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Population fluctuations in insectivores and small rodents in northernmost Fennoscandia

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Abstract

Investigated regional and interspecific synchronization and demographic characteristics of rodent and insectivore fluctuations in northernmost Fennoscandia.

Small mammals were sampled by index methods in 1965–70 on a transect from Lofoten islands to the Norwegian-Russian border. About 9000 small mammals, more than half of them shrews, were caught in taiga and subalpine forests, mires, hay meadows, alpine and tundra areas.

Pronounced fluctuations in abundance were found, with peaks mainly in 1966 and 1969 to 1970. However, some regions deviated slightly from this pattern. In northwestern Norway largest fluctuations were due to the shrew *Sorex araneus*, while rodents (*Clethrionomys rutilus* and *Microtus agrestis*) showed small and rather stable populations on some maritime islands. On the Fennoscandian mainland largest fluctuations appeared in the rodents (*Clethrionomys* and *Microtus* species).

Fluctuating rodent and *S. araneus* populations were divided into increase, peak and low density phases. In both the rodents and the shrew, phase-dependent changes were found in population structure, sex ratios and weight distributions. Reproductive parameters were less affected by the density variations. A qualitative deterioration (e. g. fewer maturing animals) was detectable in rodents that were approaching peak densities.

Introduction

Many populations of small mammals fluctuate in a more or less regular cyclic way. Reasons and nature of such fluctuations are still obscure. In order to investigate extreme conditions sampling was performed in 1965–70 in northernmost Fenno-

scandia, where the most pronounced variations in small rodent density were expected. The regional synchronization of the population dynamics of separate species were studied in populations from islands outside the northwestern parts of Norway through the north of Sweden and to the northernmost part of Finland and Norway. Local and regional synchronization of the population dynamics of various species are also elucidated.

This study forms part of comprehensive investigations on the dynamics of small mammals and their ectoparasites at the Department of Animal Ecology in Lund. Some preliminary notes on the small mammal material presented here have been published earlier (e. g. ANDERSSON and HANSSON 1966; ASKANER and HANSSON 1967; NILSSON 1971; LUNDQVIST et al. 1973; HANSSON 1974 a). On the ectoparasite material reports dealing with ticks (NILSSON 1974 a, b, 1975) other mites (EDLER and LUNDQVIST 1977; EDLER and MEHL 1972; EDLER and MRČIAK 1975) and fleas (BRINCK-LINDROTH 1972) have been published.

Methods

Collections were made in late summer. Tab. 1 shows the dates for the total sampling periods. However, the main parts were performed during some three weeks in the beginning — middle of August. The localities were sampled in the same order during the various years. The trapping was performed in two ways, i. e. index trapping and survey collection.

Table 1

Total catches of small mammals during the expeditions to northernmost Fennoscandia in 1965—70. For each year, apart from catch numbers, the time of sampling and total number of trap-nights (Tn) are recorded.

Species	1965 6/8—5/9 6 938 Tn	1966 6/8—28/8 3 318 Tn	1967 29/7—24/8 4 598 Tn	1968 26/7—16/8 3 660 Tn	1969 18/7—18/8 2 995 Tn	1970 28/7—26/8 3 074 Tn	Σ 18/7—5/9 24 583 Tn
<i>Sorex minutus</i> L.	0	1	2	25	20	12	60
<i>Sorex araneus</i> L.	1 842	538	426	584	593	515	4 498
<i>Sorex isodon</i> Turov	0	1	0	0	0	0	1
<i>Sorex caecutiens</i> Laxm.	173	33	7	18	5	10	246
<i>Sorex minutissimus</i> (Zimm.)	0	0	0	1	0	0	1
<i>Sorex</i> indet.	52	2	0	0	0	1	55
<i>Neomys fodiens</i> (Penn.)	25	5	4	3	6	3	46
<i>Lemmus lemmus</i> (L.)	0	5	0	0	0	13	18
<i>Clethrionomys rutilus</i> (Pall.)	268	205	73	76	255	297	1 174
<i>Clethrionomys glareolus</i> (Schr.)	43	160	12	7	89	150	461
<i>Clethrionomys rufocanus</i> (Sund.)	339	237	41	29	238	402	1 286
<i>Clethrionomys</i> indet.	1	0	3	0	5	1	10
<i>Arvicola terrestris</i> (L.)	0	0	0	0	1	0	1
<i>Microtus agrestis</i> (L.)	21	73	9	50	180	138	471
<i>Microtus oeconomus</i> (Pall.)	39	189	1	0	109	169	507
<i>Micromys minutus</i> (Pall.)	0	0	0	0	0	1	1
<i>Mus musculus</i> (L.)	84	1	0	0	0	1	86
<i>Mustela nivalis</i> L.	0	8	1	0	0	12	21
All species	2 887	1 458	579	793	1 501	1 725	8 943

Index trapping according to HANSSON (1967 a) was performed in certain habitats, with large areal extension in the selected localities. One multiple-catching live trap was put on each trapping station with intervals of 25 m between stations on trapping lines with variable length. The trap was located in the best place in the station, which had a radius of 2 m. The traps were distributed about 17.00 hr and the catch removed about 09.00 hr the following morning.

Methodological studies (HANSSON 1967 a, 1975) have shown that there are clear relations between index catch of most rodent species, expressed as e. g. mean number of animals caught per trap, and population density (as far as we are presently able to measure the latter). For shrews (*Sorex* spp.) no such correlation has been found. One reason may be that small rodents occupy the traps or in other ways prevent the shrews from entering them (HANSSON 1972 and unpubl.). From the methodological studies, it is obvious that species are attracted to the traps to different degrees. Granivorous species are caught in larger proportions than herbivorous ones. Of the present species, *C. rutilus* and *C. glareolus* may be expected to be caught in relatively higher numbers than *C. rufocanus* and the *Microtus* and *Lemmus* species. Common shrews (*S. araneus*) were found to be highly attracted to the trap type used (HANSSON and HOFFMEYER 1973).

At survey collection the live traps were distributed roughly in proportion to the areal extension of the habitats in each locality (except for human habitations and cultivated fields). The traps were placed in the most suitable location in each habitat. Trapping was performed both night and day, with removal in the morning and afternoon. The number caught in the daytime after removal trapping at night was rather small, usually less than 10 % of the 24 hour total (ANDERSSON and HANSSON 1966).

From 1968 we gradually introduced traps with smaller mesh size, which permitted capture of *S. minutus* and *S. minutissimus*. Comparisons between trap types in northwestern Norway did not show any difference in trapping efficiency as regards other species.

The animals were killed with diethyl ether fumes and weighed usually with "Pesola" spring balances. They were then classified as to functional categories (cf. below), examined

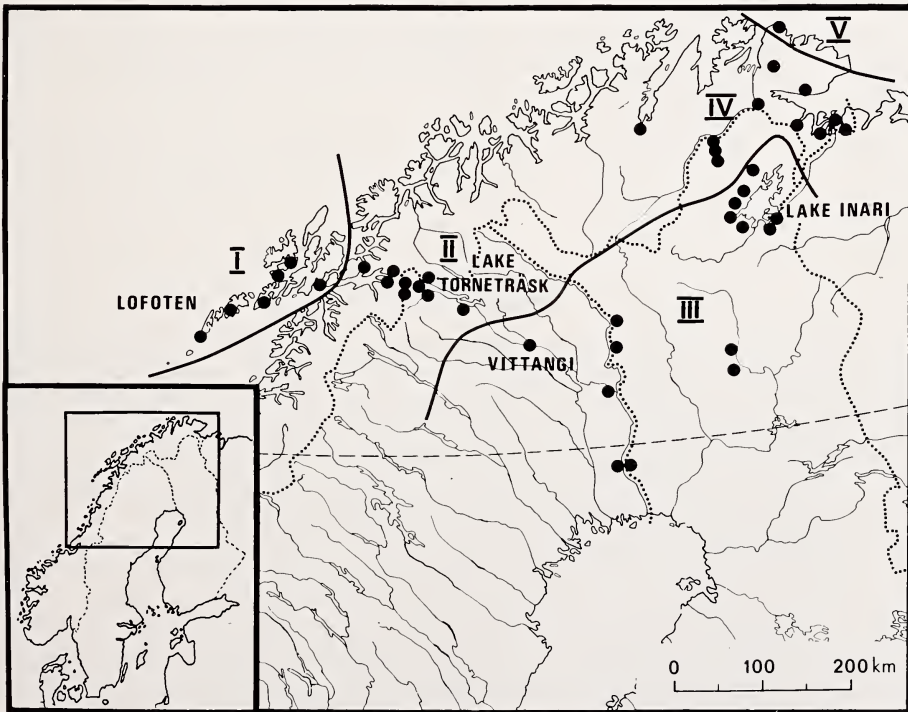


Fig. 1. The trapping localities in northernmost Fennoscandia, divided into five regions due to geographical and biotic characteristics

for external signs of reproduction (mainly for lactation) and preserved in a mixture of equal amounts of 80 % ethyl alcohol and 4 % formaldehyde solution. Some dead specimens were damaged (bitten by other trapped animals) and were not used any further. Reproductive status was examined more closely in the laboratory by autopsy.

Study areas and habitats

Trapping was performed in a number of localities across northernmost Fennoscandia, from the Lofoten islands to the Norwegian-Russian border (Fig. 1). The localities were situated in five main regions:

Region I. The Lofoten and Vesterålen islands. This area is characterized by the small number of small mammal species occurring on the islands (ANDERSSON and HANSSON 1966). The climate is comparatively mild for a location north of the Polar Circle. Most trapping was performed in climax birch forests. According to HÄMET-AHTI (1963) these forests are "submaritime birch forests" characterized by large trees and a rich flora. Index trapping occurred also on comparatively dry and oligotrophic bog areas.

Region II. The Scandinavian mountain range between the Norwegian seaboard (close to the town Narvik) and the eastern end of Lake Torneträsk. Index trapping was performed in the mainly subalpine climax birch forests, in oligotrophic mires, in dwarf shrub areas in the low alpine belt and in boulder areas in the middle alpine belt.

Region III. Northern taiga areas in Sweden and Finland, i. e. between Vittangi and Lake Inari. Small mammal indices were obtained from both spruce and pine forests, from successional birch forest and from abandoned hay meadows.

Region IV. Birch forest areas in northernmost Finland and Norway, at low altitude close to Barent Sea. Regular trapping occurred in subalpine climax birch forests, in eutrophic mires, in dwarf-shrub areas in the low alpine belt and in abandoned hay meadows.

Region V. Coastal tundra with dwarf-shrub communities on the Varanger peninsula.

Results

Species composition

About 9000 small mammals were caught during the six years of trapping (Tab. 1). More than half were insectivores, with the common shrew (*S. araneus*) as the very dominating element. Material sufficient for detailed analysis was also obtained for *C. rutilus*, *C. glareolus* (only from region III), *C. rufocanus*, *M. agrestis* and *M. oeconomus*. *M. musculus* is not included in the following analysis, as trapping in and around buildings was very erratic. Catches of *S. minutus* were almost only obtained after the 1968 changeover to traps with smaller mesh size. The catches of *S. caecutiens* were concentrated to the first two years 1965–1966. Numerous *L. lemmus* were seen, caught by hand, or found dead, but few were caught in the live traps. Some additional trapping with snap traps baited with "Polish wicks" (GRODZINSKI et al. 1966) gave more lemmings. All lemmings were caught during the peak years 1966 and 1970. This was also the case, with one exception, of the captures of weasels (*M. nivalis* "forma rixosa"). Some rare species (*S. isodon*, *S. minutissimus*, *M. minutus*) and accidentally also *A. terrestris* were caught as single specimens, demonstrating the difficulties of obtaining a true picture of their geographical distribution.

Density variations

Index catches

Most index trapping was performed in birch forest so the density variations in this habitat will be treated in some detail (Fig. 2). There were pronounced changes in density indices in the climax forests of region I, II and IV. In region I *S. araneus* dominated the catch with a mean of between 0,5 and 1,0 shrews per trap in the peak years 1965 and 1968–69. Rodents were very scarce (neither *C. rutilus* nor *M. agrestis* occurred with a mean greater than 0,05 animals per trap) in this region, with small peaks in 1966 and 1969. Both rodents and shrews underwent population decreases in 1967 and 1970. In region II shrew density was highest in 1965 and 1970. The rodents there had peaks in 1966 and 1969–70, but *C. rutilus* tended to decline in 1970. *S. araneus* and *C. rufocanus* were about equally common in the catches and showed peak values around 0,4 animals/trap except for the especially high *S. araneus* index in 1965. However, the ratio between maximum and minimum density was

much greater in the rodent. During peak years low numbers of both *M. agrestis* and *M. oeconomus* were obtained in the birch forest of region II. In the successional birch forest in region III *C. rutilus* dominated at the unregular trapping, while *Sorex* spp. and *Microtus* spp. were rare. No index trapping was performed in region IV in 1965 and densities of all species were rather low in 1966. The trap indices of *S. araneus*, fluctuating around 0,20, showed no clear tendencies during the following years, while *C. rufocanus* increased during 1969 and 1970 and *C. rutilus* showed a peak in 1969 and a small decline in 1970.

There were large differences in the *S. araneus* mean population level in the various regions and a decrease from west to east is noticeable. Only birch forests

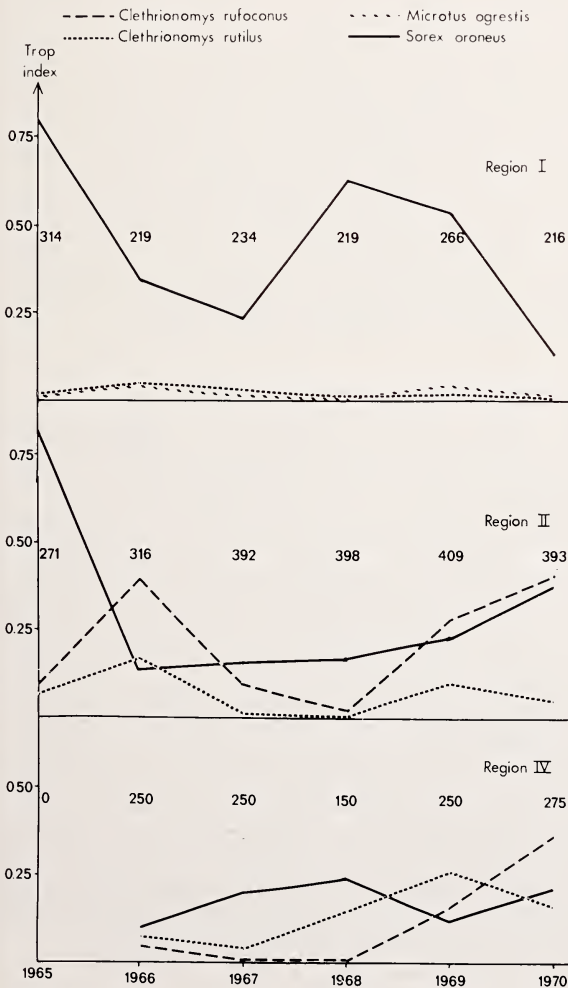


Fig. 2. Index catches in birch forest habitats. The trap index equals the mean number of animals caught per one multiple-catching live trap. The figures inside each graph refer to the number of trap nights each year

close to the western Norwegian sea shores kept both high insectivore and rodent populations. In the mountain localities and in eastern Fennoscandia the rodents were more numerous at peaks than the shrews. Thus, large *S. araneus* populations and fluctuations, being independent of rodent population levels, could only be ascertained from the low-altitude trapping in maritime areas in Northwest Norway.

The annual density variations were similar in the other habitats sampled with the index method. *C. rutilus* and *C. glareolus* dominated in the coniferous forests in region III. In the abandoned hay meadows the two *Microtus* spp. were most abundant but *S. araneus* was fairly common and in region III many *C. glareolus* were caught in this habitat. In mires *S. araneus* was the only regular species in region I, while *M. agrestis* and *M. oeconomus* were more abundant than *S. araneus* in mires in region IV. In the low alpine belt and tundra areas *C. rufocanus* was the most common species but *S. araneus* appeared also in numbers in these habitats.

Total catches

Mean nightly catch per total number of trap nights in all habitats was computed separately for all insectivores and small rodents in each region (Fig. 3). The resulting relative catches and temporal variations were similar to the index values. Insectivores dominated in region I. The less common rodents showed peaks in 1966 and 1969, while insectivore peaks occurred in 1965–66 and 1969. In region II the relative catches of insectivores and rodents were similar, with rodent peaks in 1966 and 1969–70 and insectivore peaks in 1965 and (with more uncertainty) in 1969–70. In region III insectivore catches were lower than those of rodents except during rodent "lows". Rodent peaks appeared in 1965–66 and 1969–70. Insectivore fluctuations were similar but not very pronounced. In region IV insectivore and rodent catches were similar except for the rodent peak 1969–70. There was an apparent peak in 1965 and the relative rodent catch was considerably lower in 1966. No regularity in the fluctuations of insectivores was detectable in this region.

Patterns of population fluctuations in 1965–70

The fluctuations in small rodent density followed generally the well-established 3–4-year rhythm of microtine populations (cf. KREBS and MYERS 1974). A 3-year interval between peaks was clearest for region I. In regions II–III there was also a 3-year interval between the 1966 peak and the start of the 1969–70 peak. These conditions were rather uncertain for region IV with peak in 1965 and in 1969–70. The small rodent numbers were in a medium level already in summer 1964 in easternmost Norway (CLOUGH 1967–68). The latter peak started to build up in 1968, so this region fluctuated partly out of phase with the other regions. There were also rather high rodent populations in region III in 1965. The peak in 1969–70 reached generally higher values than in 1965–66. In summer of 1971 rodents were very scarce in northernmost Sweden (ANDERSSON 1976), so the 1969–70 peak "crashed" on the mainland of northernmost Fennoscandia in the winter of 1970–71 (cf. also MYRBERGET 1973). This is supported by the small catches obtained in region IV in the winter 1971–72 (NILSSON unpubl.). The amplitude in the fluctuations varied considerably between regions with the smallest density variations in region I (being almost imperceptible in the index values). There were a few differences in dynamics between species (e. g. *C. rutilus* sometimes declining before other rodent species) but they were not clear enough to warrant separate treatment of the various rodent species.

Insectivore fluctuations were only pronounced in regions I and II. Peak numbers appeared in 1965 and 1969 in region I and in 1965 and 1969–70 in region II. In all regions the 1965 populations were highest.

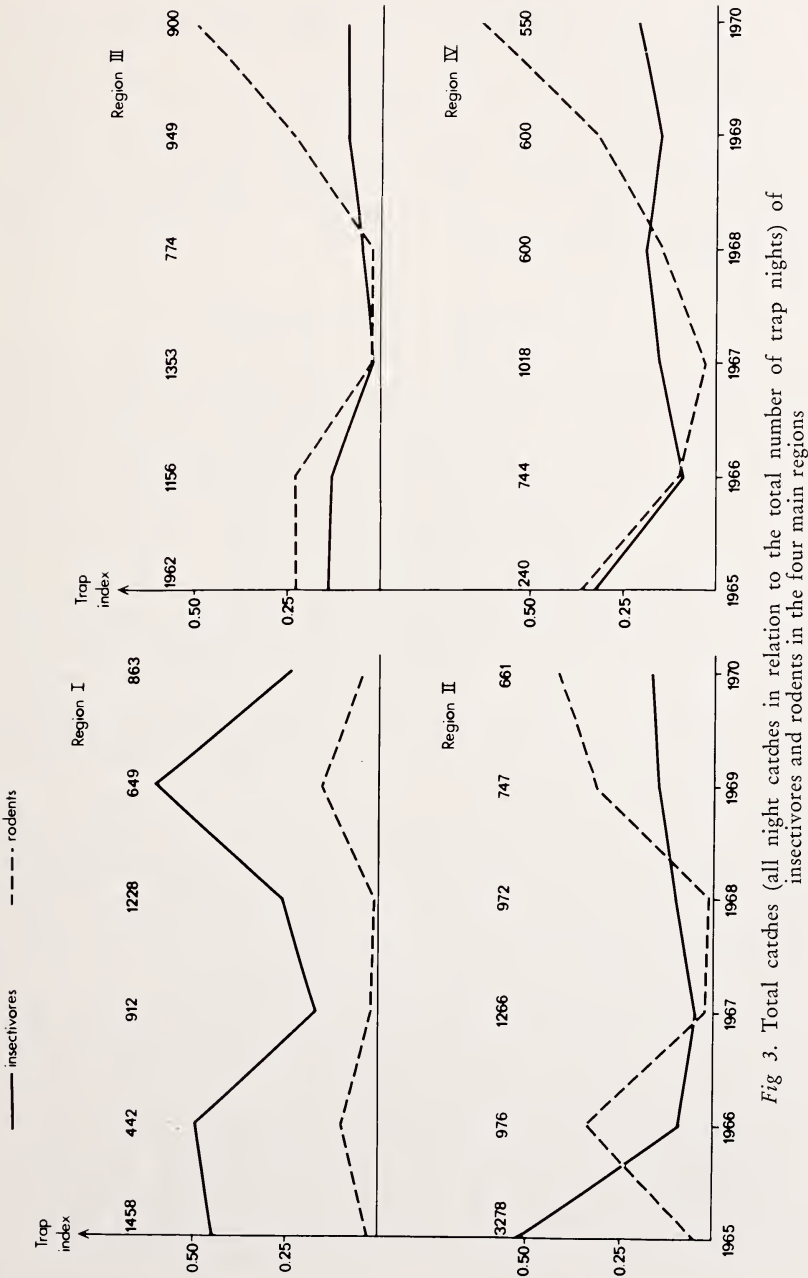


Fig. 3. Total catches (all night catches in relation to the total number of trap nights) of insectivores and rodents in the four main regions

Population structures and reproduction

In following sections population structures and demographic parameters will be compared between insectivores and rodents as regards increase, peak and decrease conditions. In this way it will be examined if the insectivore fluctuations show the same general patterns as the rodent "cycles". The following peak years form the basis for classification into phases of abundance:

Rodents: Region I, 1966 and 1969. Region II–III, 1966 and 1970. Region IV, 1965 and 1970. Region V, 1970.

Insectivores: Region I, 1965 and 1969. Region II, 1965 and 1970. Regions III–V will not be dealt with further as regards insectivores.

Thus, years of rodent increase were 1965 in regions I–III, 1968 in region I and 1969 in regions II–V. Remaining years are treated as decrease and bottom years ("low population" phases). For *S. araneus* 1968 was an increase year in region I and 1969 in region II. Remaining years in region I and II are regarded as years of decreasing or low shrew populations.

Composition of functional categories

The animals were divided into the following functional categories (MYLLYMÄKI 1970 a): adult (reproductive) males and females, juveniles still bearing remains of their first pelage, subadults in at least their second pelage but with immature gonads, and postreproductive animals with regressed gonads. The composition of these categories in the catch differed between population phases in all species with enough numbers for statistical analysis (Tab. 2). However, this difference was less for *S. araneus* than for the rodents. Following examinations (Tab. 3 and following tables) are based on the assumption that the trappability of the various categories was independent of population density or structure.

The proportion of reproductive females affects the potential of population increase. A change in the proportion of adult females (adult females/all adult animals) during the three phases was evident in the *Clethrionomys* species (Tab. 3). In *C. rufocanus* the change was pronounced, in *C. glareolus* also significant and in *C. rutilus* on the border of significance. In all three species lowest proportion of adult females was found in the low populations, while there was only a faintly higher proportion in peak than in increase populations.

The mean number of juveniles per adult female shows the juvenile recruitment (reproduction minus juvenile mortality) of young. However, the trappability of juveniles is generally low (cf. HANSSON 1971), so only an index of recruitment was obtained. Juvenile shrews are not trappable because of the long period they remain in the nest so only rodents were examined. No consistent trend could be found but this net production was rather low in several species during the phase of increase. Species differences are due to e. g. different age at weaning.

In rodents the proportions of young entering adulthood during the summer varies considerably. Also the proportion of adults regressing to postreproductive states seems to vary. The ratio of adults to subadult and postreproductive animals will describe certain aspects of the "quality" of the population at the end of the summer. This quality is thus estimated from the reproductive development during the summer but is assumed to reflect fundamental states in individual conditions. This index varied significantly in all rodents and was consistently lowest at peak density. For most rodents this index was higher in low than in increasing populations, while remaining species, *M. oeconomus*, showed rather similar values at these two phases. In shrews in northern areas, juveniles do not mature during summer and regression of adults

Table 2
Functional groups of shrews and rodents in the total samples from different phases of abundance

Species	Increase					Peak					Low					Difference p			
	♂ Ad	♀ Ad	Juv	Sub- ad	Post- repr	Σ	♂ Ad	♀ Ad	Juv	Sub- ad	Post- repr	Σ	♂ Ad	♀ Ad	Juv		Sub- ad	Post- repr	Σ
<i>S. araneus</i>	38	23	—	396	—	457	108	76	—	1 863	—	2 047	61	43	—	760	—	864	< 0.05
<i>C. rutilus</i>	87	93	85	230	0	495	80	76	55	266	1	478	75	44	58	23	1	201	< 0.001
<i>C. glareolus</i>	20	27	10	75	0	132	28	44	12	215	11	310	12	4	0	3	0	19	< 0.001
<i>C. rufocanus</i>	101	167	158	85	0	511	66	222	190	211	1	690	35	29	16	6	0	86	< 0.001
<i>M. agrestis</i>	23	55	22	31	2	133	29	70	86	94	3	282	8	19	24	3	0	54	< 0.001
<i>M. oeconomus</i>	17	43	19	69	0	148	15	17	28	251	20	331	1	7	5	15	0	28	< 0.001

Table 3

Indices of the state of the population as appearing from sample compositions at three population phases

Species	Increase					Peak					Low					Difference, P				
	\bar{x}		% Ad + juv		%	Σ animals	\bar{x}		% Ad + juv		%	Σ animals	\bar{x}		% Ad + juv		%	Σ animals		
	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀		Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀		% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀		Ad ♂ ♀	
																				% Ad ♂ ♀
	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀	% Ad ♂ ♀	Ad ♂ ♀		
<i>S. araneus</i>	38	—	13	—	41	9	—	12	—	41	—	12	—	NS	< 0.05	—				
<i>C. rutilus</i>	52	0.9	54	17	49	0.7	0.7	88	29	37	1.3	88	29	< 0.05	< 0.001	< 0.001				
<i>C. glareolus</i>	57	0.4	43	8	61	0.3	0.3	25	0	25	0.0	84	0	< 0.001	< 0.001	NS				
<i>C. rufofuscus</i>	62	1.0	83	31	77	0.9	0.9	45	19	45	0.6	93	19	< 0.001	< 0.001	< 0.05				
<i>M. agrestis</i>	71	0.4	75	17	71	1.2	1.2	66	30	70	1.3	94	44	NS	< 0.001	< 0.001				
<i>M. meonomus</i>	72	0.4	53	13	53	1.7	1.7	18	8	88	0.7	46	18	NS	< 0.001	NS				

Table 4
Sample sex ratios in various population categories during the three population phases

Species	Increase				Peak				Low			
	Juv δ/\varnothing	Subad δ/\varnothing	Adult δ/\varnothing	Postrepr δ/\varnothing	Juv δ/\varnothing	Subad δ/\varnothing	Adult δ/\varnothing	Postrepr δ/\varnothing	Juv δ/\varnothing	Subad δ/\varnothing	Adult δ/\varnothing	Postrepr δ/\varnothing
<i>S. araneus</i>	39/46	NS	228/168	<0.01	38/23	NS	142/88	<0.01	32/26	NS	429/381	<0.01
<i>C. rutillus</i>	6/4	NS	142/88	<0.01	87/93	NS	149/117	<0.05	0/0	NS	20/3	<0.001
<i>C. glareolus</i>	92/66	<0.05	33/42	NS	20/27	NS	130/85	<0.05	8/4	NS	28/44	NS
<i>C. rufocanus</i>	11/11	NS	53/32	<0.05	101/167	<0.01	127/84	<0.01	99/91	NS	66/222	<0.001
<i>M. agrestis</i>	8/11	NS	26/5	<0.001	23/55	<0.001	55/39	NS	50/36	NS	29/70	<0.001
<i>M. oeconomus</i>			30/39	NS	17/43	<0.001	122/129	NS	17/11	NS	13/17	NS

Table 5
Frequency of pregnancy and lactation at various population phases. At small samples figures from low and increase phase were pooled

Species	Increase				Peak				Low				Difference, p		
	Pregnant + lac-tating	Only pregnant	Only lac-tating	Neither pregnant nor lac-tating	Σ repro-ductive females	Pregnant + lac-tating	Only pregnant	Only lac-tating	Neither pregnant nor lac-tating	Σ repro-ductive females	Pregnant + lac-tating	Only pregnant	Only lac-tating	Σ females	Classi-fied females
<i>S. araneus</i>	3	5	14	1	23	6	14	34	22	76	4	9	26	43	NS
<i>C. rutillus</i>	14	45	17	17	93	5	40	5	26	76	2	17	4	44	<0.05
<i>C. glareolus</i>	0	11	1	15	27	0	16	0	28	44	0	4	0	4	NS
<i>C. rufocanus</i>	9	66	27	65	167	10	76	35	101	222	6	11	2	29	NS
<i>M. agrestis</i>	11	38	12	0	61	9	27	20	14	70	0	14	4	19	NS
<i>M. oeconomus</i>	2	19	7	14	42	0	4	0	13	17	0	3	0	5	—

was not found. Thus the corresponding percentage of adults in shrew populations is related to reproductive output and/or different survival rather than to population quality. In *S. araneus* this index differed significantly, but less than for the rodents, with lowest value in the peak populations.

The percentage of juveniles in a population may indicate the immediate state of increase. This index differed between population phases in *C. rutilus*, *C. rufocanus* and *M. agrestis*. In *C. rutilus* and *M. agrestis* it was highest in low populations, while the reverse was true of *C. rufocanus*.

Sex ratios

In several species there was a surplus of females in the reproductive groups (Tab. 2). To examine if this surplus emanated from birth the sex ratio was computed for various categories (Tab. 4).

In *S. araneus* there was a surplus of males in both subadult and adult animals but it deviated significantly from an 1:1 ratio only in subadults in low and increasing populations and in adults in peak populations. Subadults of *C. rutilus* in all population phases showed a significant surplus of males and this was also the case with adult *C. rutilus* in low populations. The same was found in subadult *C. glareolus* in low populations. *C. rufocanus* was the only species with a significant male surplus in the juvenile component but only in increasing populations and with a weak deviation from parity. In increasing and peak *C. rufocanus* populations as well as in most cases for *M. agrestis* and *M. oeconomus* there was a surplus of females in the adult category. In these same species there was often at the same time a significant surplus of males amongst the subadults. There was a general surplus of males among postreproductive animals.

Reproduction

Adult females were classified as follows:

I. pregnant and lactating simultaneously

II. only pregnant

III. only lactating

IV. neither clearly pregnant nor lactating

The last group (i. e. "unclassified females") contained animals with well developed gonads and possibly in early pregnancy. However, many of the female rodents were probably just entering the postreproductive state. Autopsies were made after preservation in formalin, making examination difficult, so animals in the last-mentioned group might have been less numerous if fresh material had been studied. Some females in juvenile pelage were also pregnant and these (e. g. *M. agrestis*) were added to the adult group to include all females in reproductive state. If numbers were too small for comparing all three phases, increase and low phase animals were pooled.

A comparison of the composition of the total female material (Tab. 5) showed significant differences with regard to cycle phase in *S. araneus*, *C. rutilus* and the two *Microtus* species. There were more unclassified animals in peak than in increasing populations (Tab. 6). In most cases the low populations were intermediate. When considering only classified females difference between phases was detectable only in *C. rutilus* with more lactating females in increasing populations. At all population levels there was a higher proportion of pregnant than lactating females in all rodent species. The conditions were the reverse for *S. araneus*, indicating an earlier termination of reproduction in the shrew than in the rodents.

Table 6

Indices of the states of reproduction at three population phases

Species	Increase			Peak			Low			Difference, P		
	% classified	Classified		% classified	Classified		% classified	Classified		% classified	Classified	
		% pre-gnant	% lac-tating		% pre-gnant	% lac-tating		% pre-gnant	% lac-tating		% pre-gnant	% lac-tating
<i>S. araneus</i>	96	36	77	71	37	74	91	33	77	<0.01	NS	NS
<i>C. rutilus</i>	82	78	41	66	90	17	52	83	26	<0.001	NS	<0.05
<i>C. glareolus</i>	44	92	8	36	100	0	100	100	0	NS	—	—
<i>C. rufocanus</i>	61	74	35	55	71	37	66	89	42	NS	NS	NS
<i>M. agrestis</i>	100	80	38	80	64	52	95	78	22	<0.001	NS	NS
<i>M. oeconomus</i>	67	75	32	24	100	0	60	100	0	<0.01	—	—

Table 7

Adult and postreproductive females without embryos classified according to series of placental scars

Species	Increase				Peak				Low				Difference, P
	series			Σ fe- males	series			Σ fe- males	series			Σ fe- males	
	0	1	2		0	1	2		0	1	2		
<i>C. rutilus</i>	0	23	1	24	7	23	2	32	0	25	1	26	NS
<i>C. glareolus</i>	6	9	1	16	16	21	2	39	0	0	0	0	NS
<i>C. rufocanus</i>	3	65	22	90	0	63	74	137	0	7	5	12	<0.001

Table 8

Litter sizes (including resorbed but still recognizable embryos) at various population phases

Species	Litter Sizes											
	Increase				Peak				Low			
	Σ litters	Range	\bar{x}	SD	Σ litters	Range	\bar{x}	SD	Σ litters	Range	\bar{x}	SD
<i>S. araneus</i>	7	3—9	6.6	2.4	10	4—10	6.9	1.7	10	3—10	7.3	2.0
<i>C. rutilus</i>	50	2—13	6.5	1.9	39	3—10	6.8	1.5	17	4—9	7.1	1.6
<i>C. glareolus</i>	11	4—7	5.3	0.8	16	2—7	4.8	1.1	4	4—7	5.5	1.3
<i>C. rufocanus</i>	68	1—8	5.4	1.2	76	1—8	5.1	1.3	10	2—8	5.3	1.7
<i>M. agrestis</i>	38	3—9	5.8	1.4	27	3—9	5.6	1.5	13	3—10	6.7	2.0
<i>M. oeconomus</i>	18	2—10	6.5	2.1	4	6—8	7.0	1.2	3	6—9	7.3	1.5

Placental scars could be easily detected and counted only in the *Clethrionomys* species. At most two series of scars were identified. As the first of the two series was easily visible, there had probably not been more than two litters in the females examined before the sampling in July–August. Postreproductive and adult females without embryos were grouped into those with 0, 1 and 2 series. Females with embryos were excluded as the presence of embryos makes the detection of scars difficult or impossible.

Table 9
Weight (g) variations as due to population phases

Population category	Species	Body weight						Low		Difference, P		
		Increase			Peak			Σ specimens	\bar{x}	SD	Distribution	Mean
		Σ specimens	\bar{x}	SD	Σ specimens	\bar{x}	SD					
Adult males	<i>S. araneus</i>	33	10.3	1.2	70	10.9	1.3	39	10.4	1.4	<0.01	<0.05
	<i>C. rutilus</i>	65	23.7	4.2	67	24.9	4.1	46	21.4	3.6	<0.05	<0.01
	<i>C. glareolus</i>	15	21.4	3.6	24	22.3	2.7	8	19.8	2.0	NS	NS
	<i>C. rufocanus</i>	65	33.0	7.0	46	37.3	7.4	18	28.0	7.3	<0.05	<0.01
	<i>M. agrestis</i>	15	35.1	9.7	19	38.6	12.0	0	—	—	NS	NS
	<i>M. oeconomus</i>	14	41.7	14.6	5	50.7	6.4	0	—	—	—	NS
Subadults	<i>S. araneus</i>	325	6.8	0.8	1271	7.1	1.2	537	6.6	1.3	<0.001	<0.001
	<i>C. rutilus</i>	141	17.1	2.4	192	16.2	2.1	14	17.7	2.7	<0.01	<0.01
	<i>C. glareolus</i>	71	16.7	2.4	206	15.3	2.6	2	13.5	2.1	<0.001	<0.001
	<i>C. rufocanus</i>	66	21.3	3.6	165	22.6	4.0	2	18.3	1.9	NS	NS
	<i>M. agrestis</i>	10	22.9	4.1	70	22.2	3.6	3	18.6	2.5	NS	NS
	<i>M. oeconomus</i>	28	24.5	4.8	86	24.5	3.0	8	23.9	1.8	NS	NS

There were great differences between the three species (Tab. 7). Almost all *C. rutilus* had just one series of placental scars. In *C. glareolus* 40% of the non-pregnant but adult females showed no scars at all and there was no difference between increase and peak phase. In *C. rufocanus* a large proportion of the females had two series of scars but this proportion was significantly higher during peak than at increase.

Litter size was examined in females with easily visible embryos (length ≥ 3 mm). Differences were found in neither distribution of numbers (χ^2 analysis) nor the litter means (as examined by one-way analysis of variance) between the various population phases (Tab. 8). In almost all species (with the possible exception of *C. rufocanus*) there was a slightly higher mean number at low densities.

Resorption of embryos (i. e. with some embryo considerably smaller or less differentiated than the rest in a litter) were very rare. For all years only 18 such cases were found in all rodents (less than 1% of the total number of 2307 embryos), while no single clear case of resorption was found in *S. araneus* (188 embryos). 11 out of the rodent resorptions were found in increasing populations but this does not significantly deviate from the total distribution of embryos in the various population phases.

Weight structure

The weight was examined for adult males and subadults (males and females being pooled) during the three population phases. In these two categories there are no rapid changes in weight due to reproduction or growth as there are in pregnant females, juveniles and postreproductive animals. Significance levels were very similar in the analysis of both weight distribution (χ^2 -analysis) and means (one-way analysis of variance) and no clear deviation from normality was apparent.

For the adult males (Tab. 9) significant differences were found in *S. araneus*, *C. rutilus* and *C. rufocanus*. However, in all species the highest weights were found during peak years. In at least all the *Clethrionomys* species the weights were much lower during the lowest densities than in increase and peak densities.

In the subadults significant differences were found in *S. araneus*, *C. rutilus* and *C. glareolus*. The variations were not as clear as in adult males but in all species except *C. rutilus* the weights were lowest at bottom densities. However, in this phase few were caught except in *S. araneus*.

Discussion

Mainly the delimitation of population phases and changes in trappability may introduce weakness in following analysis. The "low populations" may include both decreasing populations and the very early start of increase and thus contain animals with different demographic characteristics. Due to the low numbers caught during the population lows a separation was impossible between late decrease and early increase. However, the main considerations have concerned the difference between the peak and the two other population phases and peak densities were easily discernable. Several studies (e. g. MYLLYMÄKI 1970 b; HANSSON 1971) have shown differences in trappability between functional categories but still there is no clear evidence of trappability changes within a functional category due to density or population structures. Shrew trappability may be affected by the presence of a large number of rodents. This was one reason why the analysis of the shrew fluctuations was restricted to the large shrew populations in the western part of the area studied.

There were very pronounced fluctuations in northernmost Fennoscandia but they did not deviate quantitatively from those in alpine and taiga areas in middle Scandinavia (e. g. HANSSON 1969; MYLLYMÄKI 1970 b). However, they were completely different from the small density variations found in southernmost Scandinavia (e. g. HANSSON 1971, 1974 b; JENSEN 1975). It seems as if pronounced population fluctuations of similar kind appear over the vast areas of Scandinavia that are characterized by long periods of continuous snow cover. However, in at least some maritime islands in northern Norway the rodent fluctuations were small and very similar to the south scandinavian ones. These islands have a somewhat shorter period of snow cover than the mainland. The rodents obtained in these birch forests were *M. agrestis* and *C. rutilus*, i. e. one herbivorous species which is usually not very common in forests and one granivorous species, which may not be expected to be extremely numerous. However, the fluctuations of *C. rutilus* were much smoother there than in corresponding habitats on the mainland.

HAGEN (1956) suggested that there was a delay for one or two years towards northeast in peak rodent occurrence in Norway. This southwestern — northeastern „movement“ of peaks was analyzed by MYRBERGET (1973) from reports on "mice" occurrence by local game boards. He found such a delay in the cycle 1961–1964,

while conditions were less clear during the periods 1965–1967 or 1968–1971. In the present study there was a one year delay in 1968–1971 between the islands in northwestern Norway and the Fennoscandian mainland, including northeastern Norway. MYRBERGET (1973) mentioned also several examples of peak occurrences in lowland areas one year before neighbouring alpine areas. Generally there was good agreement between the fluctuations found in the present study and in that by MYRBERGET (1973). However, for examining regional displacements of cycles all Fennoscandia should be sampled. Such a study during 1971–75 (MYLLYMÄKI et al. 1977) gave also evidence for a north- or northeastern delay in the attainment of peaks.

Another new finding in this study was the extremely high number of shrews and their fluctuations in northwestern Norway. The traps used were favoured by shrews but there was a clear difference in relative shrew catches in the western and eastern part of the study area. Furthermore, in similar studies in alpine and taiga areas in Swedish Lapland (HANSSON 1969) and in South Swedish forest habitats (HANSSON 1967 b) no similar numbers of shrews were caught in these traps. The areas with the highest *S. araneus* densities (Lofoten and Vesterålen islands and the coastal Norwegian mainland) were characterized by intense grazing by sheep and cattle (in a few places goats). Lumbricides aggregate in sheep dung (SVENDSEN 1957) and an analysis of the contents from 90 stomachs of *S. araneus* from Vesterålen revealed that 73.9 % contained lumbricides (HEIKURA, pers. commun.). Thus the forest grazing may be beneficial for shrews. Food conditions were also suggested by HANSSON (1974 b) to determine shrew numbers in reforestation areas with rotting slash in southern Sweden, where also large shrew populations were found. The forest grazing appeared also at the western Atlantic shores so it obviously did not affect the rodent densities or a possible competition between rodents and shrews.

The differences in population structures between various phases of rodent abundance agreed in many cases well with the compilations of world-wide data in KREBS and MYERS (1974). It has thus been found earlier that litter size is a rather constant factor in the population dynamics and that resorption of single embryos has very small or no effect on population growth. The similar recruitment in various population phases indicates that variations in mortality outside the breeding season was a more important factor for population development than changes in juvenile mortality. However, the recruitment was possibly different in spring. The most pronounced and consistent change during the population cycle was the high number of subadults at peak densities. Also the high number of unclassified adult rodent females (probably just entering postreproductive state) at peaks was indicative of a decline in the conditions of individual animals. There was thus a clearly lower quality in the rodent populations at their highest numbers but it is not clear whether this quality change was brought about by nutritional deficiencies, social-endocrinal stress (FRANK 1953; CHRISTIAN and DAVIS 1964) or genetical changes (CHITTY 1970). The weights of adult males was highest at population peak but this may well be due to the population growing old (cf. ZEJDA 1964). Low weight of subadults at low densities may also be due to low age of the subadult animals, i. e. subadults appearing only late in summer.

The commonly occurring variations or deviations in sex ratio seem related to population development. However, according to the survey by KREBS and MYERS (1974) the sex ratio has not been found to vary in any *Microtus* or *Clethrionomys* species during cycle phases. In an early study by REICHSTEIN (1956) such a biased sex ratio was found, however. A general late-summer surplus of adult females, as here in *C. rufocanus*, *M. agrestis* and *M. oeconomus*, was earlier also found in *M. agrestis* from temperate areas (MYLLYMÄKI 1975). The latter study showed a continuous in-

crease in the proportion of adult females during summer. In this study such a female surplus appeared at all phases. In *C. rufocanus*, however, female surplus was only found in increase and peak populations as also observed by KALELA (1971). In these two species there was at the same time a surplus of males in the subadult component, demonstrating different maturing rates in females and males. The male surplus of subadult *C. glareolus* in peak populations and following adult male surplus in late summer low populations is interesting in the context of the cycle as HANSSON (1969) found a male surplus of *C. glareolus* juveniles from low or increase years and also an adult male surplus in the spring of the peak year. A similar two-year-change appeared in this study in *C. rutilus* and *S. araneus*.

There might be some compensation in various demographic variables. *C. glareolus*, obtained at the northern limit of its geographical distribution, showed low litter size and few litters. Both *C. rutilus* and *C. rufocanus* are common species in northernmost Fennoscandia but they differed in their reproductive traits. *C. rutilus* showed high litter size but few litters while *C. rufocanus* had a low litter size but relatively more litters. However, the true numbers of litters is unknown, and is affected by the proportion of overwintered and springborn adult females and the possibly different mortality of these two groups.

The dynamics of *S. araneus* agreed in several demographic and reproductive aspects with those of the rodents. However, it was not possible to establish any quality changes, as the young shrews never mature during the year of birth and as females were never found in a postreproductive state. The structural changes in the shrew populations are thus provisionally explicable solely in terms of variations in age- and sex-dependent mortality affecting age structure, reproductive output and weight distributions.

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Zusammenfassung

Populationsschwankungen bei Insektenfressern und kleinen Nagetieren im nördlichsten Fennoscandien

In den Jahren 1965—1970 wurden im nördlichsten Fennoscandien von den Lofoten im Westen bis zur norwegisch-russischen Grenze im Osten rund 9000 Kleinsäuger gesammelt. Über die Hälfte der Ausbeute bestand aus Spitzmäusen, vorwiegend *Sorex araneus*. Gefangen wurde in der Taiga, in subalpinen Wäldern, auf Mooren, Wiesen, in alpinen Gebieten und in der Tundra. Die Kleinsäugerpopulationen zeichnen sich durch erhebliche Dichteschwankungen aus mit Höchstwerten in den Jahren 1966 und 1969/70. Besonders großen Schwankungen unterlagen die Waldspitzmäuse (*S. araneus*) im nordwestlichen Norwegen. Vergleichsweise stabil waren die Populationen von Rötelmäusen (*Clethrionomys rutilus*) und Erdmäusen (*M. agrestis*) auf einigen maritimen Inseln. Auf dem fennoscandischen Festland dagegen wiesen Rötelmaus und Erdmaus große Dichteschwankungen auf. Bei Arten mit auffallenden Änderungen der Populationsdichte wurden drei Entwicklungsphasen unterschieden: Niedrige Dichte, zunehmende Dichte, hohe Dichte. In Abhängigkeit davon änderten sich die Populationsstruktur, das Geschlechterverhältnis und die Gewichtsverteilung; Fortpflanzungsparameter waren weniger betroffen, lediglich der Anteil geschlechtsreifer Tiere nahm bei hoher Dichte bei Nagetieren, nicht dagegen bei Spitzmäusen, ab.

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Trap mortality in *Microtus agrestis* (L.)

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A certain amount of trap mortality seems to be an inevitable by-product of any small mammal live-trapping programme, even when adequate food, bedding and shelter are available to the captured animals. If the cause of death is readily identifiable, steps can often be taken to reduce the mortality. For example, if wet bedding appears to be responsible (CORKE 1967), traps can be provided with waterproof and insulating covers (SHAW and MILNER 1967). In a recent study of trap mortality, PERRIN (1975) concluded that no single factor was responsible, but that environmental variables including extremes of temperature, rainfall and insolation were particularly important. In many respects, it is the remaining unexplained mortality which is of the greatest interest, because it may provide a clue to the physiological condition of the animals in the population under investigation. For example, PLATT (1968) has suggested that trap mortality tends to be high when populations are undergoing declines and that the number of trap deaths may, therefore, provide an indication of population "stress". The present study was carried out only a few

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