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DOI: 10.1111/j.1600-0587.1992.tb00029.x

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Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos

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

Densities of microtine rodents in two habitat complexes in the tundra of Finnmarksvidda, Norwegian Lapland, were studied during 1977–89 by means of snap trapping (Small Quadrat Method). Predator populations were studied by mapping breeding raptors and by snow-tracking small mustelids. During 1977–85, snow-tracking was conducted only during peak and decline years, whereas during 1986–89, snow-tracking was conducted every winter (November–December) and live-trapping (in August) was used as an additional method.

Lowland vole populations had regular density fluctuations with peaks in 1978–79, 1982–84 and 1987–88. Highland vole populations fluctuated less regularly and at lower over-all densities. Highland lemming populations had two outbreaks, in 1978 and 1988, ending in abrupt winter crashes. In the lowland, outbreak levels were reached only in 1978. All microtine declines in relatively productive lowland habitats were accompanied by intense activity of small mustelids, whereas avian predators were common only in 1983. Lowland declines also showed clear between-habitat asynchrony: they started in areas with an exceptional abundance of productive habitats and then spread to more barren areas. These lowland data are consistent with the hypothesis of a mustelid-microtine limit cycle, although also several other hypotheses remain unrefuted. The highland lemming data suggest a simple exploiter-victim interaction between lemmings and the vegetation.

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Introduction

There is still no general agreement concerning the causes of sustained, multiannual population fluctuations in herbivorous small mammals. However, we are beginning to understand their geographical distribution. They occur at high latitudes (or altitudes) in areas with long, snowy winters (Keith 1974, Fitzgerald 1977, Batzli et al. 1980, Hansson and Henttonen 1985, Hansson 1987, 1988). Analysis of long-term data sets (L. Oksanen 1990) suggests that the fluctuations can be subdivided into two categories, each associated with a different geography. Boreal taiga and subarctic brushwood areas are characterized by genuine, periodic cycles of voles

(or hares), while typical tundra areas show extremely violent but chaotic (aperiodic) lemming fluctuations.

The pattern of population fluctuations has implications to the underlying causal mechanism. Chaotic fluctuations can be generated by strict resource-limitation in a seasonal environment (L. Oksanen 1990, see also May and Oster 1976). Cyclic fluctuations, in turn, can be created by cyclicity in external factors (Tast and Kalela 1971) or by density dependent regulation with substantial time-delay (May 1981). Such mechanisms include induced chemical defenses of food plants (Haukioja and Hakala 1975, Rhoades 1985), predation by specialists (L. Oksanen 1990, Hanski et al. 1991), a combination of predation and moderate food shortage

Accepted 12 March 1991

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(Hansson 1969, 1979, 1987, Keith 1974) and diseases, alone (Anderson 1981) or linked with malnutrition (Hansson 1988, 1989). Social regulation has also been claimed to work this way (Chitty 1960, Krebs and Myers 1974), although it seems to be difficult to generate sufficient time delays in social interactions without resorting to biologically unreasonable assumptions (Stenseth 1981a, 1986).

Further clues to the causes of cyclic fluctuations can be seen in the degree of between-habitat synchrony. External sources of cyclicity predict synchrony between habitats. Similar synchrony should also be observed if the decline were initiated by forage depletion and severe malnutrition, because starving animals must be expected to disperse widely in a desperate search for remaining habitats still supplying forage. Predation, in turn, should generate substantial asynchrony in areas with large differences in habitat quality. Basic theory of habitat choice (Fretwell 1972) predicts that predators should always fill the best habitat first and become interested in low-quality habitats only after prey densities in the best habitats have been substantially depressed. Other hypotheses (induced defense, diseases, purely intrinsic mechanisms) are compatible with various degrees of between-habitat synchrony.

In the present paper, we report a relatively long record (1977 to 1989) of population changes in microtine rodents in an area at the transition between typical vole and lemming habitats. We also report some data on predator numbers, especially for the last four years of the study. The trapping program is connected to a set of studies that aim to test the hypothesis of exploitation ecosystems (Fretwell 1977, Oksanen et al. 1981, L. Oksanen 1990, T. Oksanen 1990), predicting that herbivore populations of barren areas are strictly resource-limited, whereas those of more productive areas are controlled by predation. In the present context, however, we focus on reporting the general pattern of population fluctuations and will consider other hypotheses, too.

Area and methods of study

The study was carried out in the Iešjávri basin, Norwegian Lapland (69°45'N, 24°E, 380–630 m a.s.l.) during 1977–1989. The basin belongs to the Baltic Shield and is limited to the north by the thrust cliff of the Scandes. The largest part of the basin can be regarded as hemiarctic or low arctic tundra (chiefly open terrain but with willow thickets and, in the lowermost parts, even patches of birch woodland in favorable sites, see Ahti et al. 1968). This part will be referred to as the lowland. Areas above 530 m a.s.l. were devoid of trees and willow thickets. All even moderately abundant plant communities were dominated by mosses, lichens, trail-

ing dwarf shrubs or graminoids. This zone will be referred to as the highland complex.

We initially tried to study small mammal dynamics by means of randomly sampled Small Quadrates (see Myllymaki et al. 1971). However, we soon realized that, with the trapping effort realistic for us, such sampling would not yield any voles during years of population lows. We thus resorted to stratified sampling. The lowland was divided into following nine habitat types whose abundances (percentages out of the whole complex) were estimated by a line transect of 32.6 km: wind-barrens (19.8%), lichen-blueberry heaths (42.1%), mossy blueberry heaths (7.6%), dry meadows (2.6%), moist meadows (0.9%), alluvial thickets (0.2%), willow mires (1.0%), cloudberry bogs (1.1%) and open bogs (24.9%). (The word "meadow" is used in the broad botanical sense, including all herb-rich habitats, actually, the "meadows" were chiefly herb-rich willow or dwarf birch thickets, see Kalliola 1939). The highland was divided into following three habitat types whose abundances were estimated by a line transect of 16.4 km: heaths and heath snowbeds (71.3%), meadow snowbeds (2.1%) and bogs (26.6%). Each habitat was initially represented by 5 Small Quadrats, each with 12 traps arranged in groups of three at intervals of 15 m, kept open for two days and checked daily. After 1982, the prevailing lichen heath habitat of the lowland was represented by 7 SQs and after 1985, the highland heath complex was represented by 6 quadrates. Trapping was performed twice a year (immediately after the snowmelt and after the tundra had turned red). There was no autumn trapping in 1980–82 or in 1985.

Although the exact location of SQs has changed during the course of the work, all fieldwork has been carried out within a radius of 15 km from Lake Iešjávri. During 1977–82 the SQs were subjectively distributed along convenient trapping routes in an area east of Iešjávri (map, Oksanen and Oksanen 1981, Fig. 1). During 1983–85, lowland trapping was performed south of the lake (map, Oksanen et al. 1991, Fig. 6) and the area was divided into two subareas: "riverside" (distance to the main river < 1 km, birch woodlots and willow thickets abundant) and "upland" (treeless tundra). In 1986, the study area was moved to the north-western part of the basin. A north-south coordinate line, running from the lowermost part of the lowland across the thrust cliff to a highland plateau, was chosen as a baseline and SQs were situated at least 50 m from each other and as close to the baseline as possible (map, Oksanen 1991, Fig. 2a). The area transected by the line was divided into five sections (one for highland, four for lowland, with vastly different habitat distributions: the "slope" immediately below the thrust cliff having the highest abundance of productive habitats, the "marsh" (at the base of the slope), "valley" (1–2 km south of the cliff) and "divide" (> 2 km south of the cliff) with successively heavier predominance of barren heaths and bogs).

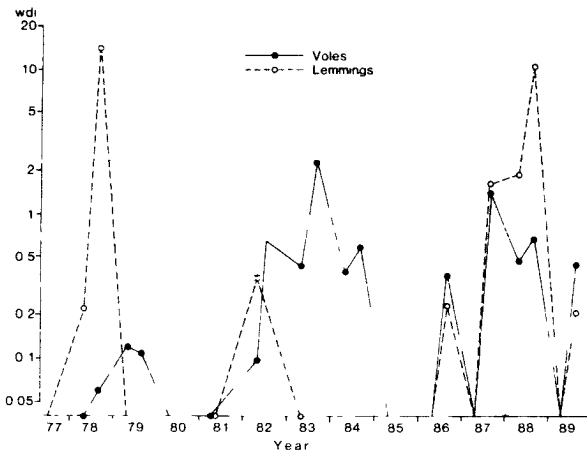


Fig. 1 Weighted density indices (wdi) for voles and lemmings in the highland complex. Sample sizes: 15–16 Small Quadrates (360–384 trap nights). Symbols along the x-axis refer to cases when microtines were captured, but wdi was below 0.05. The star refers to a data point which was largely determined by a single specimen, captured in the abundant heathland habitat. The twist in the curve without a dot refers to an estimated autumn density, for which trapping data were not available, but foraging signs indicated comparatively high winter densities (computed by assuming 33% reduction of the density index over the winter).

The bias due to over-representation of the rare, favorable small mammal habitats was removed by using weighted density indices ($w_{di} = \sum d_i p_i$, where d_i = captures per 100 trap nights in habitat i and p_i = the fraction of the complex consisting of habitat i). Due to the low p_i -values of favorable habitats, this method leads to relatively low index values. Notice also that the wdi's are only loosely related to absolute numbers of captured voles (e.g. $w_{di} = 0.25$ for the lowland can stand for 150 voles captured from alluvial thickets or for a single vole captured from lichen heaths). Consequently, the reliability of low wdi-values is strongly dependent on between-habitat distribution of voles (good if voles are concentrated to the best habitats, poor if they are also trapped in the abundant barren habitats). In order to facilitate the identification of dubious data points, we have commented all cases where wdi's are based on fewer than 20 captured specimens and used specific symbols for wdi's which are heavily influenced by a single capture.

In addition to wdi's for the entire lowland and highland complexes, we also provide separate records for the three barren lowland habitats (windbarrens, lichen heaths, open bogs) for the four moderately productive ones (mossy blueberry heaths, dry meadows, willow mires and cloudberry bogs) and for the two luxuriant ones (moist meadows, alluvial thickets). For periods 1983–85 and 1986–89, we also present data for different subareas; here, we use unweighted density estimates (udi). In the statistical treatments of the material, sam-

ple sizes refer to numbers of SQ's (the smallest statistically independent sampling units). Sample sizes for the highland complex were thus 15–16 SQ's and for the whole lowland complex, 45–47 SQ's (15–17 SQ's for barren habitats, 20 SQ's for the moderately productive habitats and 10 SQ's for the luxuriant ones). In comparisons between subareas in 1983–84, sample sizes were 10 and 20 SQ's for "riverside" and "upland" subareas, respectively (only productive habitats were included). Comparisons between different subareas during 1986–89 were based on 5 SQ's per subarea (the ones which were closest to the midpoint of the subarea, see Oksanen et al. 1991).

All vole species have been pooled in computations. Except for alluvial thickets, frequently dominated by root voles *Microtus oeconomus*, the pooled vole indices are practically identical to density indices of grey-sided voles *Clethrionomys rufocanus* (see Oksanen and Oksanen 1981).

Until 1986, studies of predators were sporadic. In late autums 1978 and 1979, we followed and mapped all fresh mustelid tracks within an area of 1.75 km² in the center of the index-trapping area during five consecutive days with good tracking conditions (fresh snow and calm weather, allowing fresh tracks to be distinguished from old ones and recorded in all habitats, see Oksanen et al. 1991). Tracks were assumed to belong to the same individual if no consistent difference in leap lengths or pit widths was observed and if the spatial distribution of tracks was consistent with the assumption of a single individual. During the winters 1983–84 and 1984–85, the same method was applied to an area covering 9 km² and encompassing all trapping quadrats (see Oksanen et al. 1991, Fig. 6). Breeding raptors, owls and jaegers were recorded within the areas covered by the traplines (30 km² in 1978–79, 9 km² in 1983–84).

Since autumn 1986, snow-tracking has been conducted on a regular basis in November–December (also in March 1989) within an area of 16 km² on both sides of the index trapping line for small mammals (4 km² highland, 3 km² slope and marsh, 5 km² valley and 4 km² divide) during at least 3 d with acceptable tracking conditions. Within the slope and marsh subareas, live-trapping of small mustelids was conducted during periods of 10 d in August in 1986–1989 with 60 traps (30 stoat traps type Erlinge and 30 microtine/weasel traps type Fix), baited with laboratory mice, covering an area of 2.5 km². From 1988 onwards, mustelids have also been captured on a microtine live-trapping grid of 4 hectares, located within the slope subarea. Captures of small mustelids obtained during the August live trapping period from this grid are included in our data; all our captures of weasels (*Mustela nivalis*) were thus obtained. Nests of breeding raptors were mapped during 1986–89 within the tracking area, in 1988 and 1989 also in its surroundings (total size of the mapping area: 70 km²).

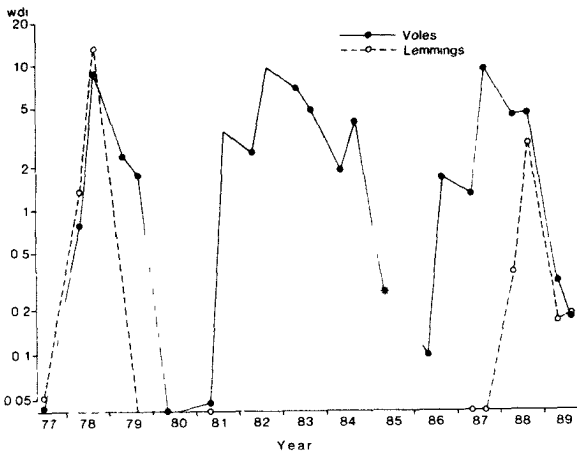


Fig 2 Weighted density indices (wdi) for voles and lemmings in the lowland. Sample sizes 45–47 Small Quadrats (1080–1152 trap nights). Symbols as in Fig 1

Results

General population trends in microtine rodents

Lemmings had two outbreaks in highland habitats, in 1978 and 1988. Both outbreaks were characterized by J-shaped growth curves, ending in abrupt crashes (Fig. 1). No lemmings were trapped immediately after the crash, but dozens of apparently intact dead bodies were found in places where lemmings were trapped in the previous fall, and the habitat was largely destroyed (Oksanen and Oksanen 1981, Moen et al. unpubl. data). The first indications of a developing lemming peak were obtained in 1977, when 11 specimens were captured in the uppermost willow thickets of the study area, at the transition between the lowland and the highland complexes (6 from regular grids, 5 from an additional trapline). In 1978, lemmings reached outbreak levels in the whole study area (Figs 1 and 2). The lemming crash ensued in 1978–79, when vole indices remained high in the lowland and low but unchanged in the highland. The next lemming outbreak in 1988 coincided with a vole decline and was largely restricted to the highland. Lemmings were present in the majority of lowland habitats, but in low numbers only. The 1988–89 decline in lowland populations of lemmings was neither dramatic (absolute numbers of captured specimens: 18 in autumn 1988, 1 in spring 1989, 2 in autumn 1989) nor accompanied by visible habitat devastation.

During the period 1979–85, only five lemmings were trapped. Two ones were caught in 1981 in the lowland and close to the lowland-highland interface. Three were captured in 1982–83 in the uppermost part of the highland (above 600 m a.s.l.), where also the first lemmings of the next outbreak were caught (two specimens in

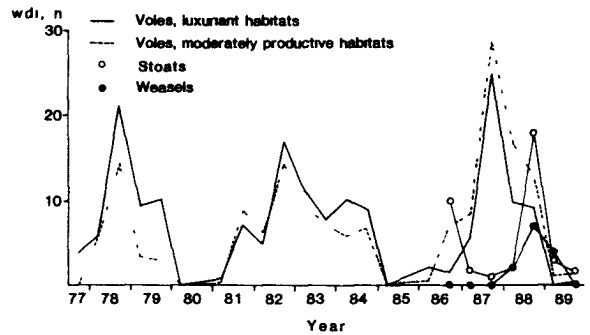


Fig 3 Weighted density indices (wdi) for voles in moderately productive lowland habitats (sample sizes 20 SQ s or 480 trap nights) and in luxuriant ones (sample sizes 10 SQ s or 240 trap nights), results of mustelid censuses (n, minimum numbers alive)

autumn 1986). Additional information of lemmings during population lows was obtained by interviewing reindeer herdsman during their spring and autumn migrations. Both in 1979 and in 1989, sightings were only reported from lowland areas.

Vole populations in the lowland fluctuated in a seemingly regular cycle with a periodicity of 4–5 yr (Fig. 2). The largest aberration in lowland wdi's was a summer decline in 1983 in the middle of an extended peak phase. (Due to the difference in reproductive status between spring and autumn, this decline in index values need not indicate an actual numerical decrease, more likely, it indicates an abnormally weak summer increase.) The 1982–84 peak was extended over a large part of northern Fennoscandia (Henttonen et al. 1987), but summer declines in density indices were not reported from other areas. The depths of population crashes also seemed variable. However, due to the low numbers of individuals captured during rock-bottom springs (1 to 12) and the relatively even between-habitat

Table 1 Numbers of captured voles in barren lowland habitats (windblown ridges, blueberry-lichen heaths and open bogs). Sample sizes 15 SQ s (360 trap nights) in 1977–82, 17 SQ s (408 trap nights) in 1983–89. – = no trapping

	spring	autumn
1977	–	0
1978	0	14
1979	6	5
1980	0	–
1981	0	–
1982	5	–
1983	17	12
1984	3	13
1985	1	–
1986	0	3
1987	1	20
1988	10	13
1989	1	2

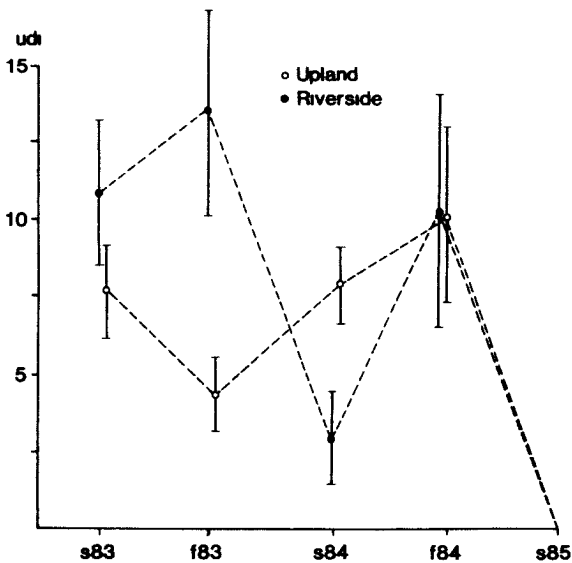


Fig. 4 Unweighted mean density indices (udi) during 1983–85 for upland and riverside quadrates representing luxuriant and moderately productive habitats collectively. Bars refer to standard errors. Sample sizes: upland 20 SQ s, riverside 10 SQ s.

distribution of voles during declines (Oksanen and Oksanen 1981, Ekerholm and Oksanen unpubl. data), the wd:s for collapsing populations have wide margins of error.

Population trends in the productive habitats (Fig. 3) by and large matched the over-all picture. The main distinctive feature was an abortive rise in 1985–86 and stagnation in 1986 within the luxuriant habitats. Actually, it was a question of two different phenomena: a stagnation at a low level within tall herb habitats (only one vole captured in spring and in autumn 1986) and a summer crash in alluvial thickets (9 root voles caught in the spring, none in the autumn). Although the numbers involved were low, this development was in such striking contrast with the strong rise in moderately productive habitats (Fig. 3) that it calls for an explanation.

In barren habitats, vole densities were always low (Table 1). The fact that some voles were captured from barren habitats during two of the three crash years suggests that the amplitude in barren habitats was essentially lower than in productive ones. The data are consistent with the idea that population fluctuations in barren habitats were basically seasonal, but the winter declines were occasionally swamped by dispersal of reproducing voles from densely populated productive habitats (see Ims 1987, 1990).

There were very few voles in the highland complex. Even during the “peaks” (1978–1979, 1983, 1987), the numbers of captured specimens per trapping occasion were low (7 to 11). The large difference in wd:s between the 1978–1979 “peak” and the two subsequent

ones was due to differences in the habitat distribution (only meadows yielded voles in 1978–1979).

Spatial differences in population trends

In broad outline, the vole fluctuations in the study area were synchronous with those of Finnish Lapland (Henttonen and Jarvinen 1981, Henttonen et al 1987, Jarvinen 1987, Haukisalml et al 1989), and fairly synchronous even with those of central Scandinavia (Hornfeldt 1991). However, strict local synchrony was limited to the final stages of the crashes, whereas the initial stages of declines showed pronounced local variations. In 1979, there was a summer crash in the largest patch of luxuriant herb habitats (mean density index in autumn 1979 2.5, sample size 5 SQ s), while in smaller and more isolated patches of the same habitats within the

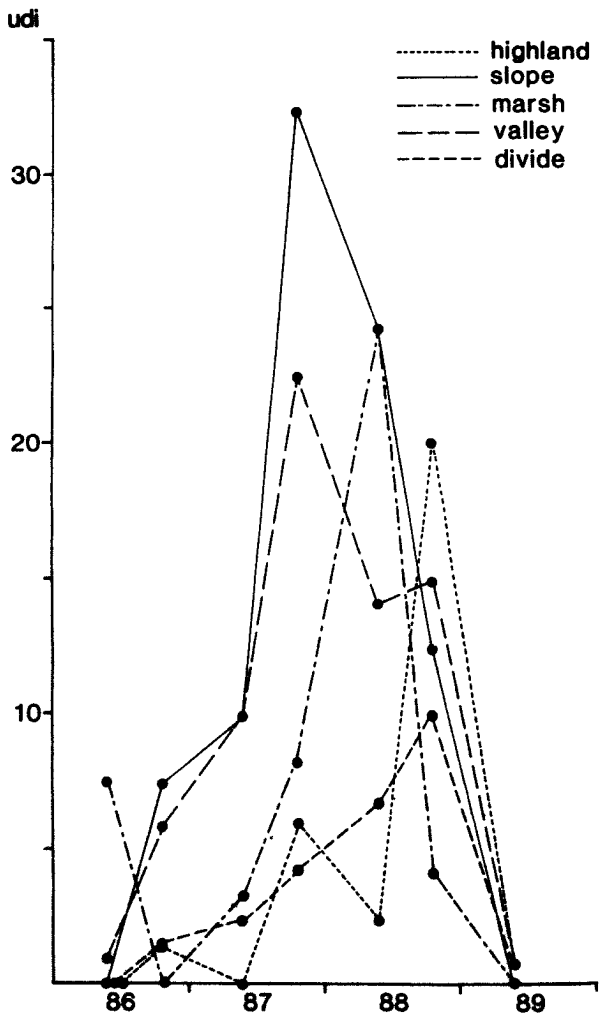


Fig. 5 Unweighted mean density indices (udi) for the four subareas of the lowland and for the highland during 1986–89. Sample sizes: 5 SQ s for all subareas.

same drainage system, populations reached peak densities (mean density index in autumn 1979 16.7, sample size 3 SQ s. see Oksanen and Oksanen 1981)

Even more pronounced asynchrony was observed during 1983–84 between the “riverside” and “upland” subareas (Fig. 4) In the “upland” subarea, density indices for productive habitats indicated fairly stable numbers during 1983–84, followed by a winter crash in 1984–85 Conversely, populations in the riverside grids peaked in autumn 1983 and were already declining in winter 1983–84 The riverside populations recovered during summer 1984 and in autumn 1984, the difference between the two subareas disappeared (however, there was much spatial density variation within each subarea, as indicated by the large standard errors in Fig. 4) The differences between subareas in seasonal variation during 1983–84 were statistically significant (For summer 1983, $t = 7.5$, $p < 0.001$, for winter 1983–84, $t = 11.7$, $p < 0.001$, $df = 28$, see Area and methods of study) Because barren habitats were excluded from the comparison, we can be fairly certain that the differences were on the scale of whole subareas, not on the scale of individual habitat patches

An even more intriguing pattern emerged in the population trends within the different sections of the trapline in 1986–89 (Fig. 5) The abortive rise of root voles in wet willow thickets of the marsh in 1985–86 was followed by a synchronous rise in 1987 In 1987–88, the synchrony was broken again In the luxuriant slope area, a persistent decline was then initiated In the marsh, the rise continued until spring 1988 By and large, this was the case in the valley, too, although the prevalence of grey-sided voles (without winter reproduction) somewhat influenced the timing of the peak there In the highland and in the divide, densities increased until autumn 1988 and then collapsed in 1988–89

The slope thus seemed to determine the fluctuations in the entire area Increases in vole densities within other subareas were aborted if they took place before the rise in the slope When the slope populations started to decline, populations in other subareas could keep on rising, but only as long as they had not reached the densities of the declining slope populations As numerical vole differences between habitats and subareas disappeared, the decline spread from the slope towards the periphery (Fig. 5, see also Oksanen et al 1991)

Changes in numbers of predaceous birds

Few avian predators attended the 1978 microtine peak within the study area No breeding pairs were located there, although a pair of rough-legged buzzards *Buteo lagopus*, breeding 1 km south of the area, occasionally utilized it. Raptors and owls were much more abundant

in areas 10–40 km south of the study area In autumn 1978, a pair of short-eared owls *Asio flammeus* was residing in the vicinity of the base camp

In 1983, five breeding pairs of long-tailed jaegers *Stercorarius longicaudus* and one breeding pair of short-eared owls were located within the 9 km² study area The density of breeding birds of prey was therefore at least 0.75 pairs km⁻² (Excluding windbarrens, where practically no voles were ever caught, the jaeger density actually exceeded 1 pair km⁻²) Jaegers were active all over the open tundra, where every substantial patch of productive habitat had a jaeger or owl nest near-by, whereas wooded areas along the river were not exploited by jaegers However, a hawk owl *Surnia ulula*, was recurrently observed in the woodlands

These high densities of predatory birds have so far not recurred No breeding avian predators were found in 1984 During the early decline in summer 1988, the new study area of 16 km² harbored only three breeding pairs of long-tailed jaegers (0.2 pairs km⁻²) This relatively low density was typical of the tundra as a whole Bondestad (unpubl. data) found only 16 breeding jaeger pairs within 70 km² of the tundra (0.2 pairs km⁻²) Also owls remained rare during the latest peak Hawk owls were observed in 1986 and 1988, and short-eared owls in 1988 However, no breeding pairs could be located, either by us or by L. Bondestad During 1987 and 1988, three pairs of rough-legged buzzards and one pair of merlins *Falco columbarius* bred in the 16 km² area, and they tried to breed there even in 1989 (Ekerholm pers. comm.) The high raptor density was local elsewhere in the 70 km² study area there were only two additional breeding pairs of buzzards in 1988 (Bondestad pers. comm.)

Numerical changes in small mustelids

Data on small mustelids during 1978–85 have been published elsewhere (Oksanen and Oksanen 1981, Oksanen et al. 1991) To summarize evidence of small mustelid activity was first obtained in autumn 1979, when the largest meadow-thicket area, where the vole populations had strongly declined (see above), was crisscrossed by tracks of a stoat *Mustela erminea*. Tracking in the 9 km² study area in the autumn 1983 revealed stoat and weasel *M. nivalis* activity in the birch forest along the river (at least one individual of each species) but not in the upland tundra During the next winter, two stoats had established winter territories in the river valley, while weasels moved on the tundra, utilizing the smaller meadows, thickets and bog margins Due to their extensive movements and lack of any indications of territoriality, numbers of weasels were impossible to estimate (see Oksanen et al. 1991, Fig. 6)

The numerical results of the mustelid studies during 1986–89 are summarized in Fig. 3 These numbers must be treated with large reservations The trapping area

(2.5 km²) was much smaller than the tracking area (16 km²). However, all small mustelids tracked during November–December entered the trapping area and would thus have been subjected to trapping if it had been simultaneously conducted. A more serious problem is provided by the fact that recapture rates were practically zero during summers of high microtine numbers, indicating that predators paid little attention to our baits when prey was freely available. Weasels *Mustela nivalis* were only caught in the 4 ha live trapping grid for small mammals, although their tracks were encountered in other parts of the study area, too (Oksanen et al. 1991).

A coarse estimate for stoat density for the mustelid peak (August 1988), obtained by dividing the number of captured stoats by the size of the live-trapping area is 7 individuals km⁻². The highest local stoat density was recorded in August 1986, when 5 stoats were captured within a 8 ha complex of alluvial thickets and managed fields (i.e. there were 60 stoats km⁻² in this area, in addition, two stoats were captured in the tall herb habitats on the slope). This high local density was found in the area where the abortive root vole rise took place.

The most reasonable estimate for weasel densities in August 1988 can be derived from the number of individuals captured in the live-trapping grid (7) and from the tracking data suggesting that weasel home ranges within this area in 1988 were of the order of 0.15 km² (Oksanen et al. 1991, Fig. 5) which yields an estimate of 45 weasels km⁻². This high value only refers to the luxuriant slope-marsh subarea.

Our data indicate that the populations of both species crashed between August and December 1988. Although the crash may have been inflated by the problems of distinguishing two animals of the same species and sex with overlapping habitat use by means of snow-tracking, a genuine decimation of predator populations obviously took place between August and December 1988. Except for the central part of the slope, the small mustelid tracks were separated from each other in December 1988. Moreover, also weasels moved extensively on the snow surface (see Oksanen et al. 1991, Fig. 5).

Discussion

Lemmings

The interpretation of the boom-crash pattern of highland lemmings seems easy. Combined with observations of obvious habitat devastation in the highland (Oksanen and Oksanen 1981, Moen et al. unpubl. data), with the scantiness of predator activity in the highland (Oksanen and Oksanen 1981, Oksanen et al. 1991) and with the virtual absence of winter nest predation, the pattern indicates chaotic vegetation-lemming fluctuations, as predicted by L. Oksanen (1981, 1990) for barren areas. This prediction is also corroborated by data on lemming populations in middle and high-arctic

(or alpine) tundra areas and on their impact upon the vegetation (Fuller et al. 1977, Batzli et al. 1980, Černjavskij and Tkačev 1982, Framstad et al. 1991).

By contrast, lowland populations of the Norwegian lemming behaved in a more complicated way. The boom-crash syndrome of 1977–79 extended to the lowland, too. In 1988–89, however, the declining vole populations of the lowland seemed to “pull” the numbers of lowland lemmings down before the boom-crash syndrome had time to develop, as typical for taiga populations of lemmings (Henttonen et al. 1987). It thus seems that a necessary condition for the development of lemming outbreaks in lowlands is that lemmings disperse there when vole populations are still rising. However, this is not a sufficient condition. A gradual lemming decline has been recorded even in a practically vole-free low arctic area (Krebs 1964).

Another implication of the lemming data is that lemming outbreaks are initiated in the highlands and/or in the uppermost edge of the lowland complex, as proposed by Kalela (1949, 1961, 1971, Kalela and Koponen 1971). Where the lemmings survive the crashes is more difficult to judge. The prevalence of lowland captures in 1981 and 1989 and the sightings reported by reindeer herdsman suggest that lowlands play a role as survival habitats immediately after crashes in highland areas.

A scenario which would account for these data and for the exceptional mobility of Norwegian lemmings (Koponen et al. 1961, Myllymäki et al. 1962, Henttonen and Jarvinen 1981, Oksanen and Oksanen 1981) is that lemmings survive extreme crashes in lowlands where predation prevents fatal overexploitation of winter food. However, in the long run, lemmings are not equipped to stand intense predation pressure in the presence of more elusive voles (Oksanen 1991). Thus, the long-term success of the emigrants depends on their ability to produce offspring which recolonize the highlands within a few years.

Voies

Even with reservations for sources of uncertainty in density estimates, we can conclude that the general fluctuation syndrome in lowland populations of voles is totally different from that of highland lemmings. The data are consistent with a regular 4.5 yr cycle, although at least one more fluctuation is needed before the existence of genuine cyclicity can be statistically tested. Moreover, the observed declines were gentle and could not be characterized as sudden crashes. Massive devastation of lowland habitats by voles was not observed during 1977–89, although the abundance of girdled mountain birches and willows in 1977 indicated copious bark-gnawing during the 1974–75 peak.

The vole data are compatible with time-delayed density dependency, as in the case of other fluctuating populations of microtine rodents in boreal, subalpine,

subarctic and low-arctic areas (Krebs 1964, Fitzgerald 1977, Vuotala 1977, Henttonen et al 1977, 1987, Andersson and Jonasson 1986, Hornfeldt 1991) Acute food shortage may have occurred in 1975 even in the best habitats, as indicated by signs of widespread bark-gnawing (above, see also Hansson 1969) During 1977–89 however, the coverages of willows and dwarf birches were more than doubled in our permanent plots (Oksanen 1988, Table 2) and massive bark-gnawing was never observed Thus, obvious food depletion in the best habitats does not form a recurrent component in the cycle

The summer decline (or lack of summer rise) in open tundra during 1983 co-occurred with exceptionally high jaeger densities (compare to Andersson 1976) Even more pronounced summer declines are common in the arctic where they are usually attributed to jaegers, owls or both (Pitelka 1973, Fuller et al 1977, Batzli et al 1980) Thus, the Korpimäki-Norrdahl (1989) hypothesis of the dampening impact of avian predators on microtine peaks seems to be sometimes applicable to tundra areas, too. However, in Fennoscandian conditions, such impacts are not regular components of the cycle

The wave-like spreading of microtine declines from areas with exceptional abundance of luxuriant vegetation to typical tundra areas seems to rule out all mechanisms where weather or synchrony in production of high-quality plant organs plays a central role (Kalela 1962, Tast and Kalela 1971, see also Laine and Henttonen 1983, Oksanen and Ericson 1987) Also Keith's (1974) hypothesis of starvation due to acute food shortage as a triggering cause for the decline is difficult to reconcile with this asynchrony, because starving animals should disperse to areas where food still is available

Two classes of hypotheses can be readily reconciled with the spatial asynchrony of population declines The first one consists those hypotheses, where the decline is tightly connected to the local population development the stress hypothesis of Christian and Davies (1964), the genetic-behavioral hypothesis (Chitty 1960, Krebs and Myers 1974), the social fence hypothesis of Hestbeck (1982), the hypothesis of inducible chemical defenses (Haukioja and Hakala 1975) and its variant which connects chemical defenses to juvenile shoot morphology (Bryant and Kuropat 1980). Under these hypotheses, local asynchrony can arise as a consequence of different timing of population rises in optimal and suboptimal areas Another class of hypotheses compatible with local asynchrony consists of those where natural enemies have a central position (Anderson 1981, Oksanen et al 1981, L. Oksanen 1981, 1990, Hansson 1987, 1988, Sinclair et al. 1988, Hanski et al. 1991). Here, the source of asynchrony lies either in infestation dynamics of pathogens or in the habitat choice of predators

Our data present some problems for both classes of hypotheses. The fact that lemmings declined in the lowland in 1988–89 without having even approached outbreak numbers (see also Henttonen et al 1987) pro-

vides difficulties for the first-mentioned class Lemmings are aggressively superior to grey-sided voles (Henttonen et al 1977) and have practically no overlap in feeding niche with them (Kalela 1957, 1961, 1971) Thus, both interspecific aggression and interspecific induction of chemical defenses seem implausible. The hypothesis of induced defense has also other problems, when applied to the interaction between grey-sided voles and blueberry twigs of the Fennoscandian tundra Changes in secondary chemistry of the blueberry do not follow the vole cycle (Jonasson et al 1986, Laine and Henttonen 1987) and heavy grazing seems to improve the quality of blueberry twigs (Oksanen et al 1987)

The problem with hypotheses emphasizing the role of natural enemies lies in numbers and in the apparent healthiness of voles in 1988 In our live-trapping study of microtines (Ekerholm et al unpubl. data), we did not find any indications of poor condition or lowered reproductive output during the decline summer Vole densities of within the slope subarea were c 50 ha^{-1} (i.e. 5000 km^{-2}) This implies a monthly production rate of c $15000 \text{ voles km}^{-2}$ Our data for the same subarea indicate a peak density of c $50 \text{ small mustelids km}^{-2}$ Thus, c 300 voles were monthly produced for each small mustelid The assumption of copious surplus killing at high prey densities (Stenseth 1981b, Abrams 1982, Oksanen et al 1985) is well needed if the summer decline is to be attributed to predation

Conclusions and perspectives for future work

The data reported here suggest that the dichotomy between vole cycles and lemming chaos (L. Oksanen 1990) exists even locally at a transition between areas with low and middle arctic characteristics The chaos can be readily understood as a consequence of interactions between lemmings and the plant cover Conversely, the cycles can be produced by a number of mechanisms incorporating time-delayed density dependence The observed spatial differences in the timing of the decline seem to rule out some candidates, but a many others remain unrefuted.

When trying to identify the sufficient conditions for the cyclic declines, we can proceed by using a population-level modification of Koch's (1881) postulates According to this approach, a factor can be regarded as a sufficient cause of the decline if (1) it is always there during population declines, (2) its experimental introduction creates a decline while surrounding populations are not declining and (3) its presence can be verified during the final stages of the experimental decline Postulates (2) and (3) can be replaced by following, logically equivalent postulates: (2') the experimental exclusion of the factor prevents a decline while surrounding populations are declining and (3') the absence of the

factor in the experimental area can be verified during the collapse of surrounding populations

In the case of natural enemies, postulate (1) is solidly corroborated for microparasites, macroparasites, avian predators and mammalian ones (above, Krebs 1964, Andersson 1976, Vutala 1977, Fitzgerald 1977, Hornfeldt 1978, Korpimäki 1985, Henttonen et al 1987, Haukisalmi et al 1989, Hornfeldt et al 1989) However, a stronger version of postulate (1), requiring presence in sufficiently large numbers to indicate a plausible causal connection to population declines remains to be verified for natural enemies other than small mustelids

Postulate (2) has been once verified for small mustelids Experimental introduction of a weasel to an island with 7 ha of productive habitat coincided with a local decline while populations on other islands increased (Oksanen and Oksanen 1981) However, the weasel was not recaptured Later attempts to repeat the experiment have failed due to technical problems (escape of a radio-collared experimental stoat, uncontrolled predator invasions, Oksanen and Oksanen unpubl data) A macro-scale test of postulate (2') was provided by the Norwegian policy to exterminate all predators during 1900–1920, which seemed to stop vole cycles (Steen et al 1990) However, the experiment suffers from the "Kaibab syndrome" (lack of control, vague data) Desy and Batzli (1989) executed a predator enclosure experiment with impeccable design, but in such small spatial and temporal scale that the results are inconclusive in the present context

The probably most fruitful way to go further consists of mesoscale experiments, focusing on postulates (2') and (3') The scale of the experiment needs to be large enough to allow treatment of entire landscape units, so that blocked dispersal can be excluded as an alternative explanation (see Krebs et al 1973) Due to financial constraints, this scale can probably be only achieved by sacrificing replication, as done in the island experiment of Marcstrom et al (1988) on the impact of martens and foxes upon population dynamics of gallinaceous birds

Acknowledgements – In the field work, the contribution of several field assistants has been indispensable The most profound contributions were made by A Lukkarı, L Bondestad, P Ekerholm, S From, A Graner, P Lundberg, M Norberg, R Nordbakke, S Oksanen and B Romsdal H Henttonen provided valuable advice in several stages of the work Also discussions with S Fretwell, L Hansson and J Moen have been instructive The logistical help of A Johnsen and H Romsdal were indispensable, and the co-operative attitude of Norwegian authorities, particularly J Halvorsrud and T Åseth, was extremely valuable Earlier drafts of the manuscript were constructively criticized by L Hansson, C King, C Otto and N C Stenseth The figures were drawn by G Marklund The study was supported by a grants from NFR (Swedish Natural Science Research Council), the Academy of Finland, the Kempe Foundation and the Hierta-Retzus foundation

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