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Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in North East Greenland: preliminary results from a long-term study

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Interactions between lemmings and stoats were documented over 6 years through systematic and comprehensive surveys of lemming winter nests in a 1 000 ha study area located in North East Greenland. The surveys revealed a cyclic pattern in the lemming population. The response of stoats to the increase of the lemming population was delayed by about 18 months. The increase phase of lemmings was featured by very low stoat densities. The collapse of the lemming population in late summer 1990 happened when, as a result of an increase in the in stoat population, young stoats dispersed to their own territories and occupied the whole area. Following the crash, stoats seem to have kept the lemming popåulation at a low level until 1992, with the subsequent local extinction of stoat during winter 1992/93. The clear-cut patterns observed in NE Greenland are probably due to the simplicity of the community and may also be related to the very deep snow cover in this part of the High Arctic. As a result, the due to vertebrate predator/prey community is simply composed of stoats, lemmings and ptarmigans over more than 2/3 of the year.

1. Introduction

A great deal of work has been devoted to the factors governing population dynamics of small mammals. Although microtine rodents have received the bulk of attention, their cyclic fluctuations in density remain controversial. A recent up-to-date review (Stenseth & Ims 1993) has shown that many of the intrinsic hypotheses, like stress and social interactions, had to be rejected as the only explanation. The driving forces behind the cyclic changes in microtine populations are now mostly sought among extrinsic factors (Hansson & Henttonen 1988, Hanski et al. 1993, Ostfeld et al. 1993). An increasing number of proponents view that interactions with predators, particularly with specialist ones, such as small mustelids, could be the trigger a cycles.

Substantial insights could be achieved in simple communities and in areas with high level of detectability. In this respect, the High Arctic ecosystems are alluring, since they provide opportunities to deal with all the predator and prey species simultaneously instead of just one predator or one prey in isolation. These considerations have lead to the inception of a long-term investigation in North

East Greenland (Sittler 1993).

The arguments favouring the predation hypothesis stress the importance of an accurate documentation of prey/predator relationships. An easily documented phenomenon in these High Arctic interactions is the nesting behaviour of the lemming in winter. Nests built for insulation not only provide information on the relative population levels of lemmings, but also on spatial distribution and reproductive activity of lemmings as well as on predation by stoats. Stoats use the lemming nests as their own wintering quarters by lining them with the fur of the prey. Data on nesting behaviour of lemmings extending over more than one field season are available only in a few studies for High Arctic sites (MacLean et al. 1974, Fuller et al. 1977) or in alpine ranges (Fitzgerald 1977).

In this paper we report the material gathered over the first six field seasons (1988 to 1993) of an ongoing long-term study (Karupelv Valley Project 1988–1998). We plan to continue these studies for several years to provide the firm body of data to test some of the hypotheses put forth.

The approach of this project was to assess in a long-term perspective the patterns and relationships of all species belonging to this simple community. In the present paper, we will concentrate on results of lemmings and their main specialist predators, the stoats.

2. Study area

The Karupelv Valley is located on the southern edge of Traill Island in North East Greenland (72°30'N, 24°W). It is part of the North East Greenland National Park and offers therefore a secure study site for long-term surveys. A short outline of its physiographic settings is given here. This High Arctic site is classified as semi polar desert by Bliss (1990) and includes some large patches fully free of vegetation. Mean temperature in July is around 5.0°C. Snow cover is continuous over more than 260 days/year. Snow depth exceeds by far what is generally reported for other arctic areas. According to measurements at Mesters Vig, a meteorological station located 30 km south of the study site, mean snow depth in March is around 140 cm (Nuna-Tek, 1989) against 35 cm in Point Barrow (MacLean et al. 1974).Furthermore, it supports one of the simplest terrestrial vertebrate communities, including the collared lemming (*Dicrostonyx groenlandicus*) and the ptarmigan (*Lagopus mutus*) as primary consumers and the stoat (*Mustela erminea*), the arctic fox (*Alopex lagopus*), the snowy owl (*Nyctea scandiaca*), the long tailed jaeger (*Stercorarius longicaudus*) as the secondary consumers.

3. Methods

3.1. Winter nest surveys

The primary source of information to assess population patterns in lemmings and stoats consisted of an extensive survey of winter nests with a tecnique similar to that by Maher (1967) and MacLean et al. (1974) in Alaska. We recorded the nests after snow melt and checked the proportion taken over by the mustelid predator. As the nests are easily detectable in the High Arctic environment and can be censused comprehensively over a large area, we could opt for a study site of ca. 1 000 ha to be investigated on a yearly basis. We recorded the total number of nests, their distributional pattern as well as any attributes that may provide information on intensity of habitat use, reproductive activity and other aspects of life history. This methodology gives indices on relative population levels during the winter, on habitat selection and spacing pattern during snow cover. Further, reproductive output and predation levels by stoats may be inferred.

The nest survey was done on a yearly basis from the end of June until the beginning of August. Based on experience gained during the first field season in 1988, nests proved to be easily seen in distances of 15 to 20 m on flat terrain, but sometimes less than 10 m in rugged topography. Nests were recorded while walking the transects spaced at distances of about 30 m in flat terrain and about 20 m in rugged topography or boulder fields. The area covered daily was labelled on an overlay of the aerial photograph to make sure that at the end of the season every part of the study area had the same census effort. This technique is labour-demanding and involves walking about 600 km per season to ensure complete coverage.

To avoid misregistration and resampling, nests were destroyed upon recording. Despite the high probability of finding the nests, a few may have escaped the detection. These could theoretically be counted in the following field season, as older nests may not always be discriminated from those of the past winter, not even by an experienced observer. In our own trials older nests (2 winters old) were compared with the recent ones (one winter old). Depending on the state and location of the nests, it was sometimes very difficult to age them, in contrast to MacLean et al. (1974). This problem concerns the first year of our survey (1988), since nests of the 1986/87 winter had not been removed. Consequently, some nests may have been attributed to winter 1986/87 or vice versa. Therefore, in all studies using this technique, data for the first year of survey may be biased and should be considered with caution.

3.1.1. Distributional pattern of the winter nests

An enlarged aerial photograph of the study area (1 000 ha) was divided into 200 grids of approx. 230×230 m in size. All nest records were assigned to one of the grids.

An initial attempt in 1988 to record distances between the nests revealed some obvious clumping pattern, with a

Fig. 1. A lemming nest that has been occupied by a stoat. (Photo Körner)

few nests grouped together, while the next ones were as a rule at a distance greater than 50 m. It appeared that the grouped nests must have been connected under the snow (tracks of latrine sites), suggesting some social relationships between inhabitants of the nests. The only previous record on this phenomenon is by Dunaeva (1948) from the arctic Siberia; she mentioned that the distance between the winter nests of collared lemmings reached up to 100 to 150 m and that nests were rarely found at a closer distance than 50–60 m. However, some nests were found in a row within 5 m, an observation attributed to a family group of lemmings. The nests were connected only in the latter case. Accordingly, we recorded nests as non-aggregated when the distance between them was more than 15 m. When two or more nests were closer than 15 m, these were considered aggregated.

3.1.2. Signs of reproduction in lemming winter nests

Examination of latrine sites during the first field season (1988) revealed pellets of different sizes. MacLean et al. (1974) working mainly with brown lemming (*Lemmus sibiricus*) were able to identify pellets from adults and young. We analysed pellets from 1989 onwards when we found a nest containing the carcass of a nestling and pellets less than 4 mm in length while other piles were made up of pellets about 6 mm in length. Near other nests, pellets with different sizes (from 4 mm upwards) were also found. We assumed that they probably were from animals growing from juvenile to adult stage.

Pellet analyses are, however, fraught with uncertainties. Most droppings, especially those from juveniles, may be overlooked when covered by vegetation or when having been removed by melt water. Furthermore, droppings lying in stagnant melt water may swell so that initial length may not be assessed.

3.1.3. Indices of stoat predation

It is well established that subnivean lemming nests may be visited and predated by mustelid predators during the winter (MacLean et al. 1974). Such nests are easy to identify due to the fur lining (see Fig. 1); the predator uses the fur of its prey for better insulation. In some nests, a light-transparent layer of hairs may be found. This is not due to the presence of a stoat but to the moulting of the lemming. As collared lemmings turn whitish in winter (from the end of September until the beginning of May), the coloration of the fur indicates the period when it has been killed. Another sign of stoat's presence are the scats or bone remains, usually within 2 meters from the nest. Scats were systematically recorded from 1990 onwards.

3.1.4. Records on vegetation

A field procedure was devised to provide information on vegetation available to lemmings, both as food supply as well as nest construction material. We first estimated the percentage cover of vascular plants within a radius of 5 m around nests. Most subnivean passages concentrate within this area, even though lemming also exploit adjacent areas. At each site, the most important vascular plants were recorded and the cover of each species was rated by a slightly modified Braun-Blanquet (1932) combined cover-abundance scale (6 classes).

3.2. Direct observations in summer

Information on lemmings in summer time was collected by recording active burrows, which are generally easy to detect due to the presence of recently excavated soil. This was

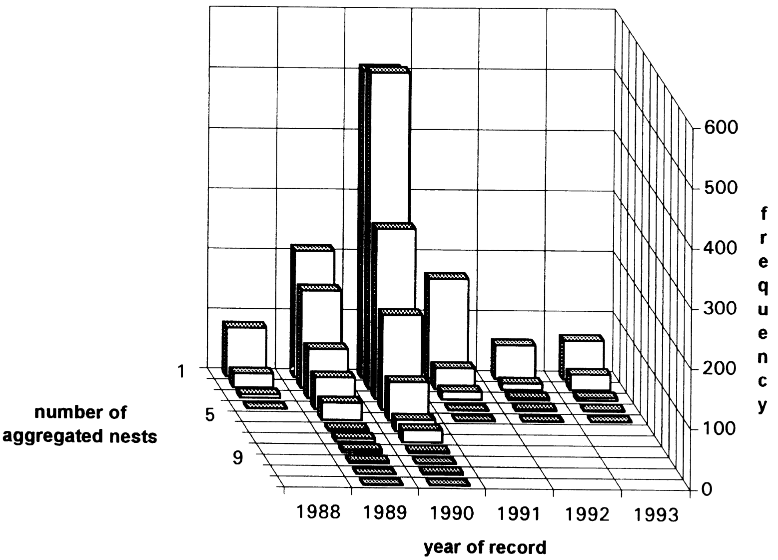


Fig. 2. Comparison of winter nest aggregations in 1988–93.

systematically done three times per field season along a permanent 1 500 m long transect line through various favourable habitats. Data obtained provide only a rought estimate of relative population levels and must therefore be accepted with some caution.

Estimating the number of stoats by direct observations is difficult. However, as time spent in the field exceeded 2 000 hours per season, direct or indirect observations were used for comparisons between the years. In contrast, numbers of all other predators (arctic fox, snowy owl and long-tailed jaegers) were easy to estimate during the breeding season by locating dens or nests.

All observed interactions between stoats and lemmings or other preys such as ptarmigan were recorded. The pluckings of the ptarmigans dating back to the winter and easily detected after snow melt were the only data that we were able to record systematically for this species.

4. Results

4.1. Population fluctuations of the lemmings

The numbers of lemming nests in the study area showed strong year to year differences (Table 1). Despite the problems in discriminating and aging nests during the first field season, it was clear that our study started from a lemming low in winter 1987/88 that persisted until the end of summer 1988. A noticeable increase occurred over the winter 1988/89. This was confirmed by the number of occupied burrows in summer 1989 as well as by regular direct observations of lemmings. Transect survey on July 4 in 1989 yielded 53 active burrows, a figure which increased to 72 on July 20.

The increase continued during winter 1989/90, with a nearly threefold increase in the number of winter nests from 1989 to 1990, when the maximum of 3687 nests was reached. On June 27, 1990, 184 active burrows were observed while on July 16 the same transect revealed 205 active burrows. The census on August 28, however, yielded only 82 active burrows, suggesting that the population was about to experience a decline.

The following winter was featured by a sharp crash as shown by the low number of winter nests (282) in 1991, a 13-fold decrease from the previous winter 1989/90. Observations made in summer 1991 reflected this low, with no direct observations of lemmings and only four burrows with signs of recent activity during the first census in June. Censuses repeated in mid- and late July failed to reveal any signs of recent activity.

The low phase continued through the winter 1991/92 and was featured by a further decrease in number of winter nests. This low level was maintained during summer 1992, with nearly no signs of freshly excavated burrows along the transect lines (neither elsewhere, not even in favourable habitats).

The low phase continued in 1993. There was a slight increase in the number of winter nests (145), but on June 28 only 3 active burrows were located along the transect line, and even they had been abandoned later in the season.

4.2. Nest aggregations

Data on nest aggregation are presented in Fig. 2 and Table 1. A more detailed analysis will be given elsewhere. Clumping was already noticed occasionally during the first field season in 1988, but it became a common feature in 1989 and 1990, when around two out of three "encounters" with lemming nests were with aggregated ones. Clumping was less common in the following 3 low years. An increase was, however, detected in 1993.

The difference in clumping between the increase — peak years and the the remaining years is interesting. Maximum number of nests aggregated was 11 both in 1989 and 1990, while maximum in low years did not exceed 5 nests. There was not a significant difference between the 1989 and 1990 data sets, while there were significant differences with the remaining years. Similarity in clumping in 1989 and 1990 may indicate that conditions leading to the increase over the first winter (1998/89) were not different from those of the second winter leading to the peak (1989/90). The difference in the absolute numbers is due to the fact that in winter 1988–1989, population started from a low level, while in autumn 1989 the population had already reached a considerable density. It seems that aggregation of 6 nests reflects a threshold value for the increase — peak phase. The high proportion of isolated nests is common to all low years.

In all years nest aggregations were linked with breeding and presence of juveniles, although the timing of nest construction is not known. Pellets attributed to juveniles confirm that breeding took place in every winter, although with significant differences in intensity (Table 2).

4.3. Population trends of stoats

Data on stoats and other predators recorded in the study area are presented in Table 3. Only the stoat material will be discussed here.

4.3.1. Direct observations during summertime

Because stoats are difficult to census by direct observation, no exact densities can be given for summer periods. However, as the field effort was similar in all years, direct observations indicate differences in relative population levels. Direct encounters were restricted to 1990, when two stoat families were located on July 8 and 10. The dens, hidden in cavities below boulder fields of a basaltic ridge, were at the distance of about 1 000 m from each other. A stoat was also observed in upper part of talus slope, at about 1 100 m a.s.l. No direct observations were made in the other field seasons (1988, 1989, 1991 and 1992). On July 27 in 1993, fresh tracks leading toward the study area were found on the shoreline.

4.3.2. Predation on lemming winter nests

Winter nest surveys showed sharp fluctuations in stoat numbers. In 1991, 28 out of 282 lemming nests were occupied. In 1989 and 1990, stoats must have been very rare because only 3 and 5 used nests were found. In 1993, no nests, respectively, were used by stoat in winter. This observation is also corroborated by the failure to detect any snow tracks during the survey started on May 14.

In most of the nests occupied by stoats, pellets from juveniles lemming were detected: in 1989, all 3 nests had pellets from juveniles; in

Table 1. Results of surveys on lemming winter nests.

	1987/88	1988/89	1989/90	1990/91	1991/92	1992/93
Winter nest survey:						
Absolute number (1000 ha)	149	1270	3687	282	105	145
Maximum number per grid (230×230 m)	6	52	91	14	11	13
Maximal nest aggregation	4	11	11	5	5	5
Proportion of isolated nest (%)	54.4	16.5	13.8	58.5	53.3	44.1
Number occupied by stoats	11	3	4	28	15	0

1990, 4 out of 5; in 1991, 17 out of 28; and in 1992, 11 out of 15 (we have no accurate data for the first year 1988).

Lemming nests covered the whole study area in all three years, even though at different densities. Still, nest occupation by stoats was very localised in 1989 and 1990, but nearly complete coverage of the study area was found during winter 1990/91 (Fig 3). This change in the stoats' distribution pattern was recorded also in adjacent areas with limited sampling and even on two offshore islands.

4.3.3. Other observations on predation

The only direct observation comes from 1990 when a stoat family (at least five individuals) in a boulder field on July 9 carried four snow bunting chicks and about 5 lemmings to a den or food cache. Indirect records of predation include either the examination of prey remains at the nest or the analysis of pellets, faeces or pluckings. In summer 1991 we discovered remains of a food cache hidden in an inaccessible cavity under boulders (no access for arctic fox), with fur remains of nearly 150 lemmings. Volume of the cache was 35×20×20 cm). This cache must have been established between August 1990 and prior the onset of the following winter as suggested by the dark summer coloration of fur remains. Other evidence for predation by stoat was mostly restricted to 1990 when an arctic tern colony was destroyed on a small island around July 20 close to our study area. Besides about 40 to 50 tern nests, other bird nests suffered from this predation: common eiders (3), oldsquaw (2) and Sabine's gulls. The winter pluckings of ptarmigan attributed to mammalian predation (35 for 1990/91 and 11 for 1991/92) may have resulted from stoat attacks in the subnivean environment.

5. Discussion

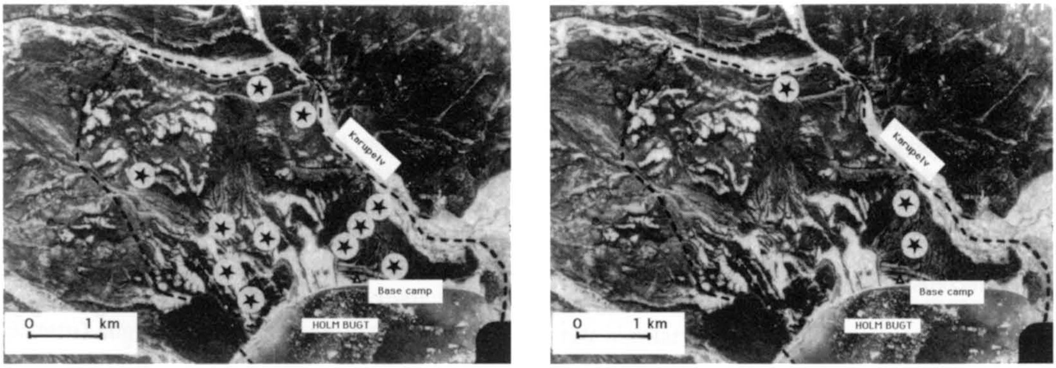
5.1. Lemming dynamics

The fluctuation pattern of collared lemmings in North-East Greenland, inferred from the number of winter nests, showed characteristics of a cyclic population: low in 1988, increase in 1989, peak in summer 1990, crash in late summer 1990, low in 1991, prolongation of the low phase over the winters 1991/92 and 1992/93 into summer 1993. The cycle length seems to be five years. Such cycle lengths of arvicoline rodents have also been reported from northernmost Fennoscandia (Hanski et al. 1991) and from some cycles at Point Barrow, Alaska (Batzli et al. 1980). However, also shorter cycle lengths are known from arctic areas, i.e. Taimyr (three or four years, Orlov 1985), while some areas show no cyclicity at all (Batzli & Henttonen 1990).

Compared with Point Barrow, where two lemming species cooccur, the Karupelv site supports clearly lower lemming numbers than the Arctic Coast of Alaska. The average number of nests/ha in Point Barrow during the peak was 41.7 against 3.7 during the peak in 1989/90 in Karupelv Valley. During the low phase, overall density of nests in our study area was around 0.1/ha. In Point Barrow, during winter 1969/70 no nests were found at all, which suggests a local extinction. These figures may, however, not be strictly comparable because sampling in Alaska was not comprehensive over a large area like in this study. In addition, in Karupelv Valley the landscape is patchy including a considerable coverage of bare land in contrast to Point Barrow where unvegetated stretches are rare. Distribution pat-

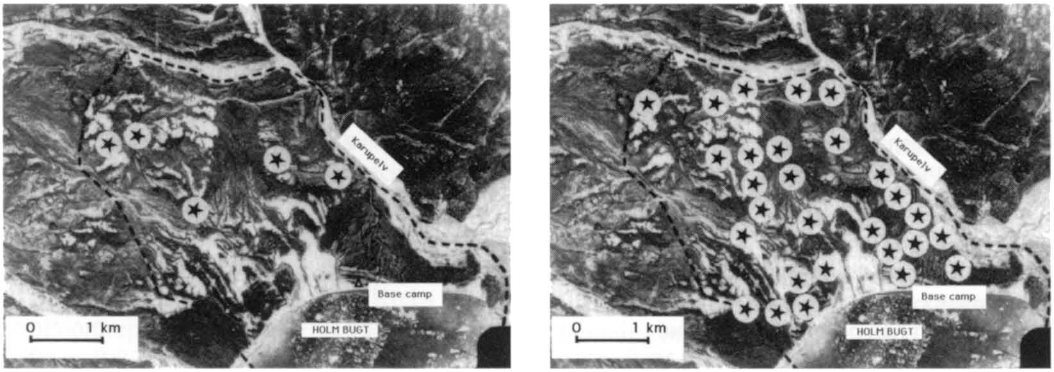
Table 2. Numbers of winter nests with or without pellets of pups or juveniles, suggesting winter breeding. Data are presented for isolated nests versus nest aggregations ($n \geq 2$). * Included here are also all cases where assessment of pellets was uncertain (e.g. pellets removed or swollen by melt water, not detectable due to obscuring vegetation, etc.). Nd = not determined for the whole data set.

	Isolated nests		Nest aggregations	
	with breeding indices	without breeding indices*	with breeding indices	without breeding indices*
1989	nd.	nd.	nd.	nd.
1990	420	90	1014	62
1991	46	120	30	21
1992	22	34	9	0
1993	35	29	31	2



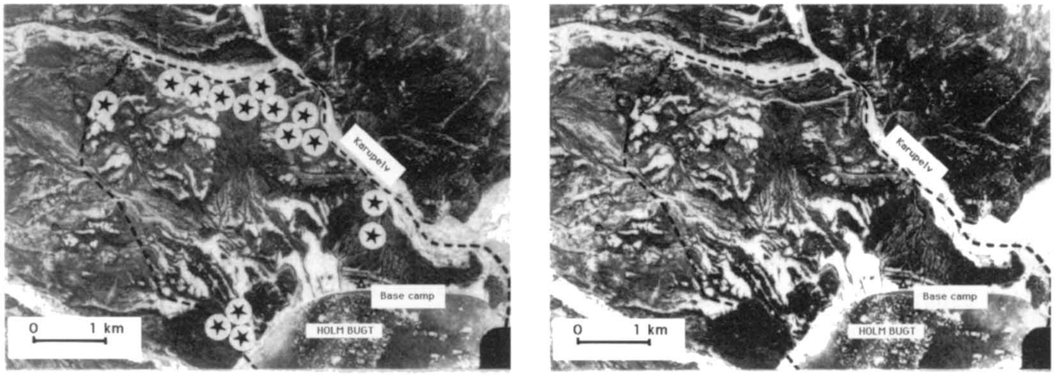
Winter 1987 - 88

Winter 1988 - 89



Winter 1989 - 90

Winter 1990 - 91



Winter 1991 - 92

Winter 1992 - 93

Fig. 3. Variation in abundance and distribution of winter nests occupied by stoats in 1988 - 93.

terns of nests in Karupelv Valley suggest, that during low density winters, large areas may be fully devoid of nests, but a few may be concentrated in some small patches.

Information on lemming winter nests confirms the importance of winter to the development of the population. The increase phase is largely due to the pronounced reproductive output in the subnivean habitat, confirming earlier observations by Dunaeva (1948), Fuller (1967), Chernjavskij & Kirjutschenko (1979), Batzli (1981), Jarrell (1987), and Henttonen & Kaikusalo

Table 3. Summary of population surveys on predators.

	1988	1989	1990	1991	1992	1993
Mammalian predators:						
ARCTIC FOX (*Alopex lagopus*)						
Breeding records in study area (1000 ha)						
Number of dens occupied	1	1	2	0	0	1
Number of juveniles (total)*	3	6	8	0	0	4
Number of the juveniles still alive end of July*	0	6	8	0	0	2
Breeding records in Karupelv Valley (5000 ha)						
Number of families (pairs with juveniles)	0	≥1	≥5	0	0	0
STOAT (*Mustela ermina*)						
Winter time records						
- Number of lemming nests used by stoats	11	3	4	28	15	0
- In 1990, an additional stoat nest was discovered in the wool of a muskox carcass			1			
Summer time records in study area						
- Direct observations of families with offsprings altogether (number of offspring) (*)	0	0	2(6)	0	0	0
- Additional observations of individuals	0	0	2	0	0	0
Avian predators:						
SNOWY OWL (*Nyctea scandiaca*)						
Breeding pairs in study area (1000 ha)	0	1	2	0	0	0
Breeding pairs in Karupelv Valley (5000 ha)	0	6	14	0	0	0
Mean clutch size (pairs recorded in study area)	0	5	7	0	0	0
Individuals observed in study area as vagrant visitor	0	–	–	0	1	0
LONG TAILED SKUA (*Stercorarius longicaudus*)						
Breeding pairs in study area (1000 ha)	0	8	13	0	0	0
Maximal flock size of vagrant non-breeding individuals	37	–	–	41	370	36
ARCTIC SKUA (*Stercorarius parasiticus*)						
Breeding pairs in study area	0	1	0	0	0	0
RAVEN (Corvus corax)						
Breeding pairs (Karupelv Valley)	0	1	1	0	0	1
Vagrant predators (P = present; A = absent)						
GREAT SKUA (*Stercorarius skua*)	A	P	A	A	A	A
PEREGRINE FALCON (*Falco peregrinus*)	A	P	P	A	A	A
GYRFALCON (*Falco rusticolus*)	A	A	A	P	P	P

*True litter size of and number of cubs lost due to postnatal mortality cannot be assessed accurately since not all cubs may stay outside the den simultaneously

(1993). Nest aggregations are a common feature during this phase. Lemming nest aggregations have never been investigated systematically, so that implications for social organisation and reproductive output remain obscure. Jarrell (1987), states that cold climate favours winter aggregation and inhibits the dispersal of winter-born offspring which consequently mature and mate with close relatives. Accordingly, dispersal and outbreeding occur during summer.

Nest aggregations, up to 11 nests clustered together (in winter 1988/89 and winter 1989/90), may reflect the production of two or more litters in winter. Careful examination of nest aggregations (location in snow pack, latrine sites of juveniles and adults, as well as their spacing pattern) suggests that they are the result of extended family formation. The initial core nest is established in fall when the snow pack is forming, and offspring establish new family groups in close vicinity. Gilg (pers. comm.) has reported similar nest aggregations (up to 10 nests within a few meters) in a survey made during a peak in lemming population on Bylot Island in the Canadian Arctic in 1993. According to Kirjutschenko (1980), Dicrostonyx may produce up to 5 or 6 litters during the snowy period in the increase phase. This is more than twice the figures reported elsewhere (Pedersen 1942, Krebs 1964).

Poor reproduction was ascertained for the winters 1987/88, 1990/91 and 1991/92, as only a limited number of nests with pellets from young lemmings were found. The subsequent summer seasons showed the lemming low. However, the winter 1992/93, while still featuring a low phase, was in clear contrast to 1990/91 and 1991/92; there was noticeable reproductive activity. Although there were relatively few nests and nest aggregations in winter 1992/93, most of them showed reproductive activity. The lemming population must have been at it deepest low at the onset of winter 1992/93 (as confirmed by observations on the whole predator community). In spite of the winter breeding, the population density was probably too low for a pronounced increase prior snow melt in summer 1993.

5.2. Responses of stoats

The interactions between stoats and lemmings are illustrated in Fig. 4. The number of nests occupied by stoats indicates relative numbers of these predators. The stoat density for the winter 1987/88 may be biased because of uncertainties in ageing the occupied nests during the first field season. Only three nests out of 1270 were occupied by stoats in winter 1988/89. This and the spacing of occupied nests suggest that probably no more than two stoats were present in the study area. Low stoat number was also suggested by the absence of any direct stoat observations in summer 1989, and that in the subsequent winter no more than 5 occupied nests were found.

Low density of stoats continued during winter 1989/90, while lemmings were increasing at a rate similar to the preceding winter, as suggested by nest aggregation pattern. Female stoats that mated in spring 1989, and were pregnant during the best food conditions until spring 1990, have probably given birth to maximal litters. According to Pedersen (1942), and as suggested by the appearance of weaned juveniles from mid-July on, births take place probably around early April. The litters produced (most likely 2 within the study area) have probably been large, around 8 to 10, as observed earlier in North-East Greenland by Pedersen (1942); he also stated that stoat breeding took place in the second summer of the lemming increase phase.

The dispersal of young stoats in the second half of July and onwards is linked with a distinct spatial change in stoat — lemming interactions. Until weaning of the juvenile stoats, predation pressure on lemming population must have been local as revealed by the distribution of occupied nests. Erlinge (1977) reported that the diameter of the area temporaily exploited by female stoats during the spring may be less then 100 m. When young stoats in Karupelv Valley reached independence they took over new territories which probably greatly expanded the range used by stoats. As a result, the study area that initially supported probably no more than 2 breeding females (and males?), had possibly to be shared by around 20 animals a few weeks later. The occupation of the whole study area by stoats started about 18 months after the initial increase of the lemmings in the late fall 1988, and persisted through the winter.

The dispersal period from August 1990 onwards coincided with the onset of the decline in lemmings. The subsequent winter was then featured by a maximum number of nests occupied by stoats. Stoats occupied the whole range, not only the study area of 1 000 ha, but also the

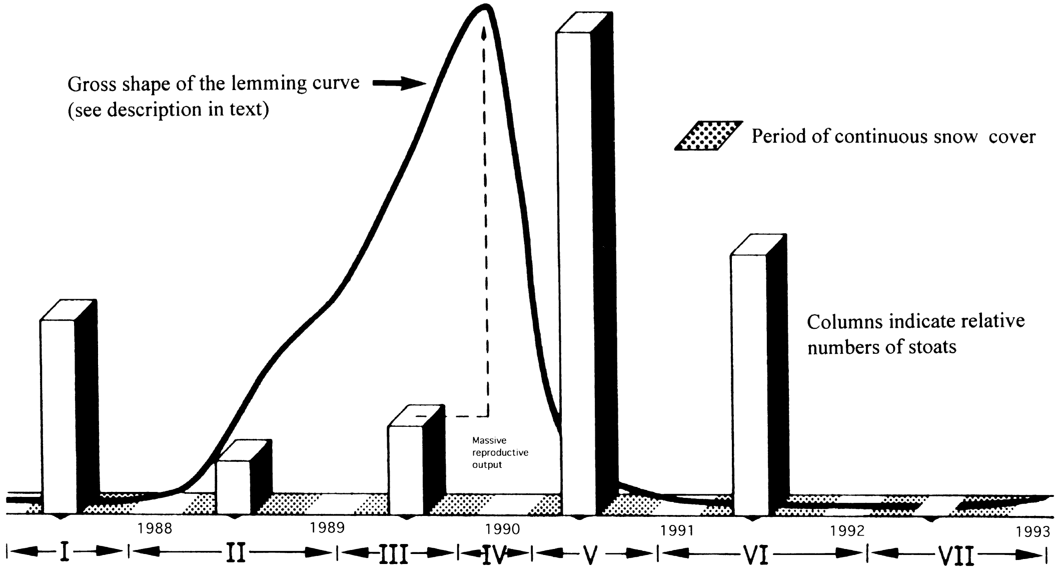


Fig. 4. Sketch to illustrate stoat-lemming interactions, as inferred from lemming winter nest surveys. Description of patterns in chronological order (see also text). **I. Winter** 1987/88. Probable deterioration of survival rates through the winter due to lowered prey availability. **II. Fall 1988 - Summer 1989.** The substantial population growth among lemmings profits only a very reduced number of stoats. But by getting in a good nutritional state, the few female stoats may have all a maximal number of ova shed during summer. **III. Fall 1989- Spring 1990.** As a result of delayed implantation and persistence of good feeding conditions over winter 1989/90, probably all embryos reached full term in spring 1990, inducing a tremendous reproductive output in stoats. **IV. Summer** 1990. Summer dispersal of juvenile stoats with comprehensive occupation of range coincides with crash in lemming population. **V. Fall 1990- Sring 1991.** Despite lowered numbers in lemming, prey caches from summer (surplus killing) and switching to ptarmigan as alternative prey helps maintaining a high number of stoats in winter. **VI. Summer 1991 - Summer 1992.** Deterioration of prey availability causes decline in overwintering stoats. Winter activity ranges limited in space, with many areas devoid of stoats. **VII. Fall 1992 - Summer 1993.** Probably all stoats must have disappeared by late autumn 1992 as not even a single nest occupied by stoats was recorded for winter 1992/93 . Fresh tracks of an individual recorded end of July 1993 on the shore suggest immigration from an adjacent area.

whole valley. The predation pressure exerted by the stoats (along with other predators?) was illustrated by the crash of the ptarmigans after good breeding in summer 1990. It is also reasonable to assume that this predation pressure contributed to the continuation of the lemming low. As a result of the prey availability in spring 1990, females (adults as well as juveniles) had probably mated. However, young born in spring 1991, just at a time when resources were already drastically depleted, seem to have had a very low survival in summer 1991. Alternatively, embryos had been resorbed well before spring 1991. A further decline of lemmings with a concomitant decrease in stoats took place through 1992. This is in agreement with other observations of extended low densities in microtines cycles (Hansson 1984, Henttonen et al. 1987). It has then lead to a local extinction of stoats at the onset of winter 1992/93, when lemmings were about to recover from the low. However, we acknowledge that even if the patterns in lemmings and stoats coincide nicely, it still remains to be demonstrated that stoats actually trigger the decline.

The time lag of 18 months in stoats' response seems to be characteristic for North East Greenland. Pedersen (1942) has reported that the response of mammalian predators (stoat and arctic fox), in contrast to the avian predators, was recorded only in the second year of the increase in lemming population. Manniche (1910) and Johnsen (1953) also noticed that stoats were most often observed in the second half of the lemming peak summer.

It is interesting to compare the pattern in Karupelv Valley to the "semi generalist" strategy adopted by stoats in more diverse communities where they can shift to alternative preys during the rodent lows. This possibility does not exist in the simple community in Greenland, where the only alternative prey, the ptarmigan, crashes in phase with the lemming, and apparently recovers with it after the low. In western Finland Korpimäki et al. (1991) found a significant lag in the response of least weasels to voles, but not by stoats. A further comparison is provided by King (1983) in New Zealand, where mice (Mus musculus) are the main prey item of stoats. The fluctuations of mice are food dependent (beech seedfall) and stoats respond with almost no lag. This difference is probably the result of the more diverse availability of alternative prey in western Finland and in New Zealand.

A curtailment in reproduction in Dicrostonyx during the summer crash has been reported also by Dunaeva (1948), Krebs (1964), and Fuller et al. (1977), as well as in other microtines by e.g. Kalela (1957) and Koshkina (1966), but see (Henttonen et al. 1987) for contrasting results. Impaired breeding has been attributed to various factors, including density-dependent social effects. However, if predation actually triggered the decline in Karupelv Valley, then it might also stop the reproduction of the prey. Cushing (1984, 1985) could demonstrate that least weasels can differentiate between oestrous and dioestrous odours of their prey, and that they selected the oestrous scent. In this regard it is interesting that Fuller et al. (1977) on Devon Island observed that female collared lemmings caught in August remained anoestrous. Furthermore, a reduced reproductive investment or breeding suppression in rodents exposed to mustelid predation has been suggested recently (for a review, see Ylönen 1994). In Karupelv Valley nest aggregations, as a result of winter reproduction, are common when stoat predation is low and limited in space. In contrast, the presence of stoats in high numbers seems to inhibit the formation of nest aggregations. Furthermore, a great proportion of nests predated by stoats showed signs of winter breeding of lemmings, an observation also made by McLean et al.(1974). If stoats actually selected reproductive females, that could explain a curtailment in reproduction.

The actual predation impact on dynamics of prey may further be reinforced by the habit of mustelids for surplus killing (Oksanen et al. 1985, own observations). Killing prey in great numbers for possible later consumption could have a great impact on population dynamics of prey.

From August 1990 on, lemmings were not only exposed to the increased predation pressure by stoats but also to the other predators, i.e. arctic fox and snowy owl that also increased noticeably during the summer 1990. Their young become independent in mid-August, one month later than stoats. Foxes and snowy owls remain in the area at least until the permanent snow cover at the end of September, and an increase in space use similar to that reported for stoats occurred. For example, we observed that a minimum number of 40 (possibly more than 50) arctic fox whelps from 5 known dens were present in the valley (about 5 000 ha) in August.

The time lag shown by stoats differed clearly from that shown by the avian predators (snowy owl and long-tailed jaeger), which responded immediatey to the increase in lemmings. The situation for foxes was somewhat intermediate, with a noticeable increase also during the peak year.

5.3. Vegetation analyses

Preliminary analyses, not presented here in detail, have shown that the site selection for winter nests depends primarily on topography, with a marked preference for the locations where snow will accumulate. Vegetation in these locations shows a great variability, both regarding cover as well as composition. In addition, large areas remain unused by lemmings in winter, as also noticed by Chernjavskij et al. (1981). According to them, only 28–55% of the suitable terrain is used in winter. A detailed analysis taking into account all aspects recorded simultaneously (geomorphology, exposition, vegetation cover and composition, spacing, clipping indices etc.) is in progress.

5.4. Future approaches

Our unpublised data show that in 1994 a strong lemming increase took place in Karupelv Valley while stoats were still at a very low level. Important future aspects be to documented are whether the time lag of 18 months in stoats' numerical response will occur again, and whether the timing of the crash will concide with the spatial increase in the stoats' predation pressure.

In addition, the actual predation impact needs more accurate documentation. Are the patterns observed for the winter nest aggregations due to differential stoat predation, which was also suggested by Madison et al. (1984)? Food caches and their composition should be monitored, especially during the critical crash period. The active lemming burrows should also be monitored because those visited by stoats are easy to detect in the High Arctic due to digging signs at the entrance of the burrow. The use of telemetry to determine activity and home ranges of lemmings as well as stoats would be highly informative. Exclosure experiments would help to assess whether the curtailment in reproduction also occurs in the absence of stoat predation.

When comparing the present study with other surveys, one should bear in mind that besides the simplicity of the community, an additional relevant difference is the unusually high snow depth in Karupelv Valley. This prevents or at least limits the predation by fox and snowy owl for more than 2/3 of the year. During the snowy time, this community is composed of lemming, ptarmigan and stoat. This could account for the clearcut patterns seldom found elsewhere.

It would also be interesting to survey similar communities in other regions using the same methods, i.e. lemmings not exposed to stoat or weasel predation like St Lawrence Island in Alaska or Wrangel Island in North East Siberia, where fluctuation patterns differ from those in Greenland (Chernjavskij 1979, Denisenko 1986, Litvin & Ovsjanikov 1990, Ovsjanikov et al. 1991).

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