) The diet of arctic foxes is measured as the percentage of whole scat equivalents (WSE) for each site. Lemming trap indices are explained in the text. Study site numbers as in Table 1.

fresh scats) at each site against the relative abundance of *Lemmus* available (proportion of *Lemmus* to all lemmings in captures) (Fig. 8). The slope of the fitted line ($y = 0{\cdot}28 + 0{\cdot}49x$) was not significantly different from 1, i.e. $y = x$ ($P = 0{\cdot}059$, $t_9 = -2{\cdot}16$). At site 6, no *Lemmus* were caught although they constituted 81% of the foxes' diet and fresh carcasses were plentiful. The reason might be that the trapping was carried out in untypical habitat. Because site 6 was an extreme outlier we excluded it from this analysis. In all other analyses this site has been included.

Discussion

LEMMING CYCLICITY IN SIBERIA

A pronounced between-year cyclic pattern characterizes the dynamics of lemmings on the Siberian tundra as shown by long-term studies on several sites we investigated, e.g. the Kola peninsula (Koshkina 1980), Yamal (Dunaeva 1948; Kalyakin 1980, 1985; Danilov 1995), Taymyr (Sdobnikov 1959; Kuksov 1974), Kolyma (Chernyavskii *et al.* 1981), and the Wrangel Island (Chernyavskii & Tkachev 1982; Dorogoi 1987).

© 1999 British Ecological Society

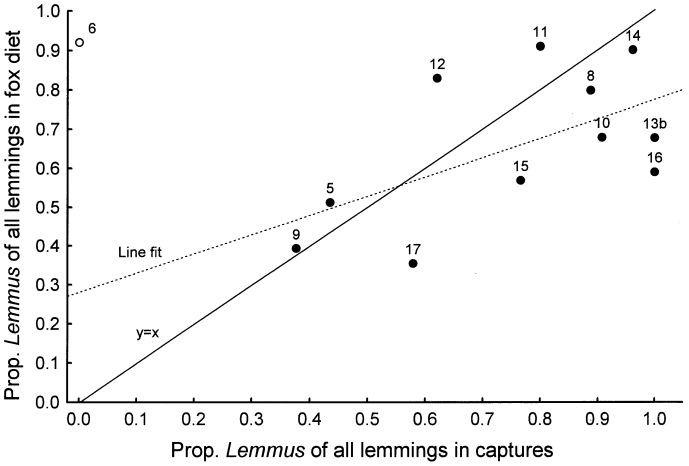

Fig. 8. Proportion of *Lemmus* in diet (measured as WSE in scats) against proportion in captures (trapping index). There was a tendency that at low relative abundance, *Dicrostonyx* constituted a higher proportion of the diet than expected ($t_9 = -2{\cdot}16$, $P = 0{\cdot}059$). Study site numbers as in Table 1. Site 6 was an extreme outlier and as such excluded from the analysis.

Generally, peak numbers have occurred with an interval of 3 or 4 years, but on the Wrangel Island the cyclic period has been 5 years (Chernyavskii & Tkachev 1982). In most cases (in 11 recorded cases out of 15 in studies we have reviewed, references above) peak numbers of co-existing Siberian and collared lemmings have coincided. In details, however, the dynamic pattern of the two species differ. Generally, the increase and the decline of the Siberian lemming populations have been more dramatic than for the collared lemming (Chernyavskii & Tkachev 1982; Dorogoi 1987). The cyclic pattern is not synchronous over the entire Siberian tundra region, but fluctuations can be synchronous over extensive areas. For example, peak numbers have generally occurred the same years on the Yamal and Taymyr peninsulas (Table 2 and references above).

How accurate is our phase determination? We have compared our suggestions with available data from recent Russian studies and reported observations at various sites in the Wader Study Group Bulletin (Tomkovich 1994a,b, 1996). On the Wrangel Island (site 17), the lemming populations were studied in detail during 1989–96 (Menyushina 1997). Both the Siberian and the collared lemming reached peak numbers in 1994 and declined in 1995 to low densities in 1996. This is in accordance with our phase determination (Table 2). On the Yamal and Taymyr peninsulas (sites 5–10), large or average number of lemmings (species not stated) were reported during 1994 and in some areas (two areas out of six in Yamal and five out of 12 in Taymyr) a declining trend was observed over the summer (Tomkovich 1996). The reports suggest peak or early decline phase in these areas. Decreasing or low numbers of lemmings were reported from these areas in summer 1992 and low or increasing densities in 1993 (Tomkovich 1994a,b). Altogether, available information indicates that on Yamal and Taymyr the lemming populations in 1994 were in various stages close to the peak phase (cf. Table 2). Furthermore, in 1994 Russian observers reported a declining lemming population in the Indigirka/Lopatka area (site 14), and an increasing population at Kolyma (site 15) (Tomkovich 1996). These reports are in agreement with our phase determination (Table 2). We have also compared our phase determinations with information from dendrochronological analyses performed during the same expedition (Danell *et al.* 1995). By this method, years of peak microtine populations are identified from the intensity of scars on willow stems, resulting from barking by rodents during winter food shortages. At Yana and Kolyma (sites 12 and 15), the last winter with high intensity of scarred willow stems had occurred in 1990/91 and Danell estimated that these populations were in the increase phase in 1994 (Kjell Danell, unpublished data). This is in accordance with our phase determination (Table 2). On Yamal and on Wrangel Island (sites 5, 6 and 17), high barking intensity had occurred over winter 1993/94 indicating high densities and populations in the peak or decline phase in summer 1994 (cf. Table 2). No data for dendrochronological analysis was obtained on Taymyr. At Olenëkskiy (site 11) we found clear indications of a recent crash from local high density during previous winter. The dendrochronological analysis from this site suggests a peak in 1989/90, but low densities since then. Obviously, the local high density in winter 1993/94 at this site was missed in the dendrochronological analysis. The sample size for this analysis, however, is limited from site 11 and the peak density might have been very local. In short, the accuracy of our phase determination is supported by data from independent Russian studies and information from dendrochronological analyses.

We have examined data from several locations to

© 1999 British Ecological Society

reveal patterns between arctic foxes and lemmings instead of following populations at a single place. To get a sample size similar to this from one site would require a 17 years study. Furthermore, even if lemming populations from different parts of Siberia might be different in their basic population pattern, arctic foxes are truly nomadic and have a capacity to migrate more than 1000 km in one season. When we measured predator response to different lemming densities across areas, it is therefore likely to be a general arctic fox response.

NUMERICAL RESPONSE

We have found that during one summer, densities of both arctic foxes and lemmings differed widely between sites along the Siberian north coast. Lemmings were the main prey item for arctic foxes, but the predatory response to *Lemmus* spp. (the Siberian and Norwegian lemmings) was different from the response to *Dicrostonyx torquatus* (the collared lemming). Our data suggest that arctic foxes responded numerically with a time lag to changes in *Lemmus* density. The observed pattern can be described as a limit cycle, generated by such a time lag (May 1976). This was supported by phase determination of the lemming populations. A high density of arctic foxes was related to a declining Siberian lemming population at site 14 and the Siberian lemming population at site 15 in the increase phase was associated with low arctic fox numbers. However, site 12 was an exception, where the lemming population was suggested to be in the increase phase but fox density was already high (Fig. 4a). This could be due to the different spatial scales of lemming and fox inventories if the lemming increase was very local, as discussed for *Lemmus* in Alaska (Garrott *et al.* 1983). Another possibility is local immigration of arctic foxes. The lemming populations on the Yamal and Taymyr peninsulas (sites 5, 8, 9 and 10) were estimated to be close to the peak phase while fox numbers were low to moderate (Table 2, Fig. 4a). The densities of *Lemmus* were moderate on these sites compared with the densities on sites 13a, 13b and 17. What seemed like peaks in these populations might be a temporary cessation of growth during summer, that could be followed by a further increase, i.e. a 'second peak'. Unfortunately, we have no information from these areas on *Lemmus* densities in 1995. The numerical response of arctic foxes relative to collared lemming densities showed a different pattern (Fig. 4b). No site had high densities of both arctic foxes and collared lemmings. However, when we combined all lemmings in the analysis, *Lemmus* dominated and we again got a pattern which to some extent fits the description of a limit cycle (Figs 4c and 9).

Lemming cycles in Eurasia have a periodicity of 3–5 years (Chernyavskii & Tkachev 1982; Hanski, Hansson & Henttonen 1991), which can be described as limit cycles. If these cycles consist of four transitions as illustrated in Fig. 9a) time lag between lemmings and arctic foxes of ≈ 12 months (9–15) can be inferred. In our study, the proportion of migrating birds was even higher in old scats than in fresh ones, implying that the old scats were from the previous summer and not winter scats. Macpherson (1969) found that ranked proportions of lemmings in the diet were correlated with ranked lemming density as measured by trapping. We found that the number of breeding arctic foxes was better predicted by the proportion of Siberian lemmings in old scats than in fresh scats. Thus, regardless of the functional response, the size of the breeding population of arctic foxes was determined by their consumption of Siberian lemmings the previous year. The strongest evidence for a limit cycle was the phase determination of the lemming cycle, as shown in Fig. 9. Arctic foxes on the Siberian tundra thus showed a numerical response with a time lag of ≈ 12 months to the Siberian lemming, but we found no evidence for a numerical response to population density changes in the collared lemming.

The time lag in numerical response was probably due to the different reproductive rates of lemmings and arctic foxes. No time lag could be detected for litter sizes. However, whereas lemmings can have several litters throughout the winter and summer, arctic foxes can only produce a single litter each year. The arctic fox can respond to high abundance of small rodents by producing litters of up to 19 cubs, although such large litters only result from high food availability during winter and early spring (Angerbjörn *et al.* 1991; Ovsyanikov 1993; Angerbjörn *et al.* 1995; Tannerfeldt & Angerbjörn 1998). Our interpretation of the pattern observed in this study, based also on other studies (Angerbjörn *et al.* 1995; Tannerfeldt & Angerbjörn 1996, 1998), is that the delay in numerical response is due to the fact that arctic foxes reproduce only once a year. In the year following a lemming peak, increased recruitment results in large numbers of reproducing arctic foxes. An alternative would be that migrating foxes that encounter a lemming peak stay and reproduce the following year. However, this would imply summer migration, contrary to known patterns (Bræstrup 1941; Elton 1949; Pulliainen 1965; Chesemore 1968; Bannikov 1970; Eberhardt & Hanson 1978). Furthermore, summer migration would not be advantageous since a peak in lemming numbers is likely to be followed by a crash (Tannerfeldt & Angerbjörn 1996). Avian predators, on the other hand, migrate over vast areas seasonally and have a numerical response without a time lag (Korpimäki 1994; Potapov 1997; Reid, Krebs & Kenney 1997).

Arctic fox litter sizes in this study were surprisingly small (Tannerfeldt & Angerbjörn 1998). The reason might be that the investigated area was in the northernmost part of Siberia, where the soil mostly consists of mud and sand with a thawing active layer less than 1 m in most soils (Goryachkin 1994). The frequent soil movements caused by permafrost may therefore

© 1999 British Ecological Society

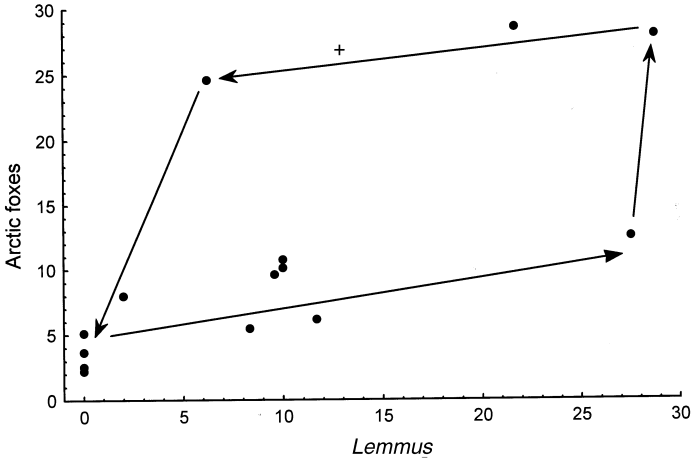

Fig. 9. Arrows added to Fig. 4(a), suggesting how arctic foxes respond numerically with a time lag to changes in lemming density. The pattern can be explained as a limit cycle, generated by such a time lag. This was supported by phase determination of the *Lemmus* populations, except at site 12 (denoted by a cross) which was suggested to be in the increase phase by *Lemmus* data and in the decrease phase according to this figure.

prevent dens from becoming very large (cf. Chesemore 1969), and small dens presumably infer larger predation risks. Arctic foxes sometimes split their litter as a precaution against predation, using two or more dens (Prestrud 1992b; Anthony 1996, personal observation). An alternative explanation to the small litters could be that foxes in these areas migrate seasonally and are not present during winter (to react to increases in lemming populations). Some authors describe 'seasonal migrations' in northern Siberia (e.g. Bannikov 1970), but there have been no studies with individually marked animals to show the exact nature of such movements. An additional problem with these litter size estimates is the long time span of the study. The age of cubs varied from $\approx$3–12 weeks and postnatal mortality will have affected litters differently (Tannerfeldt & Angerbjörn 1998).

FUNCTIONAL RESPONSE

The functional response for *Lemmus* followed a Holling's type II curve, but for *Dicrostonyx* it was a type III curve. For all lemmings combined the functional response was described by a type II function since *Lemmus* was the dominating prey (Fig. 7). Arctic foxes base their diet on lemmings at densities so low that we had difficulties to trap even a single animal. The functional response curves are therefore unclear at low densities. Nevertheless, there was a marked difference in arctic fox preference between the lemming species, with a steep functional response curve for *Lemmus*. At densities that were low relative to *Lemmus*, however, there was still a considerable proportion of *Dicrostonyx* in the diet (Fig. 8). This is expected if it is important for arctic foxes to sample prey densities in different types of habitat within their territory. Many of their prey species fluctuate and these fluctuations are not always synchronized (e.g. Batzli & Lesieutre 1995). Several studies have shown that the arctic fox, while often being dependent on lemmings for breeding, is an extremely curious opportunist that will utilize almost any type of food source (e.g. Fay & Stephenson 1989; Stickney 1989; Birks & Penford 1990; Hersteinsson & Macdonald 1996).

A functional response curve of type III can be caused by prey switching or a longer handling time at low prey densities (Taylor 1984). It is thus possible that arctic foxes search for *Lemmus* rather than for *Dicrostonyx* at low densities. The two lemming genera are found in different habitats, especially at low densities, with *Lemmus* in wet areas and *Dicrostonyx* in dry areas (Rodgers & Lewis 1986). However, it is important to note that the scale of habitat heterogeneity is smaller than an arctic fox home range and both habitat types are normally available for a single fox. The second alternative, that handling time is longer for *Dicrostonyx* at lower densities than at higher densities and than for *Lemmus*, is also possible. Because *Dicrostonyx* dig extensive burrows, they may be better protected against predation. This would be more pronounced at low population densities when burrows and food are plentiful. A similar phenomenon was suggested by Hanski & Henttonen (1996) for *Clethrionomys* and *Microtus* rodents.

The total predatory response (the product of functional and numerical responses) determines the effect of predation on a prey population (Pech *et al.* 1992). We cannot quantify this total response in our material, but a qualitative comparison following Pech *et al.* (1992) implies that the predation rate for *Lemmus* will decrease with increasing prey density, while it for *Dicrostonyx* will increase at low to medium densities but decrease at higher densities. This suggests that predation by arctic foxes may regulate a population of *Dicrostonyx* at low and moderate densities. According to theoretical models, a time lag in numerical

© 1999 British Ecological Society

response, as the one observed for *Lemmus*, might generate cyclicity in a predator–prey system (Hanski & Korpimäki 1995). Many authors have argued that cyclic rodent oscillations in the northern boreal zone are generated by mustelid predation (Hansson & Henttonen 1985; 1988; Hanski *et al*. 1991, 1993; Hanski & Korpimäki 1995; Hanski & Henttonen 1996; Turchin & Hanski 1997). Their models are based on the fact that small mustelids are specialized predators with a type II functional response and a time lag in numerical response to rodent population fluctuations. This system can not be applied to areas where mustelids are absent, e.g. on the Wrangel Island. However, arctic foxes might play the same role on the tundra as mustelids are suggested to do in boreal areas. For *Lemmus*, they have a time lag of approximately one year in their numerical response to prey population peaks and a functional response characteristic for a specialized predator. We therefore argue that for *Lemmus* as prey, the arctic fox falls into the general category resident specialists (*sensu* Andersson & Erlinge 1977), where also small mustelids belong. For *Dicrostonyx*, arctic foxes instead act as generalists. The effect on these prey species will therefore be very different.

In conclusion, arctic foxes seem to have the capacity to deepen and prolong the crash phase of *Lemmus* cycles and thereby increase both amplitude and period of cycles (e.g. Henttonen *et al*. 1987; Hanski & Korpimäki 1995). For *Dicrostonyx*, their predatory patterns instead suggests a capacity to dampen oscillations (Andersson & Erlinge 1977; Turchin & Hanski 1997). There was only one site with a very high *Dicrostonyx* density, the polar desert at Cape Chelyuskin (site 9) on the northernmost point on the Eurasian mainland. It is possible that *Dicrostonyx* have an advantage over *Lemmus* in this type of environment (Rodgers & Lewis 1986). The relationship between the arctic fox and a lemming species cannot be analysed in detail without taking other co-existing prey species into account (cf. Boutin 1995; Pech *et al*. 1995; Schmitz 1995). For a more thorough understanding of the tundra community, we also need data from areas where the lemming species are allopatric. There also seems to be a need for theoretical models of population fluctuations that include several prey species for which the predatory responses are different (Schmitz 1995; Abrams & Matsuda 1996; Hanski & Henttonen 1996).

Acknowledgements

V. Fedorov and K. Fredga trapped the collared lemmings and several people, especially E. Isaksson and N. Kjellén, helped us with inventories of fox dens. We are immensely indebted to D. Fucik for his patience and skill in helping us with analyses of fox scats. We thank P. Frodin, D. Hasselquist, P. Nilsson, and M. Svensson for help with lemming trapping and analysing these data, K. Danell for providing unpublished data from his dendrochronological analyses, and L. Baskin for translating Russian papers on lemming studies in Siberia. We are very grateful to the Swedish Polar Secretariat for organizing the Tundra Ecology Expedition 1994. Financial support was obtained from NFR (B–BU 3324–308) to Erlinge and Fredga, and from the Ymer foundation to Angerbjörn.

References

Abrams, P.A. & Matsuda, H. (1996) Positive indirect effects between prey species that share predators. *Ecology*, **77**, 610–616.

Andersson, M. & Erlinge, S. (1977) Influence of predation on rodent populations. *Oikos*, **29**, 591–597.

Angerbjörn, A., Arvidson, B., Norén, E. & Strömgren, L. (1991) The effects of winter food on reproduction in the arctic fox (Alopex lagopus): a field experiment. *Journal of Animal Ecology*, **60**, 705–714.

Angerbjörn, A. & Tannerfeldt, M. (1995) Life history ecology of the arctic fox in Siberia. *Swedish-Russian Tundra Ecology—Expedition ñ94. A Cruise Report* (eds E. Grönlund & O. Melander), pp. 118–121. Swedish Polar Research Secretariat, Stockholm.

Angerbjörn, A., Tannerfeldt, M., Bjärvall, A., Ericson, M., From, J. & Norén, E. (1995) Dynamics of the arctic fox population in Sweden. *Annales Zoologici Fennici*, **32**, 55–68.

Anthony, M. (1996) Den use by arctic foxes (Alopex lagopus) in a subarctic region of western Alaska. *Canadian Journal of Zoology*, **74**, 627–631.

Bannikov, A.G. (1970) Arctic fox in the U.S.S.R. Biological premises of productivity. *Productivity and Conservation in Northern Circumpolar Lands* (eds W. A. Fuller & P. G. Kevan), pp. 121–130. IUCN and Natural Resources, Morges.

Batzli, G.O. (1993) Food selection by lemmings. *Biology of Lemmings* (eds N. C. Stenseth & R. A. Ims), pp. 281–301. Academic Press Ltd, London.

Batzli, G.O. & Lesieutre, C. (1995) Community organization of arvicoline rodents in northern Alaska. *Oikos*, **72**, 88–98.

Birks, J.D.S. & Penford, N. (1990) Observations on the ecology of arctic foxes *Alopex lagopus* in Eqalummiut Nunaat, West Greenland. *Meddelelser om Grønland, Bioscience*, **32**, 1–28.

Boutin, S. (1995) Testing predator–prey theory by studying fluctuating populations of small mammals. *Wildlife Research*, **22**, 89–100.

Boutin, S., Krebs, C.J., Boonstra, R., Dale, M.R.T., Hannon, S.J., Martin, K., Sinclair, A.R.E., Smith, J.N.M., Turkington, R., Blower, M., Byrom, A., Doyle, F.I., Doyle, C., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D.L., Nams, V., O'Donoghue, M., Rohner, C. & Schweiger, S. (1995) Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos*, **74**, 69–80.

Bræstrup, F.W. (1941) A study on the arctic fox in Greenland. *Meddelelser om Grønland*, **131**, 1–102.

Chernyavskii, F.B., Kiryushchenko, S.P. & Kiryushchenko, T.V. (1981) Data on winter ecology of Siberian (*Lemmus sibiricus*) and hoofed (*Dicrostonyx torquatus*) lemmings. *Ecology of Mammals and Birds on the Wrangel Island*, pp. 99–122. Vladivostok (in Russian).

Chernyavskii, F.B. & Tkachev, A.V. (1982) *Population Cycles of Lemmings in Arctic*. Nauka, Moscow (in Russian).

© 1999 British Ecological Society

Chesemore, D. (1968) Distribution and movements of white foxes in northern and western Alaska. *Canadian Journal of Zoology*, **46**, 849–853.

Chesemore, D. (1969) Den ecology of the arctic fox in northern Alaska. *Canadian Journal of Zoology*, **47**, 121–129.

Collett, R. (1911–12) *Norges Pattedyr*. Aschehaug & Co., Kristiania.

Corbett, G.B. & Hill, J.E. (1991) *A World List of Mammalian Species*, 3rd edn. Oxford University Press, Oxford.

Danell, K., Roininen, H., Olofsson, E.-B., Ericsson, L. & Palo, Th. (1995) Interactions between willows and herbivores. *Swedish-Russian Tundra Ecology—Expedition No. 94. A Cruise Report* (eds E. Grönlund & O. Melander), pp. 49–55. Swedish Polar Research Secretariat, Stockholm.

Danilov, A.N. (1995) On the role of lemmings in biological connections at southern Yamal. *Ecologiya*, **3**, 203–207 (in Russian).

Dorogoi, I.V. (1987) *Ecology of Microtine Predators of the Wrangel Island and Their Role in Numbers Dynamics of Lemmings*. Academy of Sciences, Vladivostok (in Russian).

Dunaeva, T.N. (1948) Comparative review of ecology of tundra voles on the Yamal peninsula. *Proceedings of the Geographical Institute, Moscow*, **41**, 78–143 (in Russian).

Eberhardt, L. & Hanson, W. (1978) Long-distance movements of arctic foxes tagged in northern Alaska. *The Canadian Field-Naturalist*, **92**, 386–388.

Elton, C. (1949) Movements of arctic fox populations in the region of Baffin bay and Smith Sound. *Polar Record*, **5**, 296–305.

Elton, C. & Nicholson, M. (1942) The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology*, **11**, 215–44.

Erlinge, S. (1987) Predation and noncyclicity in a microtine population in southern Sweden. *Oikos*, **50**, 347–352.

Erlinge, S., Frodin, P., Hasselquist, D., Nilsson, P. & Svensson, M. (1995) The cyclic lemmings. *Swedish-Russian Tundra Ecology-Expedition ñ94. A Cruise Report*. (eds E. Grönlund & O. Melander), pp. 135–142. Swedish Polar Research Secretariat, Stockholm.

Erlinge, S., Göransson, G., Högstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylvén, M. (1984) Can vertebrate predators regulate their prey? *American Naturalist*, **123**, 125–133.

Erlinge, S., Göransson, G., Högstedt, G., Liberg, O., Loman, J., Nilsson, I.N., Nilsson, T., von Schantz, T. & Sylvén, M. (1983) Predation as a regulating factor in small rodent populations in southern Sweden. *Oikos*, **40**, 36–52.

Fay, F.H. & Stephenson, R.O. (1989) Annual, seasonal, and habitat-related variation in feeding habits of the arctic fox (*Alopex lagopus*) on St. Lawrence Island, Bering Sea. *Canadian Journal of Zoology*, **67**, 1986–94.

Frafjord, K., Becker, D. & Angerbjörn, A. (1989) Interactions between arctic and red foxes in Scandinavia-predation and aggression. *Arctic*, **42**, 354–356.

Fredga, K., Fedorov, V., Gelter, H., Jarell, G. & Thulin, C.-G. (1995) Genetic studies in lemmings. *Swedish-Russian Tundra Ecology-Expedition ñ94. A Cruise Report* (eds E. Grönlund & O. Melander), pp. 235–242. Swedish Polar Research Secretariat, Stockholm.

Garrott, R.A., Eberhardt, L.E. & Hanson, W.C. (1983) Summer food habits of juvenile arctic foxes in northern Alaska. *Journal of Wildlife Management*, **47**, 540–545.

Garrott, R.A., Eberhardt, L.E. & Hanson, W.C. (1984) Arctic fox denning behaviour in northern Alaska. *Canadian Journal of Zoology*, **62**, 1636–1640.

Goryachkin, S.V. (1994) Soils and permafrost. *Diversity of Natural Ecosystems in the Russian Arctic*. A *Guidebook* (eds S. V. Goryachkin, R. I. Zlotin & G. M. Tertitsky). Reprocentralen at Lund University, Lund.

Hagen, A., Stenseth, N.Ch., Østbye, E. & Skar, H.-J. (1980) The eye lens as an age indicator in the root vole. *Acta Theriologica*, **25**(4), 39–50.

Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialised predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, **60**, 353–367.

Hanski, I. & Henttonen, H. (1994) Traces of population dynamics past. *Trends in Ecology and Evolution*, **9**, 2–4.

Hanski, I. & Henttonen, H. (1996) Predation on competing rodent species: A simple explanation of complex patterns. *Journal of Animal Ecology*, **65**, 220–232.

Hanski, I. & Korpimäki, E. (1995) Microtine rodent dynamics in northern Europe: parameterized models for the predator–prey interaction. *Ecology*, **76**, 840–850.

Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. (1993) Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, **364**, 232–235.

Hansson, L. & Henttonen, H. (1985) Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia*, **67**, 394–402.

Hansson, L. & Henttonen, H. (1988) Rodent dynamics as community processes. *Trends in Ecology and Evolution*, **3**, 195–200.

Hedberg, D. (1995) General review of Swedish projects ^ terrestrial and marine. *Swedish-Russian Tundra Ecology-Expedition ñ94*. A *Cruise Report* (eds E. Grönlund & O. Melander), pp. 22–29. Swedish Polar Research Secretariat, Stockholm.

Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. (1987) How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos*, **50**, 353–365.

Hersteinsson, P. (1990) The fertility of Icelandic arctic fox vixens. *Wildlife Management News (Iceland)*, **6**, 19–27. (In Icelandic with English summary.)

Hersteinsson, P. & Macdonald, D.W. (1996) Diet of arctic foxes (*Alopex lagopus*) in Iceland. *Journal of Zoology*, **240**, 457–474.

Hiruki, L.M. & Stirling, I. (1989) Population dynamics of the arctic fox, *Alopex lagopus*, on Banks Island, Northwest Territories. *Canadian Field-Naturalist*, **103**, 380–387.

Jarrell, G.H. & Fredga, K. (1993) How many kinds of lemmings? A taxonomic overview. *Biology of Lemmings* (eds N. C. Stenseth & R. A. Ims), pp. 45–57. Academic Press Ltd, London.

Kaikusalo, A. & Angerbjörn, A. (1995) The arctic fox in Finnish Lapland, 1964–93. *Annales Zoologici Fennici*, **32**, 69–77.

Kalyakin, V.N. (1980). Number dynamics of lemmings at the southern Yamal. *Mechanisms of Regulation of Numbers of Lemmings and Voles at the Extreme North*, pp. 60–65. Vladivostok (In Russian).

Kalyakin, V.N. (1985) Mammals in ecosystems of the southern Yamal. *Mammals in surface ecosystems*, pp. 69–99. Nauka, Moscow (in Russian).

Korpimäki, E. (1994) Rapid or delayed tracking of multiannual vole cycles by avian predators? *Journal of Animal Ecology*, **63**, 619–628.

Korpimäki, E. & Norrdahl, K. (1989) Predation of Tengmalm's owls: numerical responses, functional responses, and dampening impact on population fluctuations of microtines. *Oikos*, **54**, 154–164.

Korpimäki, E., Norrdahl, K. & Rinta-Jaskari, T. (1991) Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia*, **88**, 552–561.

Koshkina, T.V. (1980) Characteristics of population cycles of small rodents of subarctic. *Mechanism of Regulation of Numbers of Lemmings and Voles in the Extreme North*, pp. 77–95. Vladivostok (in Russian).

Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K. & Turkington,

© 1999 British Ecological Society

R. (1995) Impact of food and predation on the snowshoe hare cycle. *Science*, **269**, 1112–1115.

Kuksov, V.A. (1974). *Density and Structure of Taymyr Population of* Lemmus sibiricus *Kerr*. The First Theriological Congress Moscow (in Russian).

Macpherson, A. (1969) The dynamics of Canadian arctic fox populations. *Canadian Wildlife Service Report Series*, **8**, 1–49.

May, R.M. (1976) Models for two interacting populations. *Theoretical Ecology, Principles and Applications* (ed. R. M. May), pp. 49–70. Blackwell Scientific Publications, Oxford.

Menyushina, I.E. (1997) *Snowy Owl Reproduction in Relation to Lemming Population Cycles in Wrangel Island*. 2nd International Owl Symposium, Winnipeg, Canada.

Myllimäki, A., Paasikallio, A., Pankakoski, E. & Kanervo, V. (1971) Removal experiments on small quadrates as a means of rapid assessment of the abundance of small mammals. *Annales Zoologici Fennici*, **8**, 177–185.

Oksanen, L. & Oksanen, T. (1992) Long term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. *Ecography*, **15**, 226–236.

Ovsyanikov, N.G. (1993) *Behaviour and Social Organization of the Arctic Fox*. Moscow (in Russian). Isdatelctvo Tsentralnoi Naushno Icsledovatelskoi Laboratori Ochtuichevo Chosjaistvoi Sapoveduikov.

Pech, R.P., Sinclair, A.R.E. & Newsome, A.E. (1995) Predation models for primary and secondary prey species. *Wildlife Research*, **22**, 55–64.

Pech, R.P., Sinclair, A.R.E., Newsome, A.E. & Catling, P.C. (1992) Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. *Oecologia*, **89**, 102–112.

Pitelka, F.A. & Batzli, G.O. (1993) Distribution, abundance and habitat use by lemmings on the north slope of Alaska. *Biology of Lemmings* (eds N. C. Stenseth & R. A. Ims), pp. 213–236. Academic Press Ltd, London.

Potapov, E.R. (1997) What determines the population density and reproductive success of rough-legged buzzards, *Buteo lagopus*, in the Siberian tundra? *Oikos*, **78**, 362–376.

Prestrud, P. (1992a) Physical characteristics of arctic fox (Alopex lagopus) dens in Svalbard. *Arctic*, **45**, 154–158.

Prestrud, P. (1992b) Denning and home-range characteristics of breeding arctic foxes in Svalbard. *Canadian Journal of Zoology*, **70**, 1276–1283.

Pulliainen, E. (1965) On the distribution and migrations of the arctic fox (*Alopex lagopus* L.) in Finland. *Aquilo Series of Zoology*, **2**, 25–40.

Reid, D.G., Krebs, C.J. & Kenney, A.J. (1997) Patterns of predation on noncyclic lemmings. *Ecological Monographs*, **67**, 89–108.

Rodgers, A.R. & Lewis, M.C. (1986) Diet selection in Arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx* groenlandicus): demography, home range, and habitat use. *Canadian Journal of Zoology*, **64**, 2717–2127.

Schmitz, O.J. (1995) Functional-responses of optimal consumers and the potential for regulation of resource populations. *Wildlife Research*, **22**, 101–113.

Sdobnikov, V.M. (1959) Number dynamics of birds and mammals on the northern Taymyr. *Zoologicheskii Zhurnal*, **38**, 1702–1709 (in Russian).

Sinclair, A.R.E., Gosline, J.M., Holdsworth, G., Krebs, C.J., Boutin, S., Smith, J.N.M., Boonstra, R. & Dale, M. (1993) Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. *American Naturalist*, **141**, 173–198.

Smith, C.A.S., Smits, C.M.M. & Slough, B.G. (1992) Landform selection and soil modification associated with arctic fox (*Alopex lagopus*) den sites in Yukon Territory, Canada. Correction of abstract. *Arctic and Alpine Research*, **24**, 324–328. Erratum published in *Arctic and Alpine Research* Vol. 25. Iss. 1. 1993. p. 78.

Smits, C.M.M., Slough, B.G. & Angerbjörn, A. (1989) *Abundance and Summer Occupancy of Arctic Fox Dens in Northern Yukon Territory 1984–88*. Yukon Fish and Wildlife Branch, Department of Renewable Resources, Government of the Yukon Territory, Whitehorse, Canada.

Stenseth, N.C. & Ims, R.A. (1993) Population dynamics of lemmings: temporal and spatial variation—an introduction. *Biology of Lemmings* (eds N. C. Stenseth & R. A. Ims), pp. 61–96. Academic Press Ltd, London.

Stickney, A.A. (1989) The foraging behavior, habitat use, and diet of arctic foxes (*Alopex lagopus*) in a goose nesting area near Kokechik Bay, Alaska. MSc thesis, University of Alaska, Fairbanks.

Tannerfeldt, M. & Angerbjörn, A. (1996) Life history strategies in a fluctuating environment: establishment and reproductive success in the arctic fox. *Ecography*, **19**, 209–220.

Tannerfeldt, M. & Angerbjörn, A. (1998) Fluctuating resources and the evolution of litter size in the arctic fox. *Oikos*, **81** (in press).

Taylor, R.J. (1984) *Predation*. Chapman and Hall, London.

Tomkovich, P.S. (1994a) Breeding conditions for waders in Russian tundras in 1992. *Wader Study Group Bulletin*, **75**, 20–26.

Tomkovich, P.S. (1994b) Breeding conditions for waders in Russian tundras in 1993. *Wader Study Group Bulletin*, **75**, 27–36.

Tomkovich, P.S. (1996) Breeding conditions for waders in Russian tundras in 1994. *Wader Study Group Bulletin*, **79**, 71–81.

Tostel, K., Sinclair, A.R.E., Walters, C.J. & Krebs, C.J. (1987) Can predation cause the 10-year hare cycle? *Oecologia*, **74**, 185–192.

Turchin, P. & Hanski, I. (1997) An empirically based model for latitudinal gradient in vole population dynamics. *American Naturalist*, **149**, 842–874.

Wiklund, C.G., Kjellén, N. & Isaksson, E. (1997) Mechanisms determining the spatial distribution of microtine predators on the Arctic tundra. *Journal of Animal Ecology*, **66** (in press).

Wilson, D.E. & Reeder, D.M. (1993) *Mammal Species of the World*. Smithsonian Institution Press, Herndon.

Received 17 October 1997; revision received 12 March 1998

© 1999 British Ecological Society