

Gradients in density variations of small rodents: the importance of latitude and snow cover

Lennart Hansson¹ and Heikki Henttonen²

¹ Department of Wildlife Ecology, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden

² Department of Zoology and Kilpisjärvi Biological Station, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland

Summary. Microtine rodents are known to show extreme population variations (cycles) but non-cyclic populations have also been recognized during recent years. The cyclic populations have been widely thought to be regulated by intrinsic mechanisms. However, such predictions for cyclic populations are usually not applicable to non-cyclic ones and extrinsic factors may have to be included in any explanation.

A hypothesis that the degree of fluctuations in small rodent numbers is related to the sustainable number of generalist predators was tested on mainly literature data by computing “indices of cyclicality” for local populations. These indices were related to latitude and snow cover (two measures) as these variables will affect the amount of alternative prey available for these generalists. Within Fennoscandia such indices for *Clethrionomys glareolus* and *Microtus agrestis* were clearly positively related to latitude and snow cover. The fraction of populations with summer declines in numbers, characterizing highly cyclic populations, increased in the same way. Cyclicality indices in Great Britain were similar to those in southern Fennoscandia, both areas being poor in snow, but were higher at the same latitudes in eastern Europe with more snow. Indices of density variations were generally low in North American *Clethrionomys* species and very variable in *Microtus* species.

The gradients observed and differences between continents are interpreted as due to microtine-vegetation interactions in northern European areas poor in generalist predators but with important small mustelid predation, and to similar snowshoe hare-vegetation interactions in mainly Canada-Alaska, where small rodents may serve as alternative prey for numerically fluctuating hare predators, at least in the forests. Western European microtine populations, and probably many others, seem to be regulated by generalist predators.

However, it has recently been realized that many small rodent populations show less violent dynamics and only fluctuate seasonally in abundance (Hansson 1971; Fuller 1977; Mihok and Fuller 1982; Krebs 1979; Bashenina 1981; Jensen 1982; Taitt and Krebs 1985). Such populations have been termed non-cyclic to denote that they still may exhibit erratic density variations.

Hansson (1971, 1979a) and Erlinge et al. (1983) argue that non-cyclic vole populations in southern Scandinavia are kept at low density and only fluctuate seasonally in numbers because of a strong functional response by generalist predators. Such predators, however, will only be effective in regions with a sustaining amount of alternative prey. The numbers and total density of alternative prey species generally decreases northwards (Simpson 1964). Density compensation in the sense of Case (1975) is hardly applicable as resources generally diminish northwards and there is no evidence of such a compensation. Generalist predators should thus be least effective in regulating microtine populations in northern Fennoscandia (for long-term data on “typical microtine cycles” in northern Fennoscandia; see Taitt and Kalela 1971; Lahti et al. 1976; Henttonen et al. 1977; Hansson 1979a; Hansson et al. 1978; Laine and Henttonen 1983). Furthermore, increased snow cover is assumed to make the hunting of generalist predator species less effective in northern than in southern Fennoscandia. There are few studies of predation in relation to snow cover but e.g. great grey shrikes (*Lanius excubitor*) change from small mammals to birds as prey with increasing snow depth (Olsson 1984). Thus the buffering effect by generalist predators is predicted to decrease northwards and small rodent populations will increase towards food-limitation; in this area the role of specialist predators will increase at least at population declines (Hansson 1979a; Laine and Henttonen 1983).

Here we examine this hypothesis further by examining variation in microtine population density in several geographic regions. We will concentrate on the following questions critical for the hypothesis:

1) How does the amplitude of population fluctuations increase with latitude in Fennoscandia?

2) Will variation in rodent numbers be better related to snow conditions than to latitude?

3) Will density variations in western Europe be similar to those in southern Scandinavia where the amount of snow is similar? Will density variation in eastern Europe (incl. European parts of the U.S.S.R.) be greater than at the same

1. Introduction

Small rodents frequently fluctuate in numbers and often these fluctuations are termed “cyclic” (Krebs and Myers 1974). Cyclic fluctuations, however, seldom or never show very regular amplitudes and frequencies but are characterized by a gradual increase to peak numbers and sometimes a sudden drop to very low numbers which prevail for an extended period. There are often 3–5 years between succes-

latitudes in southern Scandinavia, which would be consistent with the idea that snow makes the hunting of generalist predators less effective?

4) Will density variation in North America increase northwards and will density variations be greater in North America than those at the same latitudes in Fennoscandia where the Gulf Stream ameliorates the climate?

5) An important question would also be whether there is any threshold length of time and/or depth of snow cover related to cyclicity? We cannot, however, study this in detail because of the unpredictability of environmental conditions in the appropriate regions.

We will make our comparisons on two common and widespread European microtine species, viz. the bank vole *Clethrionomys glareolus* and the field vole *Microtus agrestis*. They are distributed from northern Fennoscandia to western and eastern Europe. They do not occur in North America but may be compared there with their taxonomical and ecological equivalents (cf. Merritt 1981; Klimkiewicz 1970) *Clethrionomys gapperi* and *Microtus pennsylvanicus*. We also compare the dynamics of two other small rodent species which occur in both northernmost Europe and northernmost North America, viz. *Clethrionomys rutilus* and *Microtus oeconomus*.

2. Methods

We have examined all known (to us until summer 1983) Fennoscandian trapping series covering four years or more. One reason for this lower limit is that population cycles in northern Scandinavia usually extend over four years between a population low and a subsequent peak-decline. A shorter number of years will cause great random effects in indices of cyclicity for these northern areas (cf. Henttonen et al. 1985) while three years may be enough in southern Fennoscandia and central Europe. Index trapping methods (with the index usually expressed as number caught per 100 trap nights) and density estimations have both been included. However, in density estimations only numbers actually caught have been used for our computations.

Fennoscandian island data were excluded from our analysis because the dynamics of insular rodent populations differ from those of mainland populations (e.g. Tamarin 1978; Pokki 1982). We have not made any use of sign indices (e.g. grazing frequencies) or questionnaires on vole abundance as valid, quantitative population estimates cannot be computed from such data.

We have mainly used series from outside Europe that have been published in major ecological journals. Longer series that contain discontinuities have been treated as two or more series because trapping methods or density levels may vary between subseries (e.g. Southern and Lowe 1982).

If there were continuous data in the same trapping series from two or more intermingled habitats only the data from the habitat with the highest densities were used because densities in suboptimal habitats are influenced by immigration from the optimal ones.

If there are several censuses a year we have used data from August–October as either representing annual peak numbers or showing the lowest numbers in bottom years of typically cyclic populations. This is further justified by the results of Henttonen et al. (1985) who found that cyclicity indices based on autumn densities differentiated best

between cyclic and non-cyclic populations. However, in several studies only one sample has been taken each year. Such data were accepted only if repeated sampling was performed at the same time in summer-autumn.

The index

$$s = \sqrt{\frac{\sum (\log N_i - \overline{\log N_i})^2}{n-1}}$$

where N_i is density or a quantitative density index at the same time of the year, has been suggested as an index of density variation ("cyclicity index") that is independent of sampling method and mean density level (Lewontin 1966; Williamson 1972; Stenseth and Framstad 1980). This index was demonstrated to correlate positively with the periodicity in a large set of field data (Henttonen et al. 1985). In certain trapping series some index values equalled 0 during low years and had to be replaced by a small positive number. We used the lowest figures in the trapping series, usually 0.1 or 0.5 animals/100 trap nights. According to our experience these values are of the right order of magnitude. In addition, we also computed the coefficient of variation ($CV = SD/\bar{x}$), although this index is more affected by trapping methods. Furthermore, because we feel that really cyclic microtine populations are characterized by summer declines during low years and because such declines may not be easily detected at each low phase, we also estimated the fractions of the studies in various regions in Fennoscandia which contained any clear summer decline.

In our analysis we divide Fennoscandia in three climatic, and hence biogeographic regions: (1) A southern zone (55 to about 59°N) with a mild climate with little snow in winter. (2) A transition zone (59–61°N) that is characterized by winters of varying snow depth and duration. (3) A zone north of 61°N characterized by 5–8 months of snow each year (except at the Norwegian coast) and a typical taiga forest in the lowlands and alpine tundra on the mountains. Data on local snow conditions were obtained from Johnson (1956), Ager (1964) and Solantie (1975, 1977). Two measures of snow were used: a mean annual period with snow and a mean maximum snow depth.

Data from southern Fennoscandia were compared with data from Great Britain and eastern Europe. As Great Britain extends between 50°N and 59°N the area covered in eastern Europe was likewise located between 50°N and 59°N. All the Fennoscandian data are compiled in Appendix A (*C. glareolus*) and B (*M. agrestis*). Papers with information on density variations (during at least 3 years) in western and eastern Europe and North America are listed in Appendix C.

3. Results

3.1. Fennoscandia

All correlations between indices of density variations and latitude, snow cover and snow thickness were significantly positive, and of the same magnitude (Table 1). However, because latitude is strongly correlated with both the period of snow cover ($r=0.96$) and snow thickness ($r=0.82$), it is difficult to separate the effects of latitude (i.e. diversity and density of sustaining prey) and snow cover (i.e. predation efficiency) upon rodent population dynamics. Partial

Table 1. Correlation matrix (Spearman's r_s) between environmental variables predicted to influence vole population stability and two measures (s and CV , see text) of population cyclicality in various Fennoscandian regions. Significance levels are ** = $P < 0.01$ and *** = $P < 0.001$

Species	Environmental variables	Indices of cyclicality	
		s	CV
<i>Clethrionomys glareolus</i>	Latitude	0.62***	0.63***
	Snow period	0.64***	0.68***
	Maximum snow thickness	0.65***	0.70***
<i>Microtus agrestis</i>	Latitude	0.61***	0.67***
	Snow period	0.60***	0.64***
	Maximum snow thickness	0.57**	0.65***

Table 2. Mean values for the cyclicality indexes and distribution of summer declines observed in trapping series in various Fennoscandian regions

Species	Latitude	Mean cyclicality index		Summer decline	
		\bar{s}	\bar{CV}	No	Yes
<i>Clethrionomys glareolus</i>	< 59°N	0.22	0.44	6	1
	59–61°N	0.47	0.78	4	3
	> 61°N	0.52	0.92	4	13
<i>Microtus agrestis</i>	< 59°N	0.30	0.61	6	0
	59–61°N	0.53	0.97	2	6
	> 61°N	0.62	1.14	1	9

correlations become very low due to the high correlations between latitude and the two snow variables. They were highest between *C. glareolus* indices and snow thickness ($r_k = 0.41$) and between *M. agrestis* indices and latitude ($r_k = 0.32$). However, we can mainly state that the cyclicality increased with both latitude and snow cover.

The mean cyclicality values increased from the southern region over the transition zone to the northern region (Table 2). That the increase from the southern region to the transition zone was greater in both species than from the transition zone to the northern taiga implies that there may be a "cyclicality threshold" bordering the transition zone. This is also reflected in the proportion of summer declines (Table 2) in intense studies with both spring and autumn trappings. There were clear differences between the southern zone and the northern taiga zone for both *C. glareolus* ($P = 0.009$, Fisher's exact probability test) and *M. agrestis* ($P = 0.001$). The transition zone did not deviate significantly from either of the other zones, except from the southern zone for *M. agrestis* ($P = 0.009$). If the data from the transition zone are added either to those from the southern zone or the northern taiga zone, then the difference in relation to either the north or south remains significant for both species (P 's 0.01–0.02, except for *M. agrestis* when the transition zone is added to northern taiga; $P = 0.006$). These patterns imply that the transition zone is really intermediate, or may have more in common with the northern taiga zone than with the southern zone.

3.2. Western and eastern Europe

Southern Scandinavian *C. glareolus* did not show any significantly different pattern in density variation from British populations (Mann-Whitney U-test). Mean s and CV values for the southern Scandinavian populations ($N = 7$) were 0.22 and 0.44 and in Great Britain ($N = 10$) 0.28 and 0.51, respectively. However, the British populations were very heterogeneous and at least one showed a summer decline. Two German studies (Schmidt 1975; Stubbe 1982) showed $s = 0.29$ and 0.40 ($CV = 0.55$ and 0.76). Comparisons between southern Scandinavia and the same latitudes in eastern Europe (Poland and U.S.S.R. west of the Urals, $N = 28$) resulted in significant differences (Mann-Whitney $U = 51$ and 48.5 respectively, $P < 0.05$) for both s and CV with most pronounced density variation in eastern Europe (mean $s = 0.31$ and mean $CV = 0.65$). Separate calculations were performed with data from southern Scandinavia and the European part of the U.S.S.R. only with the thicker snow cover, but the differences and levels of significance remained the same.

Population data for *M. agrestis* were available only from western Europe. Five series from Great Britain did not differ from southern Scandinavia ($N = 8$). The mean values of s were 0.32 and 0.30 and of CV 0.64 and 0.61 for Great Britain and southern Scandinavia, respectively. The first study at Lake Vyrnwy (Chitty 1952) showed pronounced cyclicality ($s = 0.95$) and a summer decline while later studies (Chitty 1962) indicated only seasonal variations ($s = 0.16$ and 0.25). Thus, as with *C. glareolus*, some British *M. agrestis* populations exhibited pronounced density variations. Some German *M. agrestis* populations showed small density variations (Kulicke 1956, $s = 0.25$; Schindler 1972, $s = 0.35$).

3.3. North America

Four population of *C. gapperi* from the U.S.A. had mean s values of 0.38 and thirteen populations from Canada had 0.42 ($CV = 0.73$ and 0.92). There was no correlation with latitude. No 3–4 year cyclic pattern was observed (cf. also Merritt 1981) but in long term studies by Grant (1976) and Fuller (1977) series of high and low density years were separated by about 10 years. Krebs and Gilbert (1984) also found a 10-year interval between peaks in *C. rutilus*. Furthermore, according to available information (West 1982; Whitney and Feist 1984) *C. rutilus*, the northern equivalent of *C. gapperi*, is not 3–4 year cyclic in central Alaska near Fairbanks at those latitudes where both *C. glareolus* and *C. rutilus* are strongly 3–4 year cyclic in northern Fennoscandia. The s and CV values for *C. rutilus* in Alaska were 0.11 and 0.20, and 0.26 and 0.51 respectively (West 1982; Whitney and Feist 1984), which correspond to the low southern Scandinavian values for *C. glareolus*. At about the same latitudes in northern Finland and Sweden the s and CV values for *C. glareolus* were 0.56–0.89 and 0.80–2.05 respectively. Values for *C. rutilus* were there of the same order.

Most studies of American *Microtus* populations have been conducted south of 50°N (Taitt and Krebs 1985) and are thus not strictly comparable with the northern European ones. Taitt and Krebs (1985) divided the fluctuation patterns observed in North America into cyclic and annual ones. 48% of the years studied showed multiannual cyclic patterns in *M. pennsylvanicus* according to the definition

of cyclicity by these authors. In other *Microtus* species this proportion was even lower (e.g. *M. townsendii* Bachm.: 29%). A long-term study (11 years) of *M. pennsylvanicus* in southern Canada (Mihok 1985, 50°N) had $s=0.48$, which is similar to central Fennoscandian *M. agrestis*. A short-term study of *M. oeconomus* populations at Fairbanks, Alaska (Whitney 1976, 65°N) gave $s=0.75$ while longer studies (17 years) of the same species at Kilpisjärvi, Finnish Lapland (Tast and Kalela 1971; Henttonen et al. 1977; Fig. 2B) resulted in $s=0.82$ ($CV=1.31$ and 1.26 respectively). In this respect *M. oeconomus* in central Alaskan taiga resembles conspecifics in northern Fennoscandia. The amplitude (peak/low in cyclic populations) in the American studies was generally about tenfold (Taitt and Krebs 1985) while in northern Fennoscandia it has often been 100-fold or more.

4. Discussion

We find the clear Fennoscandian correlations with both latitude and snow cover convincing, although data used in the analysis were obtained by several different trapping methods. The CV index of cyclicity gave consistently better correlations than the s index, so the variability in the data acquisition did not seem to influence the results in any profound way. Correlations might have been still better but the northernmost records in Fennoscandia were from the margins of the distribution of *C. glareolus* and *M. agrestis* and there their abundance, and especially peak numbers, will be affected by interspecific competition from other small rodents (Henttonen and Hansson 1984). *M. agrestis*, for example, is forced into marginal habitats by *M. oeconomus* (Tast 1968; Henttonen et al. 1977) and consequently the northernmost cyclicity index for *M. agrestis* was fairly low. Environmental heterogeneity in the transition zone is another error. The snowy period is relatively short but variable, and snow cover is shallow along the shores of the Baltic, especially far into the mainland in SW Finland.

One explanation of the gradients in cyclicity in Fennoscandia could be differences in predator-prey relationships. The effective element in the hypothesis of population regulation by predation is a set of alternative prey species for generalist predators. These alternative prey may be sustained by various means, e.g., little snow, a considerable proportion of agricultural land (Angelstam et al. 1984) or diverse habitats (or landscape heterogeneity, Hansson 1977, 1979b). Most such conditions are negatively related to the severity of the environment. An alternative explanation of the trend in cyclicity in Fennoscandia can be based on the relations between rodents and variations in plant productivity and quality (e.g. Laine and Henttonen 1983). However, the present data do not permit us to separate between these hypotheses. Laine and Henttonen (1983) and Hansson (1984a) discuss reasons why the decline in northern Fennoscandia is probably triggered by changes in food resources. But if microtines in northern Fennoscandia followed only the rhythms of their food plant species, for example, which are in fairly good but not in total synchrony, more interspecific variation in the decline should be expected among sympatric microtine species due to specific feeding preferences. Instead, all sympatric microtine species (up to 8 species in a community) in northern Fennoscandia have the deepest low phase simultaneously (Hansson 1969; Tast and Kalela 1971; Henttonen et al. 1977; Hansson et al. 1978; Laine

and Henttonen 1983; Henttonen in prep.), a fact consistent with the role of specialist predators (small mustelids, cf. also Oksanen and Oksanen 1981; Hansson 1984b; Henttonen 1985). The cyclic synchrony of sympatric microtines decreases southwards, and in the transition zone sympatric *C. glareolus* and *M. agrestis* may or may not be in phase (Korpimäki 1981; Pankakoski 1984; Hansson in prep.). In any case, we discuss our data further without denying any effect of possible multiannual variation in plant production on microtine cycles.

Stable populations of microtines in southern Fennoscandia and central Europe appear to be controlled by generalist predators (Hansson 1979a; Erlinge et al. 1983), and during seasonal lows of voles these predators are supported by alternative prey. *C. glareolus* is generally adapted to mature forest habitats with a more complex fauna of predators and alternative prey, while *Microtus* spp. are colonists of disturbed areas and early successional plant communities with a less complex fauna. Southern *Microtus* populations may therefore be more likely to show cyclic behaviour than corresponding *Clethrionomys* populations. There were some clearly cyclic microtine populations also in western Europe. One example is the early *M. agrestis* population at Lake Vyrnwy which later seemed to change to a non-cyclic one (Chitty 1952; Chitty and Chitty 1962). This change followed an alteration in the landscape from a vast area with abandoned fields and conifer seedlings to diverse forest habitats interspersed with open fields. The predator and alternative prey community might have showed a pronounced development during this landscape transition. Other areas in central Europe with cyclic populations may be characterized by similar conditions, e.g. large agricultural areas in Poland harbouring cyclic *Microtus arvalis* populations (Ryszkowski et al. 1973).

There has been a long-lasting debate whether factors intrinsic (e.g. physiological stress or genetic behavioural polymorphism) or extrinsic (e.g. food and predation) to microtine populations cause the cyclicity (e.g. Krebs and Myers 1974). The clear relationship between the level of cyclicity and environmental conditions in Fennoscandia seems to demonstrate the overriding importance of extrinsic factors. Gradients in cyclicity can hardly be explained by any intrinsic factors. On the other hand, microtine populations, also at southern latitudes, have obviously the potential to become cyclic if environmental conditions (habitat structure, fauna, quality of seasonality) permit (Chitty 1952; Ryszkowski et al. 1973).

Non-cyclic (or "annual") population variations have been observed in several North American *Clethrionomys* and *Microtus* species. Merritt (1981) states that "there seem to be no 3–4 year oscillation in *C. gapperi*". This also appears to apply to *C. rutilus* in northern Canada and Alaska. No geographical trend in cyclicity has been observed in North American *Microtus* species (Taitt and Krebs 1985) but such a trend has been reported for snowshoe hares *Lepus americanus* (Wolff 1980). Thus, there seems to be a basic difference in microtine dynamics between Fennoscandia and North America.

One possible explanation is that in northern North America the small (forest) rodents are alternative prey for the predators driven by the pronounced snowshoe hare cycles. Then a 10-year periodicity should be expected in *Clethrionomys* in areas with snowshoe hare cycles, but only annual changes with stable hare or rabbit populations. If so,

more than one alternative mechanism could be possible. 1) Generalist predators might increase during the hare increase phase until the peak, but will suddenly lose the greatest part of their food basis during the first years of the hare decline. During these years there should be severe pressure on small rodents but the latter cannot be supposed to sustain these predators for any longer period. Thus, a few years after the start of the hare decline, predation pressure should have lessened considerably and the small rodents will be free to increase considerably in numbers. Specialist predators need a certain period of high small rodent numbers in order to reproduce and increase, and a rodent peak may appear before hares and generalist predators increase again. 2) Another alternative is that predation on abundant hares releases the pressure from forest microtines, but in this case *Clethrionomys* peaks should coincide with the hare peak and earliest decline, and *Clethrionomys* should decline with hares. 3) Yet another possibility is that predation by generalist predators on small specialist ones at the end of the hare decline will release a *Clethrionomys* increase, and specialist predators would recover after the decline of the generalists. In this case a *Clethrionomys* peak should also occur a few years after the hare peak.

Some data to test these ideas are available. High *Clethrionomys* numbers were found a few years after hare peaks by Fuller (1977 and pers. comm.) in Canadian NW Territories, and by Krebs and Gilbert (1984 and pers. comm.) in southern Yukon. Such conditions seem also evident in unpublished data supplied by Mihok (pers. comm.) from Manitoba. Grant (1976) concluded that peaks in the abundance of *C. gapperi* occurred at 10-year intervals in Quebec, as they do in the snowshoe hare. These data seem to refute the second alternative. The third alternative assumes considerably densities of specialist predators, but at least in some *Clethrionomys* study areas, pygmy weasels, for instance, are rare (Fuller pers. comm.; Krebs and Gilbert pers. comm.). So with the few data available we find the first alternative most plausible.

There is also another difference between Fennoscandian and North American vertebrate communities, which might stabilize small rodents dynamics in the latter area. Various species of hibernating ground squirrels and chipmunks not found in Fennoscandia could sustain predators that would otherwise prey on microtines in summer. Extreme summer declines of the north Fennoscandian type might be prevented this way.

We suggest that the driving force in the 3–5 year cycles in central and northern Fennoscandia is a microtine-food interaction (Kalela 1962; Hansson 1969, 1979a; Tast and Kalela 1971; Laine and Henttonen 1983). In northern Fennoscandia all predators preying on microtines decline after a microtine crash (Pulliainen 1981; Kaikusalo 1982) due to shortage of alternative food, and consequently predators exhibit a time lag in their response to the microtine increase. Also the pattern of game population dynamics, including

the mountain hare *Lepus timidus*, in central and northern Fennoscandia seems to be a 3–5 year cycle (Hörnfeldt 1978; Pulliainen 1982; Angelstam et al. 1984). Bulmer (1974, 1975) concluded statistically that the driving force in the North American 10-year furbearer cycle is the snowshoe hare, and several authors have suggested that this cycle is caused by an interaction between the hare and its food (Keith 1974, 1983; Keith et al. 1984; Bryant 1981) that is modified by predators (Keith 1974). In this comparison between northern North America and Fennoscandia some species are especially interesting. The muskrat *Ondatra zibethicus* in North America shows a 10-year pattern (Elton and Nicholson 1942; Bulmer 1974, 1975), but as an introduced species in Europe has, in northern Sweden, a 4-year rhythm which seems to be caused by predation by red foxes after microtine declines (Danell 1978). In spite of its preference for microtines the American marten in the boreal zone is in phase with the snowshoe hare (Bulmer 1975). The red fox is another generalist hunting both microtines and hares, and its cycle clearly follows that of hares (Bulmer 1975). In central and northern Fennoscandia the red fox and pine marten have 3–4 year cycles (Pulliainen 1981; Kaikusalo 1982; Angelstam et al. 1984).

In this context we would also draw attention to the differences in the quality and quantity of snow between northern North America, and central and northern Fennoscandia. Over large areas of boreal North America the winter climate is continental, resulting in a powder-like soft snow cover, which in many areas is not very thick. On the other hand, warm spells are common in the more maritime Fennoscandian winter; the thick snow cover is dense and often encrusted. These differences probably also influence the hunting success of generalist predators. Differences in the thickness of snow cover in North America are not, however, large enough to cause clear differences in the fluctuation pattern of *Clethrionomys*, since the few study areas with very thick snow cover (Weckwerth and Hawley 1962; Merritt 1978) have annual patterns similar to regions with less snow.

The increasing stability of microtine populations towards southern, more diverse, biotic communities fits well with the old paradigm, “diversity begets stability”, being forcefully contradicted during recent years (e.g. May 1973; Goodman 1975; Pimm 1982). However, in the present context a “sub-community” consisting of generalist predators and several abundant alternative prey species (obviously from different taxonomic and ecological groups, e.g. microtines, hares and squirrels) is considered to cause stability and no relationship is assumed to the total biotic community. An equally large sub-community of many specialist predators and one main prey species or species group (e.g. microtines) is predicted to cause instability. Thus, the quality and not the quantity of species constituting an interacting unit seems to be important for the numerical stability of separate species populations.

Appendix A

Cyclicality indexes of *Clethrionomys glareolus* in Fennoscandia

Reference	Locality	Years	<i>s</i>	<i>CV</i>	Summer decline
Hansson 1974	Björnstorp, S, 55.5°	1968–72	0.15	0.38	No
Hansson 1979a	Björnstorp, S, 55.5°	1971–75	0.49	0.58	Yes
Hansson 1979a	Stensoffa, S, 55.5°	1971–75	0.17	0.40	No
Hansson 1967	Lund, S, 55.5°	1963–66	0.11	0.24	No
Bergstedt 1965	Fågelsång, S, 55.5°	1958–64	0.29	0.59	No
Hansson 1971b	Kullaberg, S, 56.5°	1964–67	0.08	0.18	No
Jensen 1982	Rönde, DK, 56.5°	1969–77	0.26	0.68	No
Curry-Lindahl 1956	Huddinge, S, 59°	1945–55	0.51	0.74	?
Hansson 1979a	Grimso, S, 59.5°	1972–75	0.44	0.86	Yes
Wiger 1979	Kviteseid, N, 59.5°	1970–75	0.66	0.97	No
Pankakoski 1984	Ahtiala, SF, 60°	1975–80	0.34	0.61	?
Forsman and Ehrnsten unpubl.	Kirkkonummi, SF, 60°	1978–82	0.50	0.71	No
Christiansen 1983	South Norway, ~60°	1971–77	0.41	0.87	?
Hansson 1982	Uppsala, S, 60°	1971–81	0.52	0.83	?
Hansson 1980	Garpenberg, S, 60.5°	1976–79	0.64	0.95	Yes
Christiansen 1983	West Norway, ~61°	1971–77	0.33	0.65	?
Hansson 1979a	Ockelbo, S, 61°	1971–75	0.44	0.80	No
Kaikusalo unpubl.	Loppi, SF, 61°	1973–81	0.38	0.63	No
Lagerström unpubl.	Ylöjärvi, SF, 61.5°	1976–82	0.46	0.67	No
Lagerström unpubl.	Teisko, SF, 61.5°	1976–82	0.16	0.33	No
Lagerström and Häkkinen unpubl.	Lempöälä, SF, 61.5°	1973–82	0.29	0.48	No
Kaikusalo unpubl.	Luhanka, SF, 62°	1957–62	0.38	0.53	?
Kaikusalo unpubl.	Värtsilä, SF, 62°	1977–80	0.37	0.72	?
Ivanter 1975	Carelia, SU, 62°	1948–55	0.45	0.89	?
Ivanter 1975	Carelia, SU, 62°	1957–72	0.47	0.96	?
Ryssy et al. unpubl.	Seinäjäki-Veteli, SF, ~63°	1977–82	0.45	0.90	?
Ryssy et al. unpubl.	Ahtäri-Karstula, SF, 63°	1977–82	0.32	0.89	?
Henttonen unpubl.	Hankasalmi, SF, 62.5°	1979–82	0.50	0.82	Yes
Korpimäki 1981	Kautiavo, SF, 63°		0.31	0.67	
Hansson 1979a	Alanäs, S, 64°	1971–75	0.65	0.95	Yes
Larsson 1976 + Hansson unpubl.	Strömsund, S, 64°	1971–82	0.65	0.85	?
Hansson and Larsson 1978	Ringvattnet, S, 64°	1972–75	0.71	1.24	?
Hörnfeldt 1978, 1980	Umeå, S, 64°	1972–79	0.75	1.00	Yes
Henttonen et al. 1977	Sotkamo, SF, 64°	1966–75	0.51	0.98	Yes
Skarén 1972	Kuhmo, SF, 64°	1957–68	0.36	0.68	Yes
Hansson 1979a	Robertsfors, S, 64.5°	1971–75	0.73	1.27	Yes
Viro 1974	Paľjakkä, SF, 64.5°	1966–71	0.35	0.67	No
Christiansen 1983	North Norway, ~65°	1971–77	0.42	0.71	?
Viro 1974	Tupos, SF, 65°	1966–71	0.62	1.23	Yes
Viro 1974	Muhos, SF, 65°	1966–71	0.56	0.80	Yes
Gustafson 1983	Ammarnäs, S, 66°	1975–82	0.89	2.05	Yes
Hansson 1969	Ammarnäs, S, 66°	1964–68	0.51	1.37	?
Kaikusalo unpubl.	Kolari, SF, 67°	1976–80	0.53	0.85	Yes
Koshkina 1966, Semenov-Tjan-Sjankij 1970	Kola S coast, SU, 67.5°	(25)	0.85	1.22	?
Henttonen unpubl.	Pallasjärvi, SF, 68°	1970–82	0.85	1.12	Yes

Appendix B

Cyclicality indexes of *Microtus agrestis* in Fennoscandia

Reference	Locality	Years	<i>s</i>	<i>CV</i>	Summer decline
Hansson 1974	Björnstorp, S, 55.5°	1968–72	0.22	0.39	No
Hansson 1979a	Björnstorp, S, 55.5°	1972–75	0.32	1.00	No
Hansson unpubl.	Stensoffa, S, 55.5°	1971–80	0.18	0.39	No
Erlinge et al. 1983	Revinge, S, 55.5°	1974–77	0.49	0.77	No
Hansson 1971a	Sjötorp, S, 55.5°	1964–70	0.28	0.51	No
Nygren 1980 + Hansson unpubl.	Stensoffa, S, 55.5°	1975–78	0.24	0.63	?
Christensen 1978	Tipperne, DK, 56°	1972–75	0.32	0.66	?
Hansson 1971a	Kullaberg, S, 56.5°	1964–68	0.31	0.50	No
Curry-Lindahl 1956	Huddinge, S, 59°	1945–55	0.37	0.71	?

Appendix B (continued)

Reference	Locality	Years	<i>s</i>	<i>CV</i>	Summer decline
Hansson 1979a	Grimsö, S, 59.5°	1972–75	0.24	0.67	No
Myllymäki 1977	Ahtiala, SF, 60°	1968–71	0.61	0.90	No
Pankakoski 1984	Ahtiala, SF, 60°	1975–80	0.51	1.05	?
Forsman and Ehrnsten unpubl.	Kirkkonummi, SF, 60°	1978–82	0.65	1.13	Yes
Christiansen 1983	South Norway, ~60°	1971–77	0.46	1.00	?
Myllymäki 1977	Ingels, SF, 60°	1958–62	0.85	1.15	Yes
Hansson unpubl.	Uppsala, S, 60°	1973–80	0.56	0.97	Yes
Hansson 1980	Garpenberg, S, 60.5°	1976–79	0.75	1.04	Yes
Kaikusalo unpubl.	Hansjärvi, SF, 61°	1973–78	0.15	0.24	Yes
Christiansen 1983	West Norway, ~61°	1971–77	0.65	1.10	?
Hansson 1979a	Ockelbo, S, 61°	1971–75	0.56	1.67	Yes
Lagerström unpubl.	Teisko, SF, 61.5°	1977–82	0.19	0.52	No
Myllymäki 1977	Central Finland, ~62°	1969–76	0.54	1.10	Yes
Kaikusalo unpubl.	Luhanka, SF, 62°	1957–62	0.54	0.66	
Kaikusalo unpubl.	Värtsilä, SF, 62°	1977–80	0.41	0.88	?
Ivanter 1975	Carelia, SU, 62°	1948–72	0.64	1.30	?
Ryssy et al. unpubl.	Seinäjäki-Veteli, SF, ~63°	1977–82	0.48	0.88	?
Ryssy et al. unpubl.	Ahtäri-Karstula, SF, 63°	1977–82	0.72	0.98	
Hansson unpubl.	Alanäs, S, 64°	1971–80	0.52	0.81	Yes
Henttonen et al. 1977	Sotkamo, SF, 64°	1972–75	0.95	0.91	Yes
Nygren 1980	Umeå, S, 64°	1974–78	0.69	1.40	Yes
Hansson and Larsson 1978	Ringvattnet, S, 64°	1972–75	0.59	1.24	Yes
Larsson 1976	Strömsund, S, 64°	1972–75	0.83	1.46	?
Hansson 1979a	Robertfors, S, 64.5°	1971–75	0.63	1.15	Yes
Larsson and Hansson 1977	Robertfors, S, 64.5°	1972–75	0.57	1.18	Yes
Christiansen 1983	North Norway, ~65°	1971–77	0.65	1.13	?
Heikura and Lindgren 1979	Oulu, SF, 65°	1966–74	0.64	1.17	Yes
Hansson 1969	Ammarnäs, S, 66°	1964–68	0.71	1.64	?
Henttonen unpubl.	Pallasjärvi, SF, 68°	1970–82	0.94	1.66	?
Henttonen et al. 1977	Kilpijärvi, SF, 69°	1959–75	0.50	1.52	Yes

Appendix C

Literature data on small rodent fluctuation patterns outside Fennoscandia

Great Britain: Ashby 1966; Brown 1964; Chitty 1952; Chitty and Chitty 1962; Flowerdew and Gardner 1978; Jewell 1966; Montgomery 1979; Newson 1963; Smyth 1968; Southern and Lowe 1982; Tanton 1969.

East Europe (only *Clethrionomys glareolus*): Andrzejewski 1975; Bobek 1973; Grodzinski et al. 1970 and Ryszkowski 1971 for Poland and a compilation of many papers from U.S.S.R. in Bashenina (1981).

North America: Mainly literature cited by Merritt (1981) on *Clethrionomys gapperi* and by Taitt and Krebs (1983) on *Microtus* spp.

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