

Functional and numerical responses of four lemming predators in high arctic Greenland

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The high-arctic tundra ecosystem has the world's simplest vertebrate predator–prey community, with only four predators preying upon one rodent species, the collared lemming (*Dicrostonyx groenlandicus*). We document the functional and numerical responses of all the four predators in NE Greenland. Using these data, we assess the impact of predation on the dynamics of the collared lemming with a 4 yr cycle and >100-fold difference between maximum and minimum densities. All predator species feed mostly (>90%) on lemmings when lemming density is $>1 \text{ ha}^{-1}$, but the shapes of the predators' responses vary greatly. The snowy owl (*Nyctea scandiaca*) is present and breeds only when lemming densities at snowmelt are $>2 \text{ ha}^{-1}$, giving rise to a step-like numerical response. The long-tailed skua (*Stercorarius longicaudus*) has a type III functional response and shifts from alternate food (mainly berries and insects) to lemmings with increasing lemming density. The skua surpasses all the other predators in summer by its total response. The type III functional response of the Arctic fox (*Alopex lagopus*) starts to increase at much lower lemming densities than the responses of the avian predators, but it has only a weak numerical response. Finally, the stoat (*Mustela erminea*) is the most specialized predator and the only one with a clearly delayed numerical response. According to their specific functional and numerical responses, each predator plays a key role at some point of the lemming cycle, but only the stoat has the potential to drive the lemming cycle. Stoat predation is greatly reduced in the winter preceding the lemming peak, and it reaches a maximum in the winter preceding the lowest lemming summer density. Stoat predation appears to maintain low lemming densities for at least two successive years. Our study provides empirical support for the specialist predator hypothesis about small mammal population cycles.

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The high arctic tundra biome harbors what is probably the world's simplest terrestrial vertebrate predator–prey community, with only one rodent species, the collared lemming (*Dicrostonyx groenlandicus*), as the main prey

of four predators: Arctic fox (*Alopex lagopus*), stoat (*Mustela erminea*), long-tailed skua (*Stercorarius longicaudus*) and snowy owl (*Nyctea scandiaca*). The open arctic landscape and continuous daylight in summer

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allow intensive study of the predators' behavior, and hence the arctic tundra provides an ideal environment to study the dynamics of predator–prey interactions at a large spatial scale.

Our long-term study in NE Greenland was initiated in 1988 (Sittler 1995). In this region, the collared lemming mainly reproduces in winter and exhibits strikingly regular cyclic dynamics with ≥ 4 -yr period and large amplitude (> 100 -fold; Gilg 2002). At times when lemmings are abundant, the Arctic fox, the long-tailed skua and the snowy owl are all common and they all feed almost exclusively on lemmings. To better understand the impact of the four predators on the lemming population, we set out to determine their functional and numerical responses to lemming density. The different predators display significant differences in their responses, reflecting their life histories and ecologies. Thus a large proportion of Arctic foxes and most long-tailed skuas defend the same breeding territories year after year, and hence the density of adult individuals remains fairly stable. On the other hand, the fox can have very large (≥ 10) litters while the skua only lays one or two eggs. The snowy owl is nomadic and only settles in the region during the lemming peak years, when it can raise a large brood. In winter, the lemming population continues to reproduce under a thick cover of snow. Of the four predators, only the stoat can continue to prey upon lemmings, using the burrow network connecting the lemming winter nests (Sittler 1995). Arctic foxes, unable to survive exclusively on lemmings in winter, become partly nomadic, rely on alternative prey and on food caches, and probably starve in large numbers in some years (Manniche 1910, Pedersen 1959, Smith 1976, Eberhardt and Hanson 1978, Anthony 1997, Anthony et al. 2000). Snowy owls move southward in winter (Salomonsen 1950), and long-tailed skua migrates back to its pelagic winter quarters where it spends most of the year (Furness 1987). Hence all the predators except the stoat are migratory or partly nomadic, and in this respect behave like generalist predators (Andersson and Erlinge 1977, Hanski et al. 1991), a situation noticeably different from the one encountered in and extensively described for southern Fennoscandia, where critical predation by generalists occurs primarily in winter and where voles reproduce primarily in summer (Erlinge et al. 1983, 1991, Norrdahl 1995).

Small mammal population cycles have been studied for decades and several hypotheses have been proposed to explain them (Hansson and Henttonen 1988, Batzli 1992, Oksanen et al. 2001, Turchin and Hanski 2001). Arctic ecologists have always emphasized the impact of predation on lemming dynamics (Pitelka et al. 1955, Watson 1957, Pedersen 1959, Maher 1967, Maclean et al. 1974), but predators were not assumed to actually maintain the cyclic dynamics (Krebs 1964). Rather, predators were thought to take the “doomed surplus”

of the prey population (Errington 1956, 1963) and at most to deepen and prolong the low phase of the cycle (Pearson 1966). The predation hypothesis, originally formulated by Elton (1942), was later reassessed by Andersson and Erlinge (1977), who distinguished between different types of predators, each having a specific impact on prey dynamics. Extensively developed in Fennoscandia in the past 20 years (Hanski et al. 2001), the specialist predator hypothesis has received much attention, but to date studies have produced conflicting evidence (Erlinge 1974, Delattre 1983, 1984, Erlinge et al. 1983, Debrot 1983, Henttonen 1985, Hanski et al. 1991, 1993, Korpimäki et al. 1991, Oksanen and Oksanen 1992, Hanski and Korpimäki 1995, Sittler 1995, Jedrzejewski et al. 1995, Norrdahl and Korpimäki 1995a, 1995b, Klemola et al. 1997, 2000, Korpimäki and Norrdahl 1998, Lambin et al. 2000, Graham and Lambin 2002, Oli 2003). Comprehensive knowledge on the functional and numerical responses of predators is a prerequisite for assessing the influence of each predator on the dynamics of their prey, but such studies are still lacking for most predator–prey communities (Boutin 1995).

The aim of the research reported in this paper was to describe the functional and numerical responses of all the four predator species in summer to provide a basis for understanding the role of predation in the dynamics of the cyclic collared lemming population in NE Greenland. In particular, we wished to assess whether predation is the cause of the decline in lemming densities that has been observed in every summer.

Material and methods

Study area

The study was conducted within an area of 75 km² approximately delimited by the 200 m contour line of the Karup Valley, Traill Island (72°30' N, 24°00' W), NE Greenland National Park (Fig. 1). The most intensive studies were done in a 15 km² area (also shown in Fig. 1) within the main study area. Most of the valley consists of quaternary undifferentiated superficial deposits (Koch and Haller 1971). Patterned grounds, solifluction lobes, raised beaches and thaw slumps are common geomorphologic features in the valley. The study area has discontinuous polar semi-desert vegetation, with dwarf-shrub heath, herb slope, moss–sedge meadows, snow-patch, organic crusts, fell-field and Tundra hummock being the main vegetation types.

The vertebrate community is extremely simple. The collared lemming, whose population dynamics are known to be cyclic in Greenland (Korte and Wattel 1988, Sittler 1995, Sittler et al. 2000, Gilg 2002), is the only microtine rodent. Dwarf-shrub heath and herb

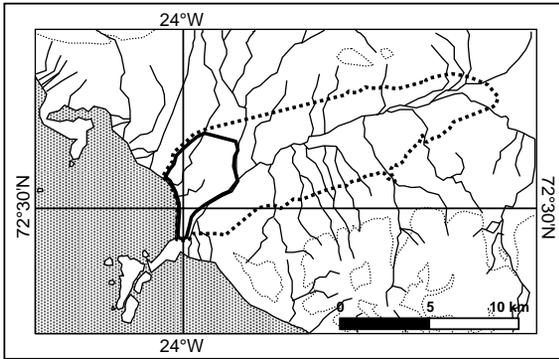


Fig. 1. Map of the 75 km² study area (bold broken line) and the 15 km² part of it (bold continuous line) used for intensive studies in the Karup Valley (scale 1:400,000). Rivers (thin continuous lines), 500 and 1000 m contour lines (thin dotted lines) and the Kong Oscar Fjord (shaded) are also shown on the map.

slope (rich in *Salix arctica* and *Dryas octopetala*) are the preferred summer habitats of the lemming (Schmidt 2000, Gilg 2002). The long-tailed skua breeds on flat tundra, gentle slopes and small mounds, while the snowy owl generally chooses a higher promontory as the nest site. The Arctic fox breeds in dens that are used for several decades (Piantanida 1979, Dalerum and Angerbjörn 2000). The stoat breeds under rocks or in screes, and it appears to move from the valley lowlands where it occurs in winter (Sittler 1995) to higher stony slopes in summer (Gilg, unpubl. radio-tracking data).

Lemming population study

Live trapping

Lemmings were live-trapped with Ugglan traps within the 15 km² intensive study area. Trappings were conducted on three main plots (total 354 burrows) in 1998–2002, and were extended to 6–15 plots (max. 1800 burrows) in 1999–2002 to increase the sampling effort during lemming decline. The burrows were accurately mapped and exhaustively trapped twice a month in 1998 and 1999 and once a month in 2000–2002. All the burrows within each plot were trapped simultaneously.

Preference for certain habitats is well known for the collared lemming in summer (Fuller et al. 1975, Rodgers and Lewis 1986, Pitelka and Batzli 1993, Predavec and Krebs 2000, Schmidt 2000) and burrow density is generally considered to be a good indicator of lemming habitat quality (Fuller et al. 1975, 1977, Danilov 1995, Predavec and Krebs 2000). Hence, the overall density of lemmings in the study area (N , ind. ha⁻¹) was calculated as the average of the estimates obtained for the trapping plots

$$N = B \times \frac{\sum \left(\frac{N_i}{B_i} \right)}{n} \quad (1)$$

where N_i and B_i are the numbers of lemmings caught and the number of burrows in trapping plot i , and B is the average burrow density per ha in the study area, calculated for a 31 km × 2 m strip transect. A detailed description of the trapping design and its rationale has been published elsewhere (Gilg 2002).

Winter nests

Lemming winter nests made of grasses and sedges become very apparent after snowmelt when they lie on the ground. The numbers of winter nests have been completely counted in the intensive study area in 1988–2002 (see Methods in Sittler 1995, Sittler et al. 2000). To estimate the lemming density at snowmelt for the period 1988–2002, we calculated the regression between lemming winter nest counts and spring density estimates (the first live-trapping session following snowmelt) for the five years (1998–2002) for which the latter data were available. A power function that was transformed to a straight line fitted the data well ($R^2 = 0.99$; $p < 0.01$),

$$\ln N' = 1.15 + 1.35 \ln W \quad (2)$$

where N' is the estimated spring density in ind. ha⁻¹ and W is the density of winter nests per ha as counted in the complete search of the 15 km² study area.

The diet of the four predators

Samples

Samples were collected in 1998–2000 and 2002. Snowy owl pellets were collected in the nests and on the perches regularly used by breeding males during the incubation period and by the fledglings after they had left the nest (pellets from 10 territories in 1998 and 2 territories in 1999). Long-tailed skua pellets were collected on the small mounds and rock outcrops used by adults as resting, watching and hunting posts (13–15 territories in all years). Fox scats were collected near dens and around the base camp (in 2000, when most dens were unoccupied). Dens were first visited as soon as possible after snowmelt and old scats (judged as such by bleaching, the growth of algae and position in the surrounding vegetation; Macpherson 1969, Angerbjörn et al. 1999) were removed, so that all scats collected subsequently could be dated (Dalerum and Angerbjörn 2000). Stoat scats were collected in the stoat traps (summer scats) and in the vicinity (0–5 m) of lemming nests that had been used by the stoat in winter (nests lined with lemming fur). Like for scats, only pellets that could be dated were collected.

Analyses

Pellets were dissected by hand and the minimum number of prey individuals was counted for each pellet according to the bone remains (e.g. the number of lower jaws for the lemming). Fox scats were analysed according to Dalerum and Angerbjörn (2000). Each scat was autoclaved, soaked in water, washed over a sieve (mesh size 1.0 mm) and the remaining macrofractions were dried and weighed to the nearest 0.001 g before separation and identification to different food categories. Each food category found in a single scat was weighed unless the separation of the categories was impossible. In the latter case, the dry weight of each food category found in a single scat was estimated by multiplying its volume (relative to the entire scat) by the total dry weight of the scat. For the long-tailed skua scats collected in 2000 and 2002, we calculated the frequency of whole scat equivalent by scoring the proportion of each prey type found in the scats (each scat accounting for 1).

Prey remains found in scats and pellets were identified by comparing them with reference material collected by the authors in NE Greenland and using published keys (Day 1966, Herrenschildt 1980, Debrot et al. 1982, Brom 1986, Teerink 1991). Tarsus length and shape were used when available to identify birds found in pellets. To assess the number of Ericaceae berries eaten by skuas, we divided the number of seeds found in pellets by eight since the mean number of seeds counted in a sample of 15 *Vaccinium uliginosum* and 15 *Empetrum hermaphroditum* berries collected in the study area was 7.9 (± 0.3 SE).

The functional responses

Functional responses were obtained by plotting the daily rates at which prey are consumed by an individual predator (daily consumption rate, DCR) against the estimated lemming density N (Eq. 1) for the same time period (Solomon 1949, Holling 1959, Korpimäki and Norrdahl 1991, Krebs et al. 2001).

Avian predators

DCR was calculated based on direct monitoring of the birds in the field. The monitoring involved five pairs of snowy owls and three pairs of long-tailed skua in 1998 and 1999 and one pair of long-tailed skua in 2002. Birds were monitored from hides with a telescope during 3 (skua) and 6 h (owl) monitoring bouts. The aim was to cover all parts of the 24 h and hence to sample possible circadian variation in predators' activity. Hides were located so that the entire territory of the focal breeding pair could be monitored. Monitoring always involved the two adults of a breeding pair. Additional monitoring bouts were done in 2000 and 2002 for non-breeding long-tailed skuas at randomly chosen points

within the study area. In this case, all individuals (single or in groups) that could be seen were monitored simultaneously. DCR was calculated as follows:

$$DCR = 24 \times \frac{\sum n_i}{\sum (P_i \times h_i)} \quad (3)$$

where n_i is the number of lemmings predated during monitoring bout i lasting h_i hours and during which P_i individual predators were monitored.

Following hatching, the number of lemmings captured by breeding adults constantly increases to meet the age-dependent needs of the offspring and hence Eq. 3 cannot be used as such. For snowy owl, the weight W_t of a t -day old young follows a growth curve during the ≈ 45 -day long fledging period (Watson 1957, Poley and Poley 1972, Scherzinger 1974, Busse and Busse 1976, Cramp 1985) that can be described by Ricklefs's equation (Ricklefs 1967):

$$W_t = \frac{A}{1 + e^{-k(t-t_i)}} \quad (4a)$$

where A is the asymptotic (adult) body weight, k is a constant and t_i is the age in days at which the inflection point of the curve ($W_t = A/2$) is reached.

The daily food requirements of young owls (X_t) follow a similar but steeper curve than W_t , the daily needs being already maximal after 20–25 days (Portenko 1972, Busse and Busse 1976). According to a detailed feeding experiment (Busse and Busse 1976), the daily food requirements of a young bird can be approximated by a variant of the previous equation, where A' is the asymptotic feeding rate in g per day (i.e. the daily food requirements of an adult bird):

$$X_t = \frac{A'}{1 + e^{-2k\left(t - \frac{t_i}{2}\right)}} \quad (4b)$$

The growth curve of young long-tailed skuas has a similar shape though their fledging period is only ≈ 25 days long (Maher 1970a). Values for k and t_i have already been published for NE Greenland (Korte 1986). Equation 4b was thus used for both the owl and the skua, and from the point of view of food consumption, every juvenile of age t was considered to represent a fraction X_t/A' of a "functional adult". Hence, DCR calculated based on the monitoring of breeding pairs with hatched young was estimated as

$$DCR = 24 \times \frac{\sum n_i}{\sum \left(\left(2 + \sum \frac{X_t}{A'} \right) \times h_i \right)} \quad (5a)$$

We note that X_t/A' is calculated separately for each young since hatching is asynchronous and hence the young in the same nest have different ages.

Arctic fox

Dry weights of prey remains found in scats can be used to estimate the number of prey individuals of each food category eaten by mammalian predators (Lockie 1959). We used the factor of 28 previously applied for the collared lemming (Reid et al. 1997, Wilson 1999) to convert the total mass of undigested lemming remains (L) found in a sample of fox scats to the lemming biomass consumed. Following these previous studies, we estimated DCR for the time period during which scats were collected as

$$\text{DCR} = \frac{28 \times L \times d}{s \times w} \quad (5b)$$

where *s* is the total mass (dry weight), *d* is the daily defecation rate (Reid et al. 1997, Wilson 1999) and *w* is the average live weight of lemmings (Gilg 2002). We could have smoothed DCR for young foxes by using the Gompertz growth curve published for this species (Prestrud and Nilssen 1995), but since the exact birth dates of foxes were rarely known and because their food requirements do not increase regularly with age (Frafjord 1994), we simply assumed that their consumption equaled adult consumption from July 10 onwards.

Stoat

Stoats have a very high metabolic rate and consume 37 to 60% (mean: 51%; *n* = 8) of their own body weight daily (Segal 1975, Erlinge 1983, Delattre 1987). According to our own measurements and the few published data (Johnsen 1953), the mean body weight of stoats in NE Greenland is 150 g (± 11 SE) for males (*n* = 7) and 122 g (± 6 SE) for females (*n* = 3). DCR was calculated based on the proportion (% of total dry weight) of lemmings in the stoat diet (*L'*), the mean body weight of stoats (136 g, assuming 1:1 sex ratio), and the daily food requirements of 60% of body weight (realistic for the harsh Arctic environment):

$$\text{DCR} = \frac{0.6 \times 136 \times L'}{w} \quad (5c)$$

The numerical responses

The numerical responses were investigated based on data collected in 1988 to 2002. Long-tailed skua and stoat responses were investigated in the 15 km² intensive study area, snowy owl and arctic fox responses in the entire study area of 75 km². The numerical response of adult predators and their reproductive output (number of fledged birds of prey and weaned mammals) are presented separately. Lemming densities needed to calculate the numerical responses were obtained from live trapping results (1998–2002) or estimated with Eq. 2 (other years).

Snowy owl

With the exception of 1999 (only 50 km² surveyed), snowy owl nests were mapped annually over the entire study area. In the first census from the beginning of June to the beginning of July, we recorded the breeding pairs and the average clutch size, while subsequent visits to selected nests allowed an assessment of the breeding success.

Long-tailed skua

Breeding pairs and clutch sizes were documented for all years, while the number of territorial pairs was mapped precisely from 1998 to 2000 (the years when we arrived at the study area in the beginning of June). Territorial pairs can be accurately counted only in early summer, because in low lemming years skuas tend to abandon their territories shortly after arrival, in early June, though they remain in the area in pairs or in larger groups (Korte 1984) and therefore continue to be active lemming predators. Breeding success was calculated for selected pairs from 1988 to 1996 and for all pairs from 1997 to 2002.

Arctic fox

Breeding foxes were counted over the entire study area by visiting the seven known dens (Dalerum and Angerbjörn 2000). Individual variation in coat coloration was used to identify non-breeding adults, which are common during low lemming years. In these years foxes regularly visited our base camp and hides and were therefore easy to record. A separate study devoted to fox home-ranges (Zakrzewski et al. 1999, Zakrzewski 2002) and involving ear tagging (young and adults) and radio-tracking (adults) was also helpful for identifying individuals in the field. Occupied dens were monitored over the summer to record the minimum number of weaned young (Macpherson 1969, Eberhardt et al. 1983, Prestrud 1992, Angerbjörn et al. 1995, 1999).

Stoat

Stoats were live-trapped in summers 1997–2002 with special mustelid traps consisting of a tunnel with a rocking floor and ending with a wooden box designed to reduce stress. Traps were baited with commercial cat food and small pieces of meet, cheese and fish. Traps were checked every four to eight hours depending on weather conditions. To assess the numerical response of stoats over a longer period (1988–2002), we recorded the numbers of lemming winter nests that had been predated and used by stoat during the winter (Sittler 1995). Additionally, we used the number of direct observations made in the field during summer.

Fitting the predator responses

To distinguish between the type II and III functional responses, we first plotted the predation rate (DCR/N) against lemming density (N). A positive slope over any range of prey densities is indicative of positive density dependence and hence type III response, whereas a consistently negative slope indicates a type II response (Trexler et al. 1988). We then fitted the classical functions used in predator–prey modeling (Holling 1965, May 1973, 1981) including studies on small rodent dynamics (Hanski et al. 2001),

$$\text{type II: DCR} = c N / (D + N) \quad (6a)$$

$$\text{type III: DCR} = c N^2 / (D^2 + N^2) \quad (6b)$$

where c is the maximum per capita consumption rate, N is lemming density per ha, and D is the half-saturation constant. The lemming density needed for each DCR estimate was calculated by assuming a linear change in density between the two trapping sessions bracketing the focal date. The maximum per capita consumption rate was determined based on data in the literature and our own data. Finally, the half-saturation constant was estimated numerically. In one instance, we had to use a different function ($c N^e / [D^e + N^e]$ with $e > 2$) to fit the data. In this case, the values of both D and e were estimated numerically.

Numerical responses of rodent predators are usually fitted with linear, logarithmic or curvilinear functions (Korpimäki and Norrdahl 1991, Jedrzejewski et al. 1996, Krebs et al. 2001). Since the density of breeding owls, skuas and foxes is limited at high prey density by the predators' territorial behavior or by the number of available breeding sites (dens) as well as by their life history traits (maximal clutch or litter size), we used sigmoid functions similar to Eq. 6b or functions with a threshold value (for species that do not breed at low lemming densities). The numerical functions used were:

Numerical response for adults:

$$\text{sigmoid function } G = b N^2 / (Y^2 + N^2) \quad (7a)$$

$$\text{step function } G = b(N' - N'_{\text{crit}}) / (Y + N' - 2N'_{\text{crit}}) \quad (7b)$$

Reproductive success:

$$\text{sigmoid function } G' = b' N^2 / (Y'^2 + N^2) \quad (8a)$$

$$\text{step function } G' = b'(N' - N'_{\text{crit}}) / (Y' + N' - 2N'_{\text{crit}}) \quad (8b)$$

where b is asymptotic density of adults, b' is asymptotic breeding success (obtained by multiplying b by the maximum clutch or litter size), Y and Y' are lemming densities at which the slopes of the curves inflect and N'_{crit} is the threshold lemming density below which the predator is not present or does not breed. In the numerical responses, N' refers to the spring density at snowmelt (Eq. 2). We determined distinct numerical responses for both adults and young to be able to

calculate the total response mechanistically for different times of the summer (e.g. before and after the birth of the young).

Total response

The total response of a predator is the total number of lemmings killed by the predator population per day as a function of lemming density. The total response can be obtained by multiplying the functional response (DCR) by the numerical response (G and/or G'), both responses being plotted against prey density (Erlinge et al. 1983, Jedrzejewski et al. 1996, Krebs et al. 2001). In our study, there are several estimates of functional response (DCR) per year calculated as functions of the current (seasonally changing) lemming density N , while there is only one yearly estimate of numerical response for the lemming density at snowmelt N' , i.e. the time when the predators initiate breeding. We can hence calculate the total response of predators only at snowmelt (when $N = N'$) or for the years for which we know both N' and N throughout the summer (1998–2002). For the calculation of the total response during the summer, G' was multiplied by X_i/A' (Eq. 4b) to convert numbers of young to adult equivalents.

Predation rate by a single predator species can be calculated for any time period by dividing its total response by the respective lemming density.

Results

Lemming population densities

Lemming densities as estimated with live trapping for the period 1998–2002 ranged from 0 to 24.8 lemmings per ha (Fig. 2; zero density estimate was set to 0.01 to allow log scale and statistical analyses). The maximal density of 24.8 ind. ha⁻¹ measured in June 1998 at the onset of

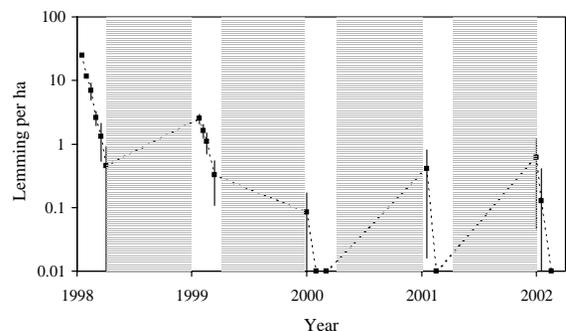


Fig. 2. Collared lemming densities (\pm SE) estimated with live-trapping in the summers 1998–2002 (zeros were set to 0.01 to allow the log scale).

snowmelt is probably an overestimate. At this time, lemmings probably gathered in the trapping plots that were already free of snow while much of the remaining ground was covered by snow. The actual maximum density over the entire study area was probably between 10 and 15 ind. ha⁻¹ as recorded during the second trapping session in 1998 (Gilg 2002). The amplitude of the lemming cycle is >100-fold. After the peak year of 1998, lemming density declined in 1999 and remained at a very low level for the following three summers. Lemming densities systematically decreased in the summer and increased in the winter (Fig. 2), with the exception of the winter 1999–2000.

The spring densities (N') estimated with Eq. 2 reveal a strikingly regular multiannual cycle with a cycle period of 4 years for the first three cycles covered by this study (Fig. 3). It is worth noting that each peak year (8–12 ind. ha⁻¹) was followed or preceded by a year with intermediate density (2–3 ind. ha⁻¹) and separated from the next year with relatively high density by at least 2 low years (<1 ind. ha⁻¹).

The diet of the predators

Snowy owl

Lemmings accounted for more than 98.5% of the 4024 prey items identified (Table 1). Other mammalian prey (stoat, arctic fox) are rare but can be important in term of biomass (arctic hare). Among the bird prey, rock ptarmigans are the most common but passerines (especially snow bunting) are also regularly preyed upon despite their small size. The proportion of lemmings found in pellets slightly decreased from July to September in both years, in line with declining lemming density (Fig. 2). The opposite increases from June to July can be explained by the fact that snow still covered part of the study area in June.

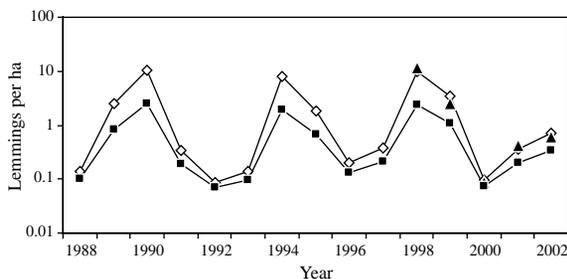


Fig. 3. Time series of the numbers of lemming winter nests per ha after snowmelt (squares) and spring densities (ind. ha⁻¹) estimated from the density of winter nests (Eq. 2; diamonds) for the period 1988–2002. Triangles show direct estimates of spring densities.

Long-tailed skua

The diet of the long-tailed skua (n = 875 pellets) included invertebrates and berries in all years, but the lemming was by far the main prey in 1998 and 1999, accounting for more than 99 and 98% of the vertebrate prey individuals, respectively (Table 2). The few pellets found in 2000 and 2002 overestimate the proportion of vertebrate prey since pellets are not necessarily produced when small prey items dominate the diet. Hence, we also analyzed two samples of fresh skua scats (n = 288) in 2000 and 2002 and calculated the frequencies of whole scat equivalents for the different prey types in low lemming years. With this method, which gives a better idea of the biomass ingested by the birds, invertebrates and berries accounted for more than 75% of the diet while lemmings dropped to less than 6% (Table 2). In the low lemming years skua can shift from an invertebrate-dominated diet (2000) to fruit diet (in 2002, when *Tipula artica* was less common than usual while *Empetrum hermaphroditum* berries from the previous year were still abundant and edible).

Arctic fox

In addition to the 343 scats analyzed in 1997 (Dalerum and Angerbjörn 2000), we analyzed 1029 fox scats for the period 1998–2002. Collared lemming was by far the most common prey over this period (Table 3). During the peak and intermediate years, lemmings accounted for 95% or more of the dry fecal weight. Only when lemming densities declined below 0.1 ind. ha⁻¹ (Fig. 2) did the other prey types account for more than 50%. During these low phases of the lemming cycle, foxes survived on seals (probably pups of *Phoca hispida*) in June and on birds (20–50% of dry fecal weight), invertebrates (10–20%) and plants (8–27%) in July and August. Bird prey individuals were generally passerines (snow bunting), shorebirds, rock ptarmigan and barnacle goose, but remains of red-throated diver, long-tailed duck, pink-footed goose, long-tailed skua, snowy owl and glaucous gull have also been found at dens. All but a few invertebrates were bumblebees (*Bombus polaris* and *B. hyperboreus*), though blue flies (*Phormia terraenovae*) were not uncommon either, especially in 2000. The few crustaceans found in winter and June scats were always associated with seal remains and have possibly been ingested with seal scats. Plant remains increased in the scats in 2000, when foxes fed on heath berries (*Vaccinium uliginosum*, *Empetrum hermaphroditum* and possibly *Arctostaphylos alpina*). The “Arctic fox remains” were most probably molt hairs of defecating animals (grooming) since they only consisted of white winter hairs and were never associated with bone fragments. The fact that 21% of the scats dated as winter 1999–2000 contained eggshells indicates that food caching occurred in the previous summer, when lemming density declined below 1 ind. ha⁻¹. Food caching has also been observed for

Table 1. Snowy owl diet in 1998 and 1999. The numbers are the absolute numbers of vertebrate prey individuals found in pellets (% in brackets).

Prey type	1998				1999		
	Jun	Jul	Aug	Sep	Jun	Jul	Aug
Mammals							
collared lemming	416 (98.3)	1976 (98.9)	408 (98.6)	395 (98.0)	156 (95.7)	463 (98.7)	151 (98.1)
arctic hare	1 (0.2)	3 (0.2)	1 (0.2)		1 (0.6)		1 (0.6)
stoat	1 (0.2)	1 (0.1)					
arctic fox		1 (0.1)					
Birds							
rock ptarmigan	1 (0.2)	3 (0.2)	1 (0.2)	3 (0.7)	4 (2.5)	2 (0.4)	1 (0.6)
snowy owl (juv.)						1 (0.2)	
ruddy turnstone	1 (0.2)						
great ringed plover		1 (0.1)				1 (0.2)	
unidentified shorebird		2 (0.1)					
snow bunting	2 (0.5)	2 (0.1)		1 (0.2)	2 (1.2)	1 (0.2)	
northern wheatear	1 (0.2)						
unidentified bird		9 (0.5)	4 (1.0)	4 (1.0)		1 (0.2)	1 (0.6)
Total	423	1998	414	403	163	469	154

lemming prey (Gilg 2002) and probably explains why most lemming fur found in fox winter scats was dark and not white as it should have been (Degerbol and Mohl-Hansen 1943).

Stoat

Altogether 663 scats were analyzed for the period 1988–2002, most of them ($n=656$) sampled in the vicinity of lemming winter nests that had been occupied by stoat under the snow. The lemming remains found in the winter scats (seven different years) always accounted for more than 98.5% of the total dry weight, the only other noteworthy food type being plant remains including a few berries (Table 4). The summer scats indicate a more diverse diet, with bird, insect, muskox and plant remains sometimes summing up to 50% of the total dry weight (in 2000), but the sample size ($n=7$) is clearly too small for any far-reaching conclusions.

The functional responses

Snowy owl

The number of vertebrate prey individuals captured by a snowy owl pair during a 6-hour monitoring bout varied from 0 to 16 (maximum for a pair with 7 young). Contrary to long-tailed skua, owls use large hunting territories and the hide was not always close enough to allow identification of the prey captured during the monitoring bout. Hence, the number of lemmings caught during a monitoring bout (n in Eq. 3 and 5a) was calculated by multiplying the total number of vertebrate prey individuals captured by the proportion of lemmings found in the pellets in the same period (from Table 1).

DCR was calculated for the five time periods (June, July and August in 1998 and June and July in 1999) for which we had both diet data (Table 1) and at least 24 h of monitoring (maximum 72 h in July 1998; total monitoring time for the five time periods: 245 h). The values of

Table 2. Long-tailed skua diet. The numbers give the absolute numbers of prey items (individuals or berries) found in pellets for the period 1998–2000 and the frequencies of whole scat equivalents for 2000 and 2002 (% of vertebrate prey in brackets).

Prey type	Pellets				Scats	
	1998	1999	2000	2002	2000 ^a	2002 ^a
N (pellets or scats)	451	381	26	17	103	185
Mammals						
collared lemming	346 (99.4)	247 (97.6)	3 (25.0)	4 (50.0)	1.9	5.9
Birds		4 (1.6)	1 (8.3)	2 (25.0)	1.0	0.4
Fishes	2 (0.6)	2 (0.8)	8 (66.7)	2 (25.0)	2.4	0.0
Invertebrates	37 ^b	70 ^b	n.d. ^c	n.d. ^c	68.9 ^d	11.1 ^d
Plants						
berries	239	105	38	50	15.5	65.6
other remains	n.d.	n.d.	n.d.	n.d.	10.2	17.0

^a scat sample: results in % of scat volume

^b insect larvae

^c lots of fragments but impossible to count individually

^d mainly crane flies (*Tipula arctica*) and spiders

Table 3. Arctic fox diet from 1997 to 2002. The numbers are percentages of dry fecal weight with frequency of occurrence (%) in brackets.

Prey type	1997 ⁽¹⁾		1998		1999			2000			2002	
	July	June	July	Winter	June	July	Winter	June	July	August	June	July
N (scats)	343	220	220	30	41	216	72	23	22	51	58	76
Mammals												
collared lemming	66.1 (77.0)	98.6 (100)	98.2 (100)	85.3 (96.7)	96.3 (97.6)	94.7 (98.6)	49.3 (55.6)	35.7 (52.2)	15.4 (9.1)	2.8 (3.9)	63.0 (72.4)	49.6 (64.5)
arctic hare	4.4 (9.9)			7.2 (6.7)	0.04 (2.4)	2.1 (2.8)	1.6 (2.8)	7.8 (13.0)	2.1 (9.1)	4.7 (7.8)	1.3 (1.7)	2.1 (2.6)
arctic fox	3.4 (7.0)	0.02 (0.9)	0.1 (0.4)			0.1 (0.9)	9.2 (27.8)	16.4 (17.4)	1.9 (9.1)	0.4 (5.9)	1.2 (1.7)	2.1 (15.8)
stoat						0.1 (1.4)	1.9 (2.8)					
muskox	0.4 (1.2)	0.02 (1.4)	0.2 (0.4)			0.2 (0.5)	4.7 (5.6)				12.0 (17.2)	2.0 (6.6)
seal	0.3 (0.6)						7.0 (13.9)	22.3 (13.0)			1.4 (5.2)	
unidentified mammal	0.7 (2.0)	0.01 (1.8)	<0.01 (0.4)	2.6 (6.7)		0.1 (1.4)	2.1 (20.8)	0.3 (8.7)	1.3 (4.6)	0.3 (9.8)	3.3 (8.6)	1.6 (5.3)
Birds	11.4 (31.5)	0.6 (5.9)	0.8 (12.3)	4.8 (16.7)	2.7 (26.8)	0.9 (7.4)	3.3 (19.4)	6.2 (21.7)	42.7 (95.5)	49.6 (90.2)	8.3 (34.5)	20.5 (47.4)
eggshells	0.03 (0.9)		0.2 (2.3)	0.03 (3.3)			1.5 (20.8)	1.6 (21.7)	0.5 (9.1)	0.03 (2.0)	0.04 (5.2)	1.6 (2.6)
Invertebrates (Insecta/ Crustacea)	8.1 (31.8)	0.4 (7.3)	0.4 (14.1)	0.1 (6.7)	0.1 (7.3)	0.8 (14.8)	1.3 (20.8)	6.3 (52.2)	19.8 (77.3)	10.8 (60.8)	4.5 (34.5)	9.5 (40.8)
Plants	3.7 (16.3)	0.3 (1.4)	<0.01 (0.4)		0.7 (2.4)	0.9 (2.8)	15.3 (41.7)	1.6 (26.1)	16.3 (50.0)	26.7 (86.3)	3.9 (22.4)	8.3 (39.5)
Human deposits	0.1 (0.6)	0.01 (3.2)	<0.01 (0.4)	0.03 (3.3)		<0.01 (1.4)	0.1 (5.6)			2.0 (5.9)		<0.01 (1.3)
Unidentified matter	1.2 (2.6)	0.04 (5.4)			0.1 (2.4)	0.1 (2.8)	2.7 (20.8)	1.7 (8.7)		2.6 (9.8)	1.1 (6.9)	2.7 (7.9)
Mean scat mass (dry weight) in g	n.d.	0.83	0.88	0.72	1.04	0.93	0.83	1.15	0.41	0.50	1.32	0.50
Mean number of prey type per scat	1.8	1.3	1.3	1.4	1.4	1.3	2.6	2.3	2.6	2.8	2.1	2.3

¹ data from Dalerum and Angerbjörn (2000).

Table 4. Stoa diet for the years 1998–2002. The numbers are percentages of dry fecal weight.

Prey type	Winter										Summer				
	1988–89	1995–96	1997–98	1998–99	1999–00	2000–01	2001–02	1999	2000	2001	2002	1999	2000	2001	2002
N (scats) ¹	40	91	31	100	235	86	73	1	4	1	1	1	4	1	1
Mammals collared lemming muskox	100	>99.9	99.7	100	>99.9	99.6	98.8	100.0	41.6	90.0	60.0	11.9	30.7	11.9	30.7
Birds															
Insects							0.05								20.0
Plants		0.02	0.15			0.38	1.08								4.64
Unidentified matter			0.15		0.002		0.02								3.09
Mean scat mass (dry weight) in g	0.16	0.17	0.17	n.d.	0.20	0.22	0.25	0.04	0.06	0.07	n.d.	0.04	0.06	0.07	n.d.

¹an approximate number since some scats were composed of several fragments.

²berries.

the parameters in Eq. 4 were $k=0.18$ and $t_i=18$. DCR varied from 3.22 to 4.73 lemmings (Fig. 4a). The best fit was obtained with a type II response with ($D=0.76$, $c=4.7$; $R^2=0.97$), but since field data were not available for low lemming densities, a type III response ($D=1.08$) fitted the data almost equally well ($R^2=0.96$). Furthermore, since snowy owl is able to feed and survive on a large number of different prey types when rodents are rare or lacking (Gross 1944, Williams and Frank 1979, Robinson and Becker 1986), a type III response is appropriate. The possible inaccuracy of the type III curve at low lemming densities does not influence the total response (below), because owls are not present in the study area at low lemming densities. The lowest DCR (open symbol in Fig. 4a) was found for a pair monitored in 1999. This pair had only one egg and the male (probably an immature based on its plumage) was unable to provide enough food for the female, which had to abandon the nest before hatching. Predation rate of snowy owl (DCR/N; insert in Fig. 5a) was maximal at a lower prey density ($N \approx 1$) than it was for the skua ($N > 1$; below).

Long-tailed skua

We monitored skua pairs for 72 h in 1998 (three pairs), 72 h in 1999 (three pairs) and 24 h in 2002 (one pair). Seven DCR estimates could therefore be calculated, each being the result of a total of 24 hours of monitoring conducted during a period of 5–14 days (mean 7.7). In addition, monitoring conducted on non-breeding adults yielded a total of 211 hours in 2000 and 96 hours in 2002 ($\sum[P_i h_i]$ in Eq. 3) and provided data for the calculation of four additional DCR estimates (two in each year). DCR varied from 0 (in 2000 and 2002) to 4.5 lemmings per day (July 1998). After removing one outlier (open symbol in Fig. 4b), the best fit, using $k=0.23$ and $t_i=9.1$ days (Korte 1986) in Eq. 5a, was obtained with type III function ($D=2.2$, $c=4.4$ and $e=4$; $R^2=0.99$; Fig. 4b). Removing the deviating data point is supported by the biased size class distribution of the lemming population in the beginning of August 1998 (Gilg 2002). Large lemmings are difficult to catch, kill and swallow by the skua, and hence small lemmings are always preferred even at low densities (Gilg and Hurstel 2000). Indeed, if we do not consider large lemmings (≥ 45 g) while plotting N on the x-axis, Eq. 6b fits the data much better (crosses). Maximum predation rate of the skua (insert in Fig. 5b) occurred at higher lemming density ($N > 2$) than it did for the other predators.

Arctic fox

The daily consumption rate of the fox was calculated for nine different time periods, namely for each summer month that we had scats available between June 1998 and August 2000 (Table 3). Winter scats were not used since they could not be dated accurately, “winter”

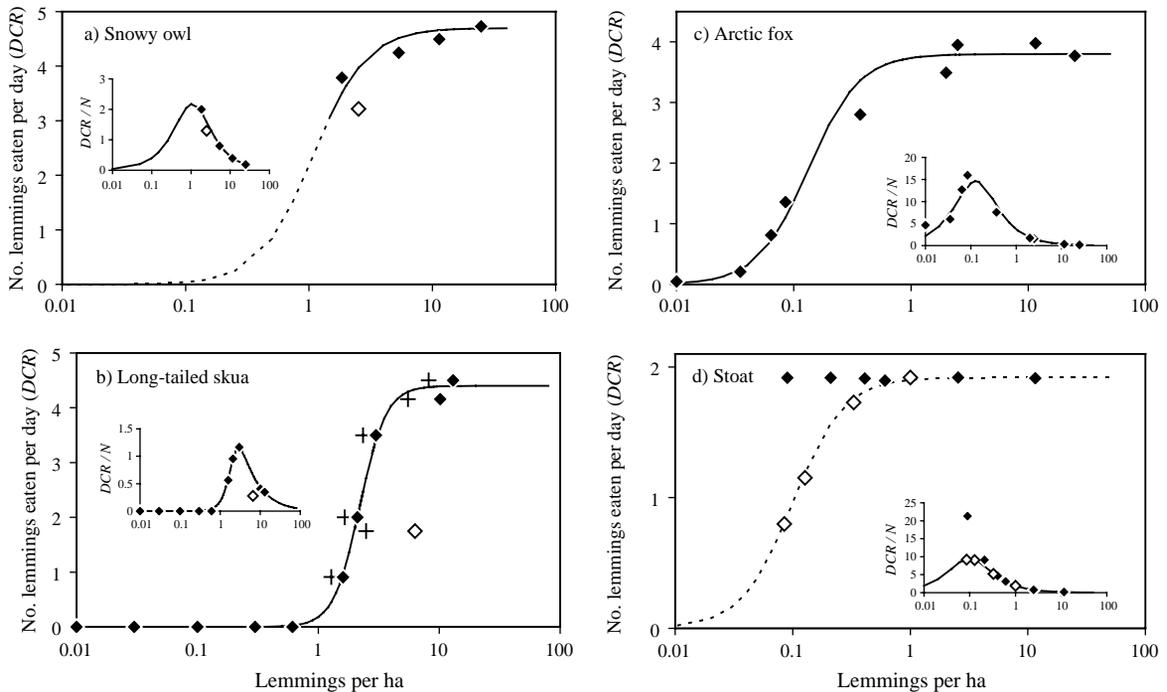


Fig. 4. Functional responses of the four predators to lemming density. The crosses in (b) were plotted for lemming densities excluding large (≥ 45 g) individuals; open symbols refer to outliers in (a) and (b) and to estimates based on summer scats in (d) (see text). Dotted lines were used to draw the poorly documented but conservative response of stoat (d) and for the undocumented part of the owl response (a) at low lemming densities (see text). With the exception of (d), where we used an estimate of spring density based on eqn (2), lemming density was estimated with live-trapping (Eq. 1). The inserts show predation rates (DCR/N against N).

referring to a 9-month long period. The daily defecation rate of foxes (d) is known to vary according to food availability (Reid et al. 1997, Wilson 1999). Following these authors, we used $d = 7$ in 1998 (lemming peak year: no food stress), $d = 6$ in 1999 (some food stress), and $d = 5$ in 2000 and 2002 (low lemming years: strong food stress). The mean lemming mass (w) calculated over five years (1998–2002) was 42.5 g (± 0.86 SE) (Gilg 2002). DCR calculated with these parameter values ranged from 0.037 (August 2000) to 4, and the best fit was obtained with a type III response ($D = 0.13$, $c = 3.8$; $R^2 = 0.98$; Fig. 4c). Foxes respond much faster to an increase in lemming density than do the avian predators, and the maximal predation rate (insert in Fig. 4c) is reached already at the density of 0.13 lemmings per ha.

Stoat

The functional response of the stoat appeared very different depending on whether winter or summer scat samples were used. In the case of winter samples, and using the lemming density at snowmelt N' , DCR remained at a constantly high level (dark symbols in Fig. 4d). In contrast, in the summer samples (Table 4), when plotted against the closest available lemming density estimate, DCR decreased with decreasing lemming density (open symbols in Fig. 4d). Rather than trying to fit the points to a poorly supported function

(Discussion), we only calculated the conservative boundary of the stoat functional response. This boundary is given by the type III function presented in Fig. 4d ($D = 0.1$; $c = 1.92$ from Eq. 5c).

The numerical responses

Snowy owl

Owls bred during 5 out of 15 summers, and their density varied from 0 (in most years) to 0.17 pair km^{-2} (Table 5). Owls did not breed in 1995 ($N' = 1.87$), but a few pairs did in 1989 ($N' = 2.52$) and in 1999 ($N' = 2.55$). Hence the critical lemming density at snowmelt (N'_{crit}) at which snowy owl starts to breed is close to 2 ind. ha^{-1} . The numerical response follows a step function at N'_{crit} , with an asymptotic density of 0.17 to 0.2 pair km^{-2} . If we ignore the 1994 data point (80% snow cover on 1 July, meaning exceptionally unfavorable breeding conditions for a bird laying eggs in May), the best fit of Eq. 7 with $N'_{\text{crit}} = 2$ was found for $b = 0.183$ and $Y = 2.86$ ($R^2 = 0.99$; Fig. 5a).

Breeding success of the snowy owl varied in a similar manner from 0 (in most years) to one fledgling produced per km^2 (in 1998). The best-fitting curve (excluding the 1994 data point) for $N'_{\text{crit}} = 2$ was obtained with parameter values $b' = 1.1$ and $Y' = 4$ ($R^2 = 0.99$; Fig. 5c).

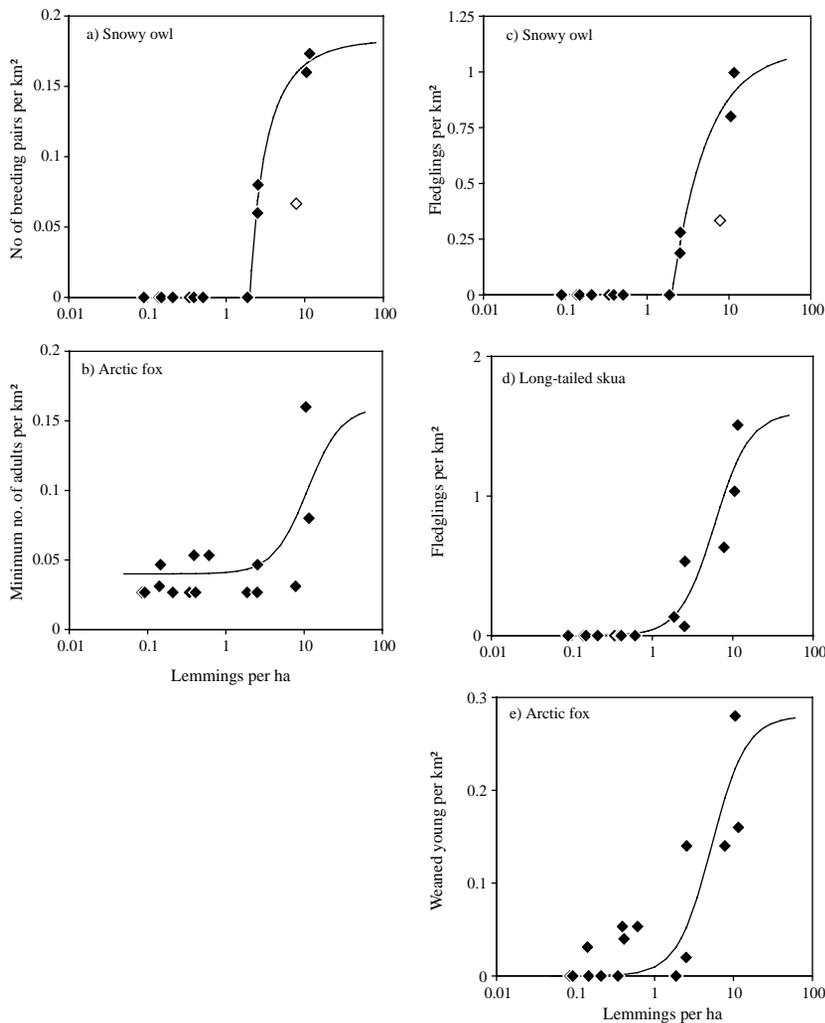


Fig. 5. Numerical responses of adult snowy owl (a), adult arctic fox (b) and breeding success of snowy owl (c), long-tailed skua (d) and arctic fox (e) as a function of lemming density at snowmelt. Open symbol in (a) and (c) refers to 1994 (see text).

Long-tailed skua

Unlike the snowy owl, the long-tailed skua shows pronounced nest site tenacity even during low rodent years (Andersson 1976). Thus though the number of breeding pairs was strongly correlated with the lemming density at snowmelt ($r=0.93$; $p<0.001$), the number of pairs defending a territory was constant at 0.97 to 1 pair km^{-2} (Table 5). Territories were precisely mapped at different lemming densities in 1998–2000 during the first week of June when the birds return to their breeding sites (Korte 1984). The density of adult long-tailed skuas is always close to 0.02 ind. ha^{-1} (Maher 1970a, Andersson 1976).

Breeding success of long-tailed skuas ranged from 0 to 1.5 fledglings per km^2 , and it was closely correlated with lemming density at snowmelt ($r=0.96$; $p<0.001$). Contrary to snowy owl, breeding attempts by long-tailed skua can be observed at low density (e.g. 1996, 1997, 2002; Table 5), and the numerical response for juveniles

(G') is therefore best fitted with a sigmoid function with $b'=1.6$ and $Y'=6$ ($R^2=0.89$; Fig. 5d).

Arctic fox

The density of fox dens used for reproduction varied from 0 to 0.08 per km^2 . The density of active dens was correlated with lemming density at snowmelt ($r=0.71$; $p<0.01$), but this relationship was less pronounced for the fox than for the avian predators. Even at low prey density ($N'<1$), some foxes attempted to reproduce in 5 out of 8 years and the number of territorial but non-breeding pairs present in the valley was never less than one in the other years. Hence, we forced the sigmoid function to start at $G=0.027$ (minimum number of adults in the study area = 2) and put a ceiling at $b=0.16$ (maximal number of breeding pairs: 6 per 75 km^2 in 1990). The best fit to the data ($R^2=0.72$) was obtained with $Y=11$ (Fig. 5b), indicating that very high fox density only occur at very high lemming density. Without

Table 5. Numbers of breeding avian predators (with mean clutch size, breeding success and median hatching date), arctic fox (with mean number of weaned young per litter) and stoat density indexes (individuals per 100 trap nights and number of occupied lemming nests during the previous winter) in 1988 to 2002. The first line gives the estimate of collared lemming density at snowmelt.

Demographic variable	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Collared lemming density estimate after snowmelt (ind./ha)	0.15	2.55	10.54	0.34	0.09	0.14	7.79	1.87	0.21	0.39	11.55	2.52	0.09	0.41	0.61
Snowy owl (75 km ²)															
no. of breeding pairs	0	6	12	0	0	0	5	0	0	0	13	3 ^a	0	0	0
mean clutch size	–	≥4	6.7	–	–	–	≥5	–	–	–	7	4	–	–	–
breeding success (mean no. of fledglings produced per nest)	–	3.5	5	–	–	–	5	–	–	–	5.75	2.5	–	–	–
hatching date of first egg (median date)	–	30 Jun	16 Jun	–	–	–	21 Jun	–	–	–	18 Jun	25 Jun	–	–	–
Long-tailed skua (15 km ²)															
no. of territorial pairs	n.d.	n.d.	≥13	n.d.	n.d.	n.d.	≥13	>10	n.d.	n.d.	15	15	14–15	n.d.	n.d.
no. of breeding pairs	0	8	12 ^b	0	0	0	13	3	5	4	14 ^b	5 ^b	0	0	3
mean clutch size	–	1.75	1.77	–	–	–	1.92	1.67	1.40	1.50	1.86	1.40	–	–	1.33
breeding success (% of eggs producing fledglings)	–	≤57	≤73	–	–	–	38	40	0	0	87	14	–	–	0
hatching date of first egg (median date)	–	19 Jul	12 Jul	–	–	–	15 Jul	7 Jul	6 Jul	6 Jul	27 Jun	23 Jul ^c	–	–	8 Jul
Arctic fox (75 km ²)															
no. of dens with reproduction (no. of dens checked)	1 (4)	1 (4)	6 (7)	0 (6)	0 (6)	1 (6)	1 (6)	0 (7)	0 (7)	2 (7)	3 (7)	1 (7)	0 (7)	1 (7)	2 (7)
mean no. of weaned young per litter ^d	0	6	3.5	0	0	2	9	0	0	2	4	1.5	0	3	2
Stoat (15 km ²)															
individuals per 100 trap nights (no. of trap nights)	–	–	–	–	–	–	–	–	–	0 (824)	0 (449)	2.7 (300)	0 (547)	0.24 (420)	0 (396)
no. of lemming nests occupied during winter (% of all winter nests)	11 (7)	3 (0.2)	4 (0.1)	28 (10)	15 (14)	0 (0)	2 (0.1)	15 (1.5)	6 (3)	1 (0.3)	3 (0.1)	7 (0.4)	16 (14)	6 (2)	12 (3)

^aonly 50 km² surveyed in 1999 due to inaccessibility of the upper valley.

^bin 3 years, an additional pair (on the same territory in 1998 and 1999) was sitting on an egg-like stone for several weeks; it was not considered as breeding.

^clate snowmelt in 1999 but only one egg for this sample.

^dminimum values at the end of July (including dens monitored in the Karup Valley outside the study area).

the highest data point (1990), the numerical response of adult foxes to lemming density would have been much weaker ($b = 0.08$; $Y = 11$; $R^2 = 0.55$). Summer 1990 was unique since it followed a year (1989) with high lemming density (Fig. 3) and good breeding success. It may be that young foxes born in 1989 already reproduced in 1990. Overall, we could not find any delayed density dependence between the number of adult foxes and lemming densities over the 15-year period ($r = -0.26$ for N'_{year-1} and $r = 0.35$ for $N' + N'_{year-1}$).

The breeding success of the arctic fox was well correlated with lemming density at snowmelt ($r = 0.87$; $p < 0.001$). The best-fitting parameter values were $b' = 0.28$ and $Y' = 5.3$ ($R^2 = 0.75$; Fig. 5e).

Stoat

The numerical response of the stoat was the hardest to assess because, contrary to the other predators, density estimates could not be calculated with direct counts. Live-trapping data for 1997–2002 showed great differences between the years, from 0 to 2.7 ind./100 trap nights (Table 5), with the highest densities one year after the lemming peak. The number of lemming winter nests occupied by the stoat provides another density index that is available for the entire study period. If the duration a stoat occupies a particular nest is density-dependent (e.g. longer during peak years), this index would be biased. However, since the mean number of scats found around the stoat-occupied nests in different years was fairly constant (mean: 12.3 ± 1.04 SE) and not correlated with N' or N'_{year-1} ($p > 0.1$), we rejected this hypothesis. Fitzgerald's (1977) results also support our decision. He showed that the mean number of winter nests used by small mustelids over the winter season remained constant over a vole cycle regardless of the vole density. The number of winter nests occupied was not correlated with the lemming density at snowmelt (N' ; Fig. 6a), but it was correlated with N'_{year-1} ($r = 0.68$; $p = 0.01$) and even more so with $N'_{year-1} + N'_{year-2}$ ($r = 0.83$; $p < 0.001$; Fig. 6b). These results suggest that stoats need two successive and successful breeding seasons to recover from the very low density they reach during the low phase of the lemming cycle (the open symbol is the data point for 2002, omitted in the calculation; Discussion). The total number of stoats annually encountered in the 15 km² study area was positively correlated with $N' + N'_{year-1}$ ($r = 0.88$; $p < 0.001$; zero values omitted: open symbols; Fig. 6c), but not with N' or N'_{year-1} separately ($p > 0.05$). Successful stoat reproduction in the study area was confirmed in 1990 and 1999, the two instances in which the focal year was the second successive year with $N' > 2.5$). The occurrence of reproduction was difficult to ascertain and it may have occurred in other years as well.

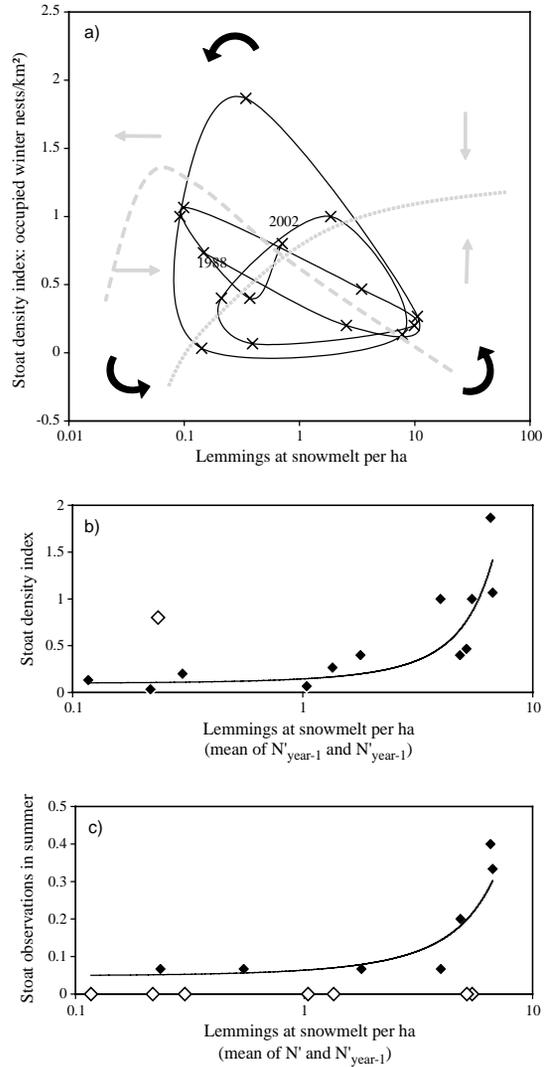


Fig. 6. Numerical response of the stoat to lemming density at snowmelt (a) and based on lagged lemming densities (b–c). In panel (b), the number of winter nests occupied by stoats per km² is plotted against the average lemming density for the two springs preceding this winter (i.e. N'_{year-1} and N'_{year-2}). In panel (c), the stoat numbers are the minimum numbers of different individuals seen in the summer per km² in the 15 km² intensive study area, plotted against the average lemming densities for the two previous springs (i.e. N' and N'_{year-1} since in this case observations were made after snowmelt). The anti-clockwise succession of yearly data points (crosses) in (a) is shown by the black arrows, with the first and the last year of the time-series labeled. The gray dotted line approximates the location of the predator zero isocline (direction of the change in predator numbers shown by vertical gray arrows), while the gray dashed line approximates the location of the prey zero isocline (direction of the change in prey numbers shown by the horizontal gray arrows). Open symbols in (b) and (c) were not used while calculating the trend lines shown in these figures (see text).

Total responses and predation rates

The total response of each predator species was calculated for the period 1998–2000, for which we

know both N and N' , by multiplying the functional response (Fig. 4) by the numerical response (Fig. 5). For stoat, the total response was calculated by multiplying the conservative estimate of its functional response (with $D=0.1$ in Fig. 4d) by its lagged numerical response (minimum number of stoats observed in the field as a function of the lemming density at snowmelt averaged for N' and $N'_{\text{year}-1}$; Fig. 6c).

The total response of predators varied more than 100-fold from >0.1 lemmings predated daily per ha in the first part of the summer in 1998 to <0.1 per km² in 2000 (Fig. 7a; mid winter predation by stoat estimated by averaging the last data point available for the previous summer with the first data point for the following summer). The contribution of each predator species varied greatly among the years, avian predators taking most of the lemmings in intermediate (1999: 71%) and peak years (1998: 88%), while the impact of mammalian predators clearly dominated during the low years (95–100% of the total number of lemmings predated in summers 2000–2002).

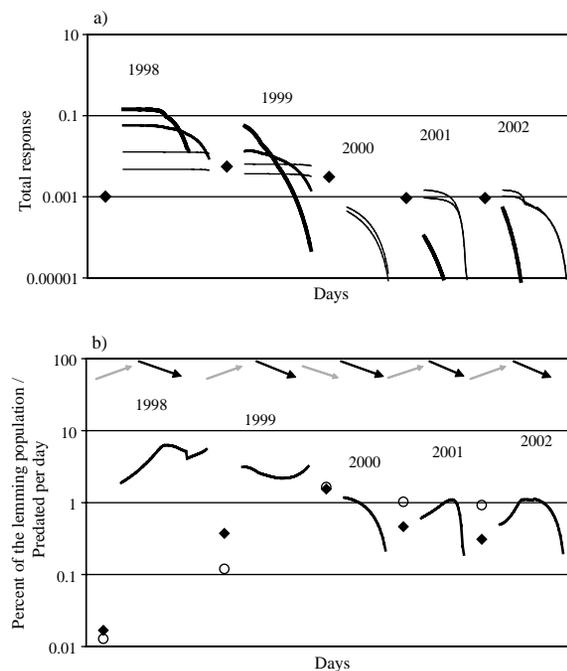


Fig. 7. (a) total response (number of lemmings predated per ha per day) of long-tailed skua (very bold), snowy owl (bold), stoat (regular) and Arctic fox (fine line) during five successive summers. Black diamonds show the estimated daily predation rate of the stoat at mid-winter, when the stoat is the only significant resident predator species. (b) daily predation rate of the collared lemming, summed up for the four predators in summer (black line) and for the stoat only in winter (black diamonds; alternative calculation: open circles, see text). Black and gray arrows indicate the trend in lemming population density in summer and winter, respectively (from Fig. 2).

Another striking result is that more than 2% of the lemming population was predated daily in the summers of high and intermediate lemming density, while the daily predation rate was $\leq 1\%$ in low lemming years (2000–2002; Fig. 7b; Gilg 2002). In winter, assuming that only stoats were significant predators, the daily predation rate was $>1\%$ only in 1999–2000 – which is the only winter with a decrease in lemming density (Fig. 2). Stoat predation was extremely low during the winter 1997–1998 preceding the peak year (Fig. 7b). The numerical response of the stoat (Fig. 6c) used for this calculation can be questioned, but an alternative estimate of the daily predation rate based on the number of occupied winter nests gives a very similar result (open circles Fig. 7b). In this second calculation, based on an independent data set, we assumed that each occupied winter nest (Fig. 6a) is used by a single stoat for one fifth of the winter season.

Discussion

Possible biases in the estimates

The equations used for the calculation of predators' responses include a number of assumptions that may potentially bias the estimates. We used methods and assumptions that would tend to underestimate rather than overestimate the predators' responses, and hence our conclusions about the impact of predation on lemming population dynamics should be conservative.

First, the functional response of avian predators takes into account the age-dependent food requirements of nestlings (Eq. 4b). Second, our calculations for mammalian predators did not include lemmings that were killed but not consumed, a behavior which can have a significant impact on prey dynamics (Oksanen 1983, Oksanen et al. 1985, Mittler 1997). Third, we did not consider the number of injured lemmings that escaped predators but subsequently died, nor non-weaned young that died following the death of their mother (Gilg 2002). Fourth, the mean weight of a stoat (136 g) was averaged based on a sample mainly consisting of subadults, hence the mean food requirements of stoat is probably higher than estimated by Eq. 5c, especially in winter and at low lemming densities when the metabolic rate is high due to low ambient temperatures and increased search time. Lastly, the mean body mass of lemmings (w) used to estimate the functional response of mammalian predators was averaged across all lemmings trapped over the cycle in 1998–2002, but most of them had been trapped during the peak year (1998), when lemmings were larger than in other years (the “Chitty effect”; Gilg 2002). A lower value of w would increase the number of lemmings required by the predators, but the shape of the functional response (determined by the half-saturation constant) would have remained the same.

Despite our conservative approach and the large number of scats that we analyzed (Table 4), the functional response of the stoat remained hard to describe. Scats produced in winter could not be dated precisely and DCR had to be plotted against the density at snowmelt (also leading to an underestimation). Summer scats were too few to provide reliable DCR estimates. We tried to fit one single response for the entire year, but it may be that while stoats are forced to specialize on lemmings in winter they may display a more complex response with several prey species in summer. Our decision to use a type III rather than a type II functional response incorporates a probabilistic “refuge” for the lemming at very low densities. It incorporates the possibility of stoats using some alternative prey when lemmings are so dispersed ($<0.1 \text{ ha}^{-1}$) that they must become very hard for stoats to locate. Empirically, birds, eggs, insects, berries, and carrion are known to be used in summer in NE Greenland (Pedersen 1926, 1931, 1942, Rodahl 1946; Table 4) as well as in other comparable arctic-alpine ecosystems (Nasimovich 1949, Martinoli et al. 2001). In this situation, with stoat density ≤ 1 per 15 km^2 , it would be unrealistic to use a type II functional response, which assumes a steeply increasing predation rate for the lowest prey densities. Furthermore, the value we used to describe the functional response of the stoat ($D=0.1$) must be conservative, since it is similar to the value estimated for the well-documented fox response ($D=0.13$), even if the Arctic fox has unquestionably broader diet (is more “generalist”) than the stoat.

The numerical responses are probably also conservative, since they were calculated with the minimum number of predators feeding on lemmings. For example, we did not consider young that died before fledging or weaning, but which would have eaten lemmings for several days. The minimum number of weaned foxes (Table 5) was probably underestimated, since the pups rarely show up all together and may leave the natal den before complete weaning (Macpherson 1969). To a lesser extent, young snowy owls spread around the nest before fledging, and some might occasionally be overlooked due to their homochromic plumage.

Despite all these considerations tending to produce underestimates, our results agree with the values presented in the literature. The maximum DCR of the snowy owl ($4.7 \text{ lemmings day}^{-1}$) is very close to those reported for captive (Gessaman 1972, Ceska 1974, Busse and Busse 1976) and wild individuals (Pitelka et al. 1955, Watson 1957, Batzli et al. 1980, Wilson 1999), while the maximum densities are often reported to be close to one pair per $4\text{--}5 \text{ km}^2$ (Miller et al. 1975). Similarly, the density of long-tailed skua in our study ($\approx 0.8\text{--}1$ pairs per km^2) was the same as in other parts of its breeding range (Maher 1970a, Maher 1974, Andersson 1976, Korte 1977), while its maximum DCR ($4.4 \text{ lemmings day}^{-1}$) is in line with

the values reported from Scandinavia (Andersson 1971) and from Alaska for the Pomarine skua (*Stercorarius pomarinus*; Maher 1970b).

The food requirements of an individual stoat ($w=136 \text{ g}$) estimated in this study equal 1.92 lemmings ($w=42.5 \text{ g}$) per day, while Wilson (1999), using a different method of calculation based on the energetic value of a lemming (Gessaman 1972) and the energetic requirements of long-tailed weasels (*Mustela frenata*; Brown and Lasiewski 1972), concluded that stoats ($w=134 \text{ g}$) would need 1.35 lemmings ($w=60 \text{ g}$) per day. Taking into account the difference in the respective prey weights, the two estimates are strikingly similar. The maximum DCR calculated for the Arctic fox ($4 \text{ lemmings day}^{-1}$) is somewhat lower than the previously published values. In Canada, Wilson (1999) reported up to three (for juveniles) to seven collared lemmings predated daily by Arctic fox, though 80% of the estimates were ≤ 4 . A physiological approach based on the energetic value of lemmings (60 kcal for a 42.5 g lemming; Gessaman 1972) and on the maintenance requirements for a 3 kg Arctic fox ($360 \text{ kcal day}^{-1}$) would predict a maximum of six lemmings per day. However, fattening periods and changes in activity patterns modify the energy budget greatly and energy requirements can vary 5-fold, which means that the food requirements can be much higher than the value suggested by our results (Batzli et al. 1980, Frafjord 1993, 1994, Fuglei and Øritsland 1999). There are two reasons for our possible underestimate. The scat samples collected at dens were a mixture of young and adult scats, hence our maximum daily consumption rate is a mean for both age classes and hence lower than published values for adults only. The factor of 28 used to convert dry weight of lemming remains to fresh weight of lemmings eaten might be too low, a view already expressed by Wilson (1999). Indeed, if lemming remains recovered in fox scats were only hairs (which was often the case), the conversion factor would have been close to 35 (Reid et al. 1995), giving a maximum DCR of 5 lemmings per day. In any case, the shape of the functional response is valid and only the estimation of the maximum rate remains underestimated.

Contrasting responses by the four predators

All predators responded strongly to changes in lemming density. Because they have to feed in a landscape devoid of shelter and under continuous daylight, lemmings are very vulnerable to predation, with 1% or more of their numbers being predated daily in most phases of the cycle (Fig. 7b). Therefore, and since the collared lemming population only rarely reaches what is regarded as high rodent densities at lower latitudes ($>10 \text{ ind. ha}^{-1}$), predators can have a great impact on lemming

population dynamics. In the summers when the spring density exceeds 2 lemmings per ha, all the four predators can feed almost exclusively on lemmings (Table 1–4) and all breed successfully (Table 5). At lemming densities higher than 2 per ha in the spring, all the four predators can be considered as lemming specialists.

In a closer examination, and considering all lemming spring densities, avian and mammalian predators display important differences in their responses. Avian predators, unable to scent and dig lemmings from their burrows at low densities, are generalists in terms of their functional ($D > 1$ lemmings ha^{-1}), numerical (successful breeding only when $N' \gg 1$) and total responses (maximum predation rate at high lemming densities; Fig. 7a). Additionally, they are only present in summer (long-tailed skua) or during peak lemming years (snowy owl). However, the skua, which is at least five times more abundant than the owl, returns to the same territory every year to raise small broods of maximally two young, while the owl is nomadic and raises large broods of up to 7–8 fledglings. In contrast, the mammalian predators are able to track lemmings at very low densities in their burrows or under the snow, and they behave as specialists with functional responses saturating at low lemming densities ($D \leq 0.15$ lemmings ha^{-1}) and total responses outscoring the responses of avian predators at low lemming densities (Fig. 7a). The arctic fox, however, is less of a specialist than the stoat. The functional response of the fox was best fitted with a value of D greater than that for the stoat (Fig. 4c), and the deep snow layer that covers the study area in winter largely prevents foxes from feeding on lemmings for most of the year in NE Greenland (Manniche 1910).

The arctic fox and the snowy owl are omnipresent in the Arctic and have been observed to have unpredictable and spectacular invasions. For these reasons they have often been considered as the key predators on arctic rodent populations (Elton 1924, Chitty 1950, Pitelka et al. 1955, Watson 1957, Batzli et al. 1980, Wilson 1999). On the contrary, because the stoats are rarely seen in the field and the skuas have small clutches and are often seen feeding on invertebrates and berries, these predators have often been neglected. In this study, we have shown that these latter predators have a very strong impact on lemming dynamics. As a matter of fact, every predator species becomes dominant at some stage of the cycle (Fig. 7a), emphasizing the need to consider all the species in this community for an adequate understanding of the predator–prey dynamics.

Impact of predation on lemming populations in summer

The numerical and functional responses of predators determine their impact on prey population dynamics

(Solomon 1949). If predation rate is density-dependent and occasionally higher than the recruitment rate of the prey, predation has a regulatory effect (Sinclair and Pech 1996, O'Donoghue et al. 1998).

To assess the role of predation in lemming dynamics, we calculated the fraction of the lemming population that is predated daily (Fig. 7b). If this daily predation rate (a_{PN}) is greater than the intrinsic growth rate of the prey (r_N), the prey density declines (Begon et al. 1996). The intrinsic rate of increase of the collared lemming in summer has been estimated at 0.6% per day (Krebs 1964) or even less (Gilg 2002). In theory, and assuming no intrinsic mortality, the maximum rate of increase could be as high as 2.3% per day, assuming that all females older than one month produce one litter of four young (with a 1:1 sex ratio) per month (Gilg 2002). A more realistic but still optimistic estimation assumes that 30% of the females reproduce monthly in summer (Wilson 1999), that the mean litter size is 3.8 young (with 1:1 sex ratio), that females start to reproduce at the age of two months, and that there is no post-weaning mortality but 10% mortality of young before weaning (Chernyavsky and Kiriushchenko 1979). These assumptions lead to a daily rate of increase of 1%.

With these values, the observed predation rate (Fig. 7b) is sufficient to explain the lemming decline in 1998–1999: the estimated predation rate (dominated by avian predators) was 2 to 6-times higher than the likely recruitment rate of the prey. In several phases of the cycle predation was even compensatory, increasing with decreasing prey density (Fig. 2, 9), indicating a time lag in the response of predators (O'Donoghue et al. 1998). In most summers, the daily predation rate was $\geq 1\%$, and since our predation rates represent conservative estimates while the 1% rate of lemming increase is likely to be an overestimate, predation most probably caused the summer decline in the lemming population (Gilg 2002). However, in low years the predation rates declined toward the end of the summer, when the lemming density N went below the mammalian predators' half-saturation constants D (≤ 0.13).

Arctic fox, long-tailed skua and snowy owl are the dominant summer predators (Fig. 7a). According to the generalist predator hypothesis, they should reduce the amplitude and length of the lemming cycle (Andersson and Erlinge 1977, Hanski et al. 1991). Instead, the amplitude (>100 -fold) and the length (≥ 4 years) of the lemming cycle are greater than what is observed in most of Fennoscandia (Hanski et al. 1991, Norrdahl 1995, Henttonen and Hanski 2000). According to Rosenzweig and MacArthur (1963), generalist predators must be relatively inefficient and have sufficient alternative prey to have a stabilizing effect on prey dynamics. These assumptions can be rejected in the present case at least for the snowy owl and the long-tailed skua, which had high hunting success (owl: 55%

($n=279$; 1998) and 67% ($n=55$; 1999) of hunting attempts successful; skua: 65% ($n=37$) and 79% ($n=19$) respectively), but are unable to breed when the lemming density is low due to the scarcity of alternative prey. These apparent discrepancies between observations and expectations based on the general notion of 'generalist predators' naturally reflect the complexity of the predator responses in the present community, which defy any simple classification.

The complex nature of the predators' responses is especially clear in the case of the nomadic avian predators, which have often been suggested to have various population dynamic impacts on their prey species (Ydenberg 1987, Ims and Steen 1990, Norrdahl and Korpimäki 2002). Another generic reason for the complexity of predators' impacts on prey populations is the fact that predators respond functionally to the current prey density (N), while their numerical responses are often determined by the past densities. For example, the critical prey density for the numerical response of the snowy owl, the long-tailed skua and to some extent the arctic fox is the lemming density at the onset of breeding season, approximately at snowmelt in the Arctic (N'). Hence, the estimated predation rate for a given density N can be very different for different values of N' . This complication has been overlooked in some studies by assuming that the prey density remains fairly constant over the breeding season. But as we have seen, in the Arctic the lemming density declines drastically in most summers, which means that it is essential to take N' explicitly into account (Maher 1970b). This is illustrated by Fig. 8, which summarizes the daily predation rate for each predator according to N and N' . Here, the owl, the skua, and the fox (four upper panels) show the typical (type III) increase in predation rate with an increase in prey density until a threshold density, above which the respective predation rate declines. However, the predation rates also depend on N' , being by far higher in peak years (e.g. 1998 with $N' > 10$) than in intermediate (e.g. 1999 with $N' \approx 1$) and in low years (e.g. 2000–2002 with $N' < 1$). Therefore, all these "generalist" predators have a stabilizing effect on the dynamics of the collared lemming, but this effect is stronger when N' is high and only the avian predators have a sufficient impact to significantly contribute to the lemming decline at high lemming densities, when they take $\geq 1\%$ of the prey population daily. The situation is very different for the stoat, which shows the highest predation rate after the peak and can impose a high predation rate ($\pm 1\%$ of the lemming population) even at low lemming densities (i.e. when both N and N' are < 1). Considering the summed predation rate (Fig. 8: last two panels), the only period when a summer increase in the lemming population could possibly take place on the assumption of 1% recruitment rate appears to be the low years preceding the peak.

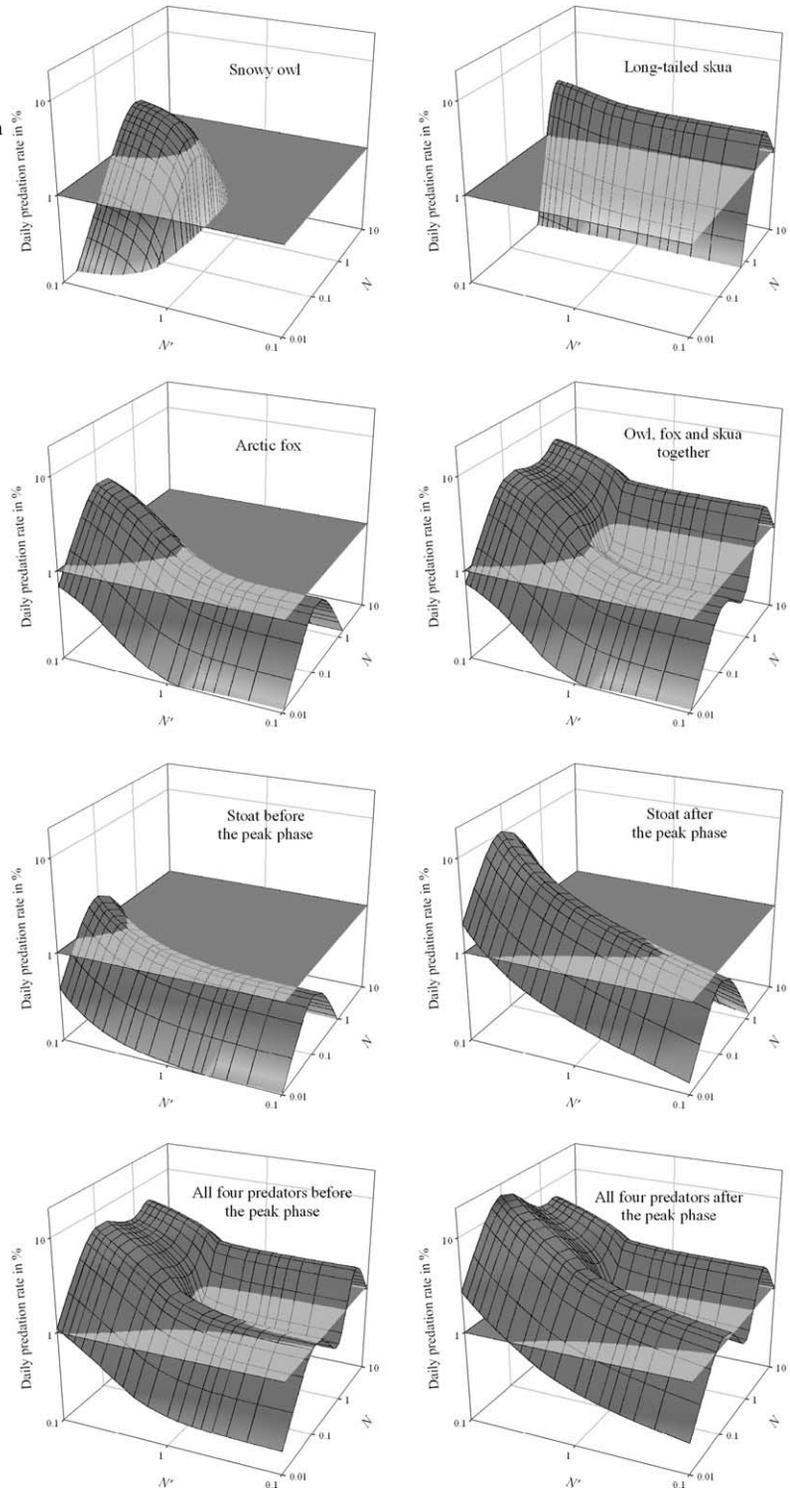
Several other studies that have assessed the impact of predation in predator–prey communities comparable to the present one have reached results similar to ours. The collared lemming summer decline appears to be often associated with high predation pressure. Enclosure experiments and studies of radio-collared lemmings indicate that predators were able to reduce lemming populations by 50–80% over a period of two months in summer in four studies (Reid et al. 1995, Wilson et al. 1999, Schmidt 2000, Gilg 2002). The long-term study conducted at Point Barrow on the brown lemming (*Lemmus trimucronatus*) also concluded that avian predators (snowy owl and pomarine skua) were the most important predators in summer, accounting for up to 88% of total mortality (Batzli et al. 1980). With the exception of June, when high predation rates were recorded due to numerous non-breeding pomarine skuas, the trends reported at Point Barrow are very similar to our results. In the peak years, predation rates of avian predators were high and increased during the summer as the lemming density declined, while in low lemming years avian predation rates were negligible.

Predation is probably more important in the Arctic, where rodents are very accessible to predators in summer, than in other regions. However, predators have been reported to kill a large fraction of some rodent populations also at more southern latitudes. In California, weasels were believed to kill more than 80% of an over-wintering vole population in some years (Fitzgerald 1977), with the lowest figures in the winter preceding the peak year (Tapper 1979). In two Polish studies, mortality of voles due to predation was always $> 50\%$ when vole density was low (Goszczyński 1977), and tawny owls (*Strix aluco*) alone were recorded to kill up to 74% of the rodent population in some months (Jedrzejewski et al. 1996). In boreal forests in Canada, coyotes (*Canis latrans*) and lynx (*Lynx canadensis*) can kill more than 50% of the snowshoe hare (*Lepus americanus*) population in winter (Krebs et al. 2001). Finally, in Sweden the extensive study of Erlinge and co-workers has shown that more than 90% of the voles and mouse produced annually in a 4000 ha study area were lost due to predation, mainly by generalist predators (Erlinge et al. 1983, 1984).

Predation and the lemming cycle

It seems obvious that predation is a key factor that explains the summer decline observed in the collared lemming population. The next questions we should attempt to answer are (1) what keeps the lemming population sparse for several successive years following the peak year, and (2) what force is suddenly released to allow the lemming population to peak within a few months?

Fig. 8. Daily predation rate in summer (percentage of lemming population predated per day) calculated with the functional and numerical responses for each predator (adults and full-grown young). Stoat predation rate (included in the four lower panels) is presented separately for the increase and the decline phases of the cycle, since the numerical response of the stoat is delayed. The stoat numbers were estimated using Fig. 6c, with $N_{\text{year}-1}$ estimated through regressions with N . The shaded layer shows the 1% threshold above which lemming reproduction can no longer compensate for losses due to predation.



In our study area, the lemming population increases only during winter (Fig. 2; Sittler 1995), though the winter increase does not occur systematically nor always to the same extent. Thus in winter 1999–2000 the lemming population actually declined, and it increased

much faster in the winter 1997–1998 (preceding the peak) than in the other winters (Fig. 2). This variation is well correlated with the inferred predation rate of the stoat in winter (Fig. 7b, 9). In winter 1999–2000, stoat predation rate was higher than the maximum growth

rate of the lemming population, apparently preventing any increase. In winter 1997–1998, predation was strongly reduced, being almost 100 times less than the 1% recruitment rate, and allowing a fast and continuous lemming increase during the winter. In the other years, stoat predation was between 0.1 and 1%, apparently allowing a moderate increase of the lemming population. Hence, predation appears to be a plausible factor not only to explain the summer decline but also to drive the entire cycle.

Long-term data collected over the 15-year period also supports the specialist predator hypothesis as the possible mechanism maintaining cyclic dynamics. With the exception of winter 1999–2000, stoat density follows systematically changes in lemming density with a time lag of less than one year (Fig. 9a). Such delayed density dependence of small mustelids to rodent densities, previously reported from many localities (Fitzgerald 1977, Tapper 1979, Debrot 1983, King 1989, Korpimäki et al. 1991), is noteworthy in suggesting a strong dynamic link between the two species, though this observation alone is not sufficient to explain the maintenance of cyclic dynamics. More significantly, the predation pressure of the stoat, as assessed by the percentage of lemming winter nests occupied by the stoat (Fig. 9b), was systematically released ($\leq 0.1\%$ of winter

nests occupied by stoat) in the winter preceding the lemming peak years: 1990, 1994 and 1998. In contrast, winter predation thus assessed was maximal (>2 and often $\approx 10\%$) before the lemming lows: 1992, 1996 and 2000, and probably also in 1988. In all but one year (winter 2000–2001), an increase in the winter predation pressure resulted in a decrease in lemming density and vice versa. Additionally, the amplitude of the lemming cycle and annual changes in winter predation pressure varied in a similar manner: when peak density was not very high (7.8 ind. ha^{-1} in 1994 versus $\approx 10 \text{ ind. ha}^{-1}$ in 1990 and 1998), predation pressure in the following winter was also reduced (1.5 to 3% vs $>10\%$).

The strikingly regular pattern in the multi-annual dynamics was somewhat disrupted in winter 1999–2000, when the stoat density index peaked during the second winter following the lemming peak (arrow in Fig. 9a), probably following two successive breeding years by the stoat; and in winter 2001–2002, when the lemming population slightly increased despite an increase in stoat winter predation (arrow in Fig. 9b). Associated with these irregularities, the long-term 4-year cyclic dynamics were also altered. One possible explanation of these irregularities is exceptional mortality of muskox in the winter 2000–2001, when at least seven full-grown individuals and one died within or in the vicinity of the 15 km^2 young intensive study area, the average figure being closer to 0–2 per winter over the entire (75 km^2) study area. The last two years have been especially warm and wet, a very harmful situation for the muskox (Pedersen 1958, Vibe 1967, Putkonen and Roe 2003). Stoat, which is known in Greenland to feed extensively on dead frozen meat in winter (Rodahl 1946), had a much higher survival rate during the 2000–2001 low phase of the lemming cycle than in the previous years (compare the data point for winter 2000–2001 with winters 1992–1993 and 1996–1997 in Fig. 9a). Thus stoat winter predation rate remained apparently too high to allow a strong increase in the lemming population in 2002. The stoat and lemming population sizes may have been close to an equilibrium point (where the prey and predator zero isoclines cross) for the past two years, an assumption also supported by Fig. 6a.

Two observations from two other localities are worth mentioning here. At the Zackenberg research station, 240 km north of our study area, similar irregularities in the lemming dynamics have been observed during the last two years in lemming populations studied since 1994 (Berg 2001). In contrast, on Ymer Island (70 km north-west of our study area), in the dry continental steppe-like Tundra zone (Feilberg et al. 1984) that is less influenced by the relatively warm and wet marine climate, the lemming dynamics have been synchronous with the dynamics in our study area since at least 1988, and the lemming populations peaked, as expected, in summer 2002 (Gilg and Sabard, unpubl.).

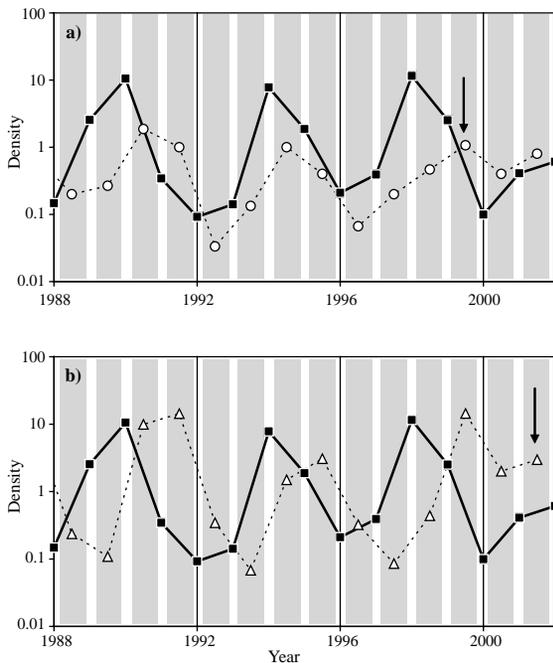


Fig. 9. Delayed response of the stoat to lemming densities over the period 1988–2002. Black squares show lemming density at snowmelt (ind. ha^{-1} ; from Fig. 3); open circles in panel (a) represent an index of stoat density (number of lemming winter nests occupied by stoat per km^2) and open triangles in panel (b) the predation pressure of stoat (percentage of lemming winter nests occupied by stoat). Winter periods are shaded. For the two arrows see Discussion.

Our study highlights the role of predation in shaping the lemming dynamics and suggests that predation is the most probable force driving the cyclic dynamics. The observations that striking population declines of the lemming were associated with an increase in the overall predation rate (depressatory predation) and that stoat predation pressure in winter was delayed density-dependent support the specialist predation hypothesis. Turchin et al. (2000) suggested that the cyclic dynamics of the moss-eating Norwegian lemming (*Lemmus lemmus*) was driven by food-lemming interactions, highlighting the possibility that dynamics of similar lemming species occurring in similar (open boreal) landscapes can be driven by different forces. Alternative hypotheses based on food and intrinsic factors (Batzli 1992, Boonstra 1994, Turchin and Batzli 2001) could not be addressed in this study and deserve further studies in NE Greenland, but these hypotheses generally predict a continuous decrease in prey population density from the peak to the low phase, while the observed decline from the peak in summer 1998 to the low in summer 2000 (Fig. 3) was interrupted by temporary increases in winter (Fig. 2). The predation hypothesis is also supported for the collared lemming by a mathematical predator-prey model (Gilg et al. 2003) parameterized with the data presented in this paper, as well as by experimental studies in Canada (Reid et al. 1995, Wilson et al. 1999).

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