Journal of Animal Ecology (1990), **59**, 753–761

PERIODIC FLUCTUATIONS IN SMALL MAMMALS AT BODA, SWEDEN FROM 1961 TO 1988

BY VIDAR MARCSTRÖM, NILS HÖGLUND AND CHARLES J. KREBS

Department of Zoophysiology, Uppsala University, S-751 22 Uppsala, Sweden

SUMMARY

(1) From 1961 to 1988 small mammals were censused on four trap lines at the Boda Research Station in central Sweden. *Clethrionomys glareolus* was the dominant small mammal, comprising 85% of the total catch of 1955 small rodents.

(2) *Clethrionomys glareolus* fluctuated cyclically with peaks averaging 3·6 years apart over the 28 years of the study and an average amplitude of 55-fold. *Microtus agrestis* and *Apodemus flavicollis*, although much less common, showed cyclic fluctuations in close synchrony with *Clethrionomys glareolus*.

(3) *Sorex araneus* was much more common in the Boda area in the 1960s than it is today, but it also has fluctuated in synchrony with the *Clethrionomys* cycle.

(4) *Clethrionomys glareolus* showed the Chitty Effect of increased body weights of adults in the peak density years.

INTRODUCTION

Vole populations in central and northern Fennoscandia are believed to be cyclic with a 3–4 year period while those in southern Scandinavia are more nearly stable (Wildhagen 1953; Kalela 1957; Myrberget 1973; Hansson 1984; Hansson & Henttonen 1985, 1988; Stenseth 1985). There are few long-term data sets to substantiate these beliefs (Anderson 1989) and it is important to provide a good description of cyclic changes in populations and to investigate their variability. In this paper we analyse snap-trap data covering 28 years from the Boda Research Station in central Sweden in an attempt to answer four questions: (i) Which small mammal species are cyclic in spruce forests in central Sweden? (ii) How synchronous are the fluctuations in the different species of voles, mice and shrews? (iii) Do cyclic declines occur primarily in summer or in winter? (iv) Do cyclic populations show the Chitty Effect of body weight changing with population size?

METHODS

Four trap lines were established in 1961 within 300 m of the Research Station at Boda, Sweden (61°32′N, 16°52′E). Each line was about 100 m long and was set with twenty-five snap-traps spaced at 4-m intervals. Lines were 200 m or more apart. Each line was trapped for 7 days in early July and 7 more days in mid- to late-August 1961–67; after 1967 the trapping sessions were moved to May and August to obtain a better fix on spring densities. Snap traps were baited with a mixture of dried apple, olive oil, and flour, and were checked once per day. Thus, 700 trap-nights were sampled twice during the growing season of each year. All individuals captured were identified to species and body weights were measured.

TABLE 1. Habitat description of trap lines at the Boda Research Station in 1987

	Line 1	Line 2	Line 3	Line 4
Logging waste % cover	50	20–50	0	0
Forest stand	Thicket stage	Thicket stage	Mature forest	Mature forest
Forest height (m)	1·3–3	1·3–3	27	26
Forest age (y)	10–15	10–15	*c.* 120	*c.* 120
Diversity	High	Moderate	Little	Little
Vegetation	Low herb without dwarf shrubs	Tall herb without dwarf shrubs	Tall herb without dwarf shrubs	Low herb with *Vaccinium myrtillus*
Tree layer	No trees	No trees	75% spruce 10% birch 10% aspen	90% spruce 5% birch 5% pine
Summer cover (%)	60–70 tall herbs	80–90 tall herbs	0–10 poor cover	10–20 few herbs
Field layer dominants (% cover)				
Deschampsia flexuosa	50–60	50–60	0	0
Herbs	10–20	20–30	50–60	10–20
Tall ferns	0	0	10–20	0–10
Vaccinium myrtillus	20–30	0–10	0–10	20–30

RESULTS

Vegetation

All four trap lines occur on fertile sedimentary soils. The general area is dominated by a 120-year old spruce (*Picea abies* (L.) Karst.) forest and at the start of the study all four areas were quite similar. In 1973 the spruce forest was logged on lines 1 and 2, and thus the vegetation of these two lines has changed dramatically during the study. After logging, however, the distance to unlogged forest was only a few meters for lines 1 and 2. These areas were replanted in 1976 and trees were thinned in 1986. Table 1 summarizes the current vegetation of all four lines. The major difference since 1973 is that the field layer is much more strongly developed, particularly in the grasses, on lines 1 and 2, and there is little grass on lines 3 and 4.

Population changes

Four species of small rodents were captured at Boda over the period 1961–88. Of the 1955 voles and mice captured by snap trapping, 85·5% were *Clethrionomys glareolus* Schreb. Of the remaining rodents, 7·7% were *Apodemus flavicollis* Melch., 6·7% were *Microtus agrestis* L., and 0·1% were *Myopus schisticolor* Lillj (two individuals). In addition to these rodents, 869 *Sorex araneus* L. were captured in snap-traps during the study.

Population indices for *Clethrionomys glareolus* and *Microtus agrestis* are shown in Fig. 1 for 1961–88. Peak densities of *Clethrionomys glareolus* (in the range of 10–20 animals per 100 trap-nights) occurred in the following years: 1962, 1966, 1969, 1973, 1977, 1980, 1983–84 and 1987, for an average cycle length of 3·6 years with a range of 3–4 years. The amplitude of the *Clethrionomys* cycle is difficult to estimate. If we assume that these trap catches are proportional to true density, them the amplitude of these cycles averages 55-fold with a large variation from 4-fold to 172-fold. These amplitude estimates are critically dependent on the estimation of the 'low' of the cycle. The index of cyclicity (s) of Stenseth & Flamstad (1980) and Hentonnen & Hansson (1985):

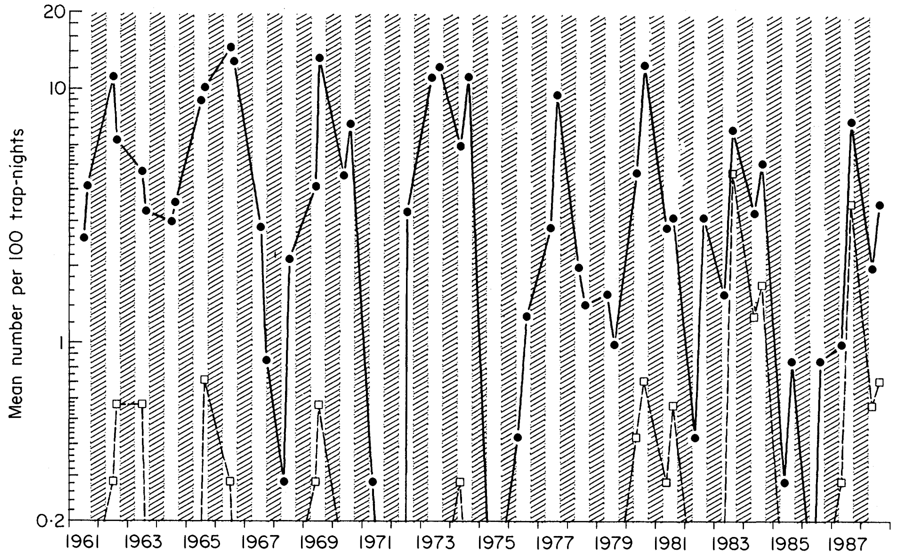

FIG. 1. Population changes in *Clethrionomys glareolus* (●) and *Microtus agrestis* (□) at the Boda Research Station, 1961–88. Winter seasons are shaded.

$$s = \sqrt{\frac{\Sigma(\log_{10}N_i - \log_{10}N_i)^2}{n-1}}$$

is 0·64 for early summer densities and 0·67 for late summer densities of *Clethrionomys glareolus*. The coefficient of variation of density for *Clethrionomys glareolus* is 1·10 for early summer and 0·85 for late summer densities. The index of cyclicity for *Microtus agrestis* is 0·46 for late summer densities, and is 0·39 for *Apodemus flavicollis* in late summer. *Sorex araneus* showed an index of cyclicity of 0·62 for late summer densities but this is confounded by a general declining density trend in this species.

Population trends in the summer after the peak year were not predictable in *Clethrionomys glareolus* at Boda. In 5 of 8 post-peak years, populations increased during the summer of the decline phase, and in 3 of 8 post-peak years populations continued declining throughout the summer period. Cyclic declines are thus highly variable in *Clethrionomys glareolus* at Boda. Catastrophic 'crash' declines can occur, as in 1970–71 and 1974–75, but other declines are much less severe (e.g. 1963, 1978).

Microtus agrestis were not common on the trapping area until 1983, by which time a dense growth of grasses had invaded lines 1 and 2. *Microtus agrestis* reached peak densities in 1983–84 and in 1987 in exact synchrony with *Clethrionomys glareolus*. Before 1983 Fig. 1 shows that the few *Microtus* captured tended to cluster in the peak years of *Clethrionomys*.

Population indices for *Sorex* araneus and *Apodemus flavicollis* are shown in Fig. 2 for 1961–88. Shrew numbers appear to have declined from high densities in the early years of the study (1961–66) to lower numbers after 1966. High densities of *Sorex araneus* occurred in 1961–62, 1965–66, 1968, 1973, 1977, 1980 and 1987. These 'peaks' are less well defined than those for *Clethrionomys glareolus*, but nevertheless there is substantial synchrony between these species in the patterns of population trends. Shrew numbers during the early years of this study are exceptionally high.

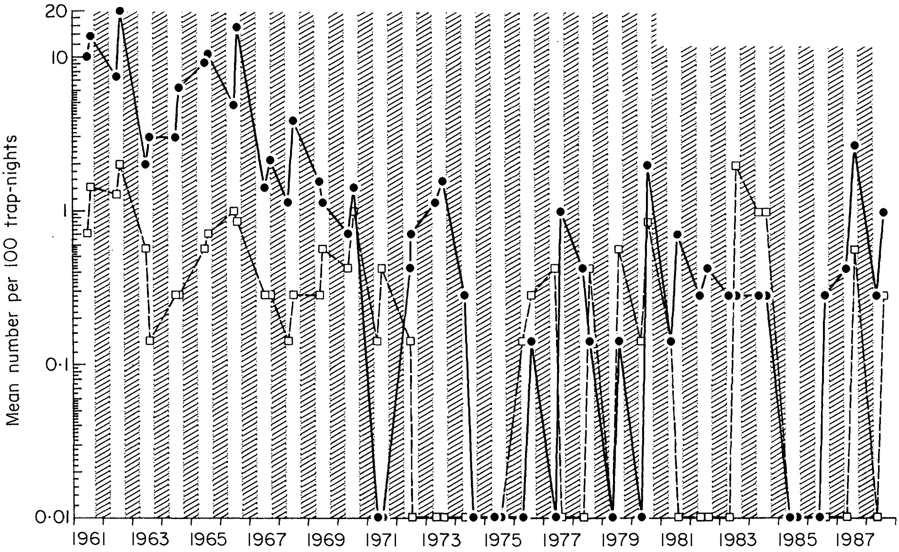

FIG. 2. Population changes in *Apodemus flavicollis* (□) and *Sorex araneus* (●) at the Boda Research Station, 1961–88. Winter seasons are shaded.

Apodemus flavicollis was never very common on the study area (Fig. 2) but occurred in small numbers in almost all years with the exception of the early 1970s. To determine whether there is a significant correlation with other small mammals in this community, we did a time series analysis of the log-transformed catches for each season, and analysed for cross-correlations between the time series plotted in Figs 1 and 2.

Table 2 gives the cross-correlations between each of the time series shown in Figs 1 and 2. Each species is significantly positively correlated with the abundance of *Clethrionomys glareolus* with zero time lag over the 28 years of data. Virtually none of the other lag correlations were significant until the lag period reached 3–4 years, at which time there was again a significant positive correlation between the time series. This time-series analysis backs up the graphical analysis given above in showing that all these small mammals are fluctuating cyclically in phase with a 3–4 year periodicity at Boda.

We investigated the relative variability of the catches of voles at Boda by plotting the variance against the mean catch for the four trap lines, and then fitting Taylor's power law to the resulting regression (Fig. 3). There is much scatter in the regression so that only 55% of the variation is accounted for by the regression line. The slope of the functional regression is 1·37 (±0·13, S.E.), slightly but significantly above 1. There is no indication that the pre-1973 (logging) data are less heterogeneous than the post-1973 data. Over a large range of densities, the variance of the catch is nearly equal to the mean, which suggests only random variation in catch among the four trap lines, rather than large-scale patchiness. This is probably a reflection of the scale of movements of these small mammals, so that the trap lines are fine-grained with respect to the small mammals.

Body size

Body weights were analysed only for *Clethrionomys glareolus* from these populations. A crude separation of young-of-the-year (juveniles) from adults (overwintered) was made at 19 g. We can use the mean body weights of *Clethrionomys glareolus* adults to determine

TABLE 2. Cross-correlations between time series of small mammal catches at Boda Research Station, 1961–88. All the species were cross-correlated with *Clethrionomys glareolus*, the dominant rodent species. Standard errors in parentheses; $n = 56$ for all zero time lags, $n = 49$ for 3·5-year lags. All catches were log $(x + 1)$ transformed before the analysis

Clethrionomys glareolus	Cross-correlations *Microtus agrestis*	 *Apodemus flavicollis*	 *Sorex araneus*
Lag 0 years	0·48	0·41	0·58
	(0·14)	(0·14)	(0·14)
Lag 3·5 years	0·36	0·38	0·36
	(0·15)	(0·15)	(0·15)

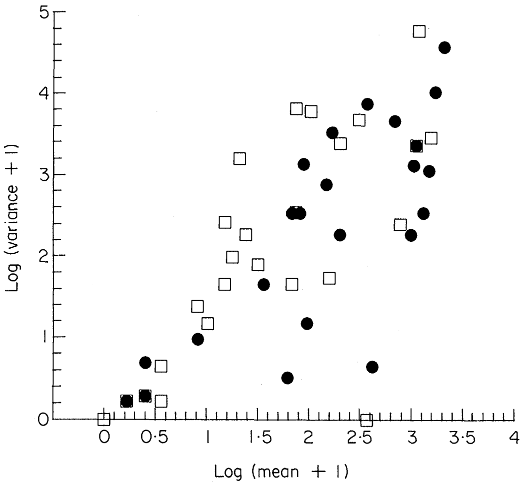

FIG. 3. Relationship between the mean trap catch of voles and the variance in catch among four trap lines at Boda, 1961–88. All data transformed by $(X + 1)$ transformation. Taylor's power law: log (variance) = 1·37 log (mean catch) − 0·38, $n = 49$, $r = 0·75$.

whether this cyclic population shows the Chitty Effect of higher body weights in peak populations. Figure 4 shows the relationship between body size and population density. There is a strong positive relationship ($r_s = 0·73$) between spring and early summer body weights of adult overwintered voles and the trap index catch, as Chitty (1952) first observed with *Microtus agrestis* in England. We do not think that these weights are a simple function of age, since virtually all the overwintered voles were juveniles of the previous summer.

Age distribution

We do not have reproductive or mortality data on *Clethrionomys glareolus* to assist us in untangling the demographic machinery that drives the population cycle in this

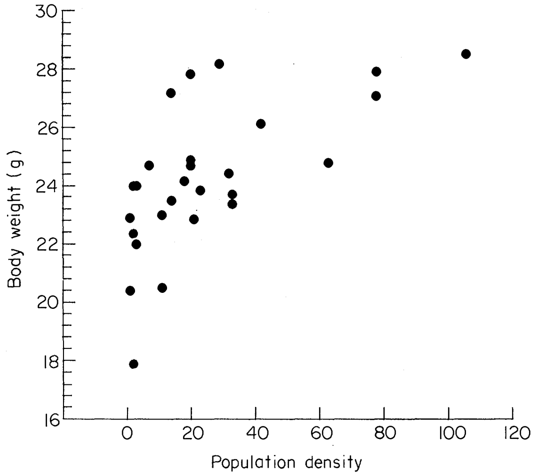

FIG. 4. Relationship between mean body weight (g) of *Clethrionomys glareolus* overwintered adults in early summer and population density estimated by total snap-trap catch of this species in early summer, $r_s = 0{\cdot}73$, $n = 27$.

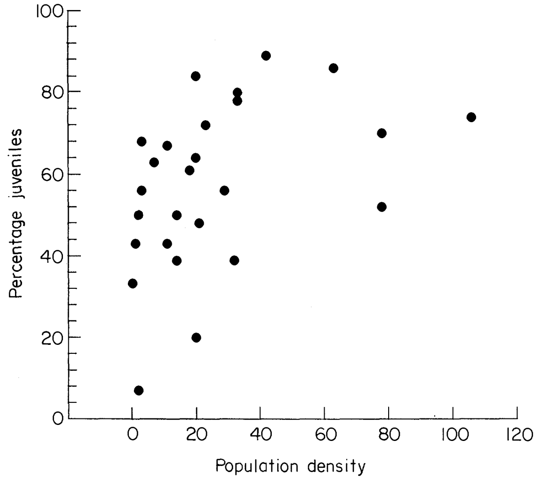

FIG. 5. Age ratios (percentage of young-of-year in August samples) as a function of early summer population density for *Clethrionomys glareolus*, $r_s = 0{\cdot}54$, $n = 27$.

population. But we can use age ratios (percentage of juveniles in late summer samples) to investigate the idea that juvenile losses are particularly severe in declining populations, less severe in peak populations, and relatively low in increasing populations (Krebs & Myers 1974). Figure 5 plots this relationship. Age ratios are highly variable in *Clethrionomys glareolus*. There is a slight tendency for age ratios to be higher when density is higher ($r_s = 0{\cdot}54$, $n = 27$), but there is much variation in age ratios at low densities that presumably are a result of mixing low densities that are declining with low densities that are entering the phase of increase. The patterns are not clear in these data, and age ratios are of little value for predicting density changes.

DISCUSSION

Long-term data sets are necessary to characterize the pattern of density variation in small rodents. This 28-year sequence of snap-trapping data from northern Sweden is the longest on record (Henttonen, McGuire & Hansson 1985; Hansson & Hentonnen 1985). Our results are in broad agreement with the conclusions of Kalela (1957), Lahti, Tast & Uotila (1976) and Hansson & Henttonen (1985) that vole populations from northern Fennoscandia show strongly cyclic population changes. Our data also agree with the conclusion of Henttonen, McGuire & Hansson (1985) that an index of cyclicity (s) of 0·5 divides cyclic from non-cyclic populations. The Boda *Clethrionomys* data are well above this border line ($s = 0{\cdot}64$ or $0{\cdot}67$) and agree closely with other northern Swedish *Clethrionomys glareolus* data summarized in Hansson & Henttonen (1985).

Fluctuations in all the small mammals at Boda seem to occur in synchrony. One possible explanation is that predation mortality caused by specialist predators keeps all species in step (Hagen 1969; Angelstam, Lindström & Widèn 1984). The major alternative hypothesis is that food resources change cyclically for all species (Kalela 1962). The Boda data cannot address these hypotheses, and experimental work is needed. Marcström, Kenward & Engren (1988) showed that the experimental removal of foxes and martens on islands in the northern Baltic had no impact on the vole cycle. It is clear from Figs 1 and 2 that synchrony among species operates broadly at Boda and also that each species shows individualistic patterns of change that may not have a common explanation.

Hansson (1984) argued that synchronous declines in shrew and vole numbers would rule out a food-based explanation for interspecific synchrony (since they eat different things), and would support a predator-based explanation. He showed that in one cycle both shrews and voles declined together at Strömsund (64°N). Henttonen (1985) and Henttonen *et al.* (1987) supported this explanation with similar data from Finnish Lapland. Figures 1 and 2 show that there is significant synchrony between shrew and vole numbers at Boda, supporting the proposition that mustelid predation might cause this synchrony between shrews and voles. We do not think that this is a likely explanation because mustelids were scarce at Boda. Furthermore, Marcström, Kenward & Engren (1988) found that mustelids were also scarce during two vole cycles in northern Sweden.

Microtine rodents at Pallasjärvi, Finland (68°N) declined abruptly in the summers of 1971, 1975 and 1979 (Henttonen 1985; Henttonen *et al.* 1984). The 1971 cyclic decline was simultaneous at Boda. The next decline at Boda occurred in the winter of 1974–75, slightly before the summer 1975 decline at Pallasjärvi, and the next decline was 1 year earlier at Boda (1978). The next decline occurred clearly in summer 1981 and 1982 at Boda, but did not occur in voles at Pallasjärvi.

Within Sweden, Hansson (1969) reported peak densities of microtines from Ammarnäs (66°N) in 1963 and 1966. By contrast, 1963 was a decline year at Boda. Hörnfeldt (1978) reported a peak from Västerbotten (64°N) in 1973–74, and Hörnfeldt, Lofgren & Carlsson (1986) reported another rodent peak in 1977–78 in the same area, a pattern very similar to that shown in Fig. 1. Marcström, Kenward & Engren (1988) trapped voles on the islands of Rånön and Bergön in northern Sweden from 1975 to 1986, and found peak populations of *Clethrionomys* in 1977, 1980 and 1984 in exact synchrony with our Boda data. While it is tempting to argue for some broad factor like weather that synchronizes populations regionally, it is clear that the null model of random synchrony between regional populations cannot be rejected until we have more long-term data from the same area for comparison. Myrberget (1973) concluded the same from his analysis of Norwegian rodent cycles.

Hansson & Henttonen (1988) have emphasized the differences in dynamics of rodent populations in northern and southern Sweden. We have seen no long-term studies for southern Sweden like the Boda series. It may be premature to dichotomize these populations with respect to the underlying dynamics without more data from southern Sweden.

ACKNOWLEDGMENTS

We thank Henning Pettersson, Sture Sundgren, and Arne Nordström for their help with the trapping field work at Boda. This research was financed by the Swedish Sportsmen's Association. The initiative and interest of Professor Alf Johnels of the National Museum of Natural History was of vital importance at the start of this study, and the cooperation of Ulf Bergström from this museum is also gratefully acknowledged.

REFERENCES

Anderson, P. K. (1989). *Dispersal in Rodents: A Resident Fitness Hypothesis.* American Society of Mammalogists, Special Publication 9, Lawrence, Kansas.

Angelstam, P., Lindström, E. & Widèn, P. (1984). Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, **62,** 199–208.

Chitty, D. (1952). Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936–39. *Philosophical Transactions, Royal Society of London*, **236,** 505–552.

Hagen, Y. (1969). Norske undersökelser over avkomproduksjonen hos rovfugler og ugler sett i relasjon til smågnagerbestandens vekslinger. *Fauna*, **22,** 73–126.

Hansson, L. (1969). Spring populations of small mammals in central Swedish Lapland in 1964–68. *Oikos*, **20,** 431–450.

Hansson, L. (1984). Predation as the factor causing extended low densities in microtine cycles. *Oikos*, **43,** 255–256.

Hansson, L. & Henttonen, H. (1985). Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia*, **67,** 394–402.

Hansson, L. & Henttonen, H. (1988). Rodent dynamics as community processes. *Trends in Ecology and Evolution*, **3,** 195–200.

Hentonnen, H. & Hansson, L. (1985). Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia*, **67,** 394–402.

Henttonen, H. (1985). Predation causing extended low densities in microtine cycles: further evidence from shrew dynamics. *Oikos*, **45,** 156–157.

Henttonen, H., McGuire, A. D. & Hansson, L. (1985). Comparisons of amplitudes and frequencies (spectral analyses) of density variation in long-term data sets of *Clethrionomys* species. *Annales Zoologici Fennici*, **22,** 221–227.

Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. (1987). How much do weasels shape microtine cycles in the northern Fennoscandian taiga? *Oikos*, **50,** 353–365.

Henttonen, H., Tast, J., Viltala, J. & Kaikusalo, A. (1984). Ecology of cyclic rodents in northern Finland. *Memoranda Soc. Fauna Flora Fennica*, **60,** 84–92.

Hörnfeldt, B. (1978). Synchronous population fluctuations in voles, small game, owls, and tularemia in northern Sweden. *Oecologia*, **32,** 141–152.

Hörnfeldt, B., Lofgren, O. & Carlsson, B. G. (1986). Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden. *Oecologia*, **68,** 496–502.

Kalela, O. (1957). Regulation of reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus* (Sund.). *Annales Academiae Scientiarum Fennicae, Series A, IV*, **34,** 1–60.

Kalela, O. (1962). On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. *Annales Academiae Scientiarum Fennicae, Series A, IV*, **66,** 1–38.

Krebs, C. J. & Myers, J. H. (1974). Population cycles in small mammals. *Advances in Ecological Research*, **8,** 267–399.

Lahti, S., Tast, J. & Uotila, H. (1976). Pikkujyrsijöiden kannanvaihteluista Kilpisjärvellä vuosina 1950–1975. *Luonnon Tutkija*, **80,** 97–107.

Marcström, V., Kenward, R. E. & Engren, E. (1988). The impact of predation on boreal tetraonids during vole cycles: an experimental study. *Journal of Animal Ecology*, **57**, 859–872.

Myrberget, S. (1973). Geographical synchronism of cycles of small rodents in Norway. *Oikos*, **24**, 220–224.

Stenseth, N. C. (1985). Models of bank vole and wood mouse populations. *The Ecology of Woodland Rodents* (Ed. by J. R. Flowerdew, J. Gurnell & J. H. W. Gipps), pp. 339–376. Clarendon Press, Oxford.

Stenseth, N. C. & Framstad, E. (1980). Reproductive effort and optimal reproductive rates in small rodents. *Oikos*, **34**, 23–34.

Wildhagen, A. A. (1953). On the reproduction of voles and lemming in Norway. *Statens Viltundersökelser*, Oslo, Norway.

(*Received 17 April 1989*)