Ann. Zool. Fennici 22:221-227. 1985

Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species

Heikki Henttonen, Anthony D. McGuire & Lennart Hansson

Henttonen, H., McGuire, A. D. & Hansson, L. 1985: Comparisons of amplitudes and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. — Ann. Zool. Fennici 22:221-227.

In order to examine geographic patterns of density variation or cyclicity in microtine rodents, a quantitative index of cyclicity is necessary. Lewontin (1966) proposed *s*, the standard deviation of the logarithmic transformation of the densities, as a general measure of density variation. Using long-term data sets of *Clethrionomys* species we compared the dominant frequency (wavelength) contribution to the time series. When seasonal information (spring and autumn indices) of density variation is available, *s* divides cyclic and non-cyclic populations perfectly. We performed a discriminant analysis for more heterogenous data sets with only a single yearly density-estimate, by separating data sets into cyclic or non-cyclic populations on the basis of *s* and then using contributions of frequency classes as variables. The discriminant analysis classified these relatively heterogeneous data sets lacking seasonal information with 91.4% accuracy. The use of *s* improves when some qualitative features of cyclicity (summer declines, interspecific synchrony) are taken into consideration. Values of *s* based on autumn densities provide the best discrimination between typical cyclic and non-cyclic populations. Our examination of the effect of length of study period on *s* suggests that variation in *s* is considerably decreased and levelled after 4 years. Since *s* is significantly correlated with the dominant wavelength of the spectral contribution to the time series and also is predictive of cyclicity we conclude that *s* is a reasonably good measure of cyclicity.

H. Henttonen, Dept. of Zoology and Kilpisjärvi Biol. Station, Univ. Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland.
A. D. McGuire, Inst. Arctic Biol., Univ. Alaska, Fairbanks, AK 99 701, USA.
L. Hansson, Dept. Wildlife Ecology, Swedish Univ. Agricultural Sciences, S-75007 Uppsala, Sweden.

1. Introduction

Geographic patterns of density variation or cyclicity in microtine rodents have attracted considerable interest. One of the reasons is that geographic differences or gradients may help to elucidate the relative importance of biotic and abiotic extrinsic factors (Elton 1942, Kalela 1962, Hansson 1971, 1979, Hansson & Henttonen 1985a, b, Laine & Henttonen 1983, Erlinge et al. 1983). Another reason is that regional differences in cyclicity have also been suggested to be correlated with life history strategies in microtines (Stenseth 1978, Stenseth & Framstad 1980, Stenseth & Gustafsson 1985), although this has been questioned by Henttonen & Hansson (1985), and Hansson & Henttonen (1985b).

An obvious problem in analyzing density variation is finding a quantitative index for the comparisons. An index which measures cyclicity should separate typical cyclic populations with a classic 3-5 year pattern from irregularly or only seasonally fluctuating non-cyclic populations. It should also be independent of various trapping methods used to estimate microtine densities. Lewontin (1966) and Williamson (1972) proposed the standard deviation of logarithmic (base 10) densities,

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

where N_i is density or some density index, and n is number of years, as a general measure of density variations. Stenseth (1977) (see also Stenseth & Framstad 1980) was the first to use *s* as an index of microtine cyclicity, and subsequently Henttonen & Hansson (1985), and Hansson & Henttonen (1985a,b) have utilized *s* in their studies comparing the geographic patterns of microtine density variations.

In this paper we compare *s*, a measure of the amplitudes of density variation, with univariate spectral analysis (Brillinger 1975, Bloomfield 1976). Univariate spectral analysis is a frequency domain approach which characterizes the time series of density variation as a sum of sine waves of different frequencies. For example, a microtine population that varies sinusoidally with a period of four years could be described by a single pure sinusoid, also with a period of four years. However, most time series are not pure sinusoids, and must be described as a sum of sinusoids of different frequencies.

We show that *s* is a reasonably good, single measure of cyclicity, although it strictly taken only measures relative variance, and that its use improves if also other characteristics of cyclicity are taken into consideration.

2. Material and methods

We used long-term data sets of *Clethrionomys* from the literature as well as some unpublished data sets for microtine populations in Fennoscandia. The minimum length of a study period to be included was 14 years for clearly cyclic data sets and 10 years for non-cyclic and intermediate data sets. These limits were mainly set by the availability of long-term data sets.

The two approaches commonly used to analyze time series are time domain analysis (Box & Jenkins 1976, Jenkins 1979) and frequency domain analysis (Brillinger 1975, Bloomfield 1976). Time domain analysis is based upon autocorrelation and attempts to generate predictive parametric models. These models imply that the population's density in a particular year can be predicted using information on densities from previous years. Frequency domain analysis, on the other hand, uses Fourier transform mathematics to describe the time series as a sum of sine waves of different frequencies. Some of the frequencies in this sum will contribute more to the description of the time series than others. Thus it is possible to determine a frequency or range of frequencies which best describe the cyclic nature, if such exists, of a time series. Although frequency domain analysis results may be used in a predictive manner, this type of analysis is primarily a descriptive tool.

We used the BMDP statistical software (Dixon 1981) univariate spectral analysis program to analyze the time series discussed in this paper. This program uses Fourier transform mathematics to generate a sum of sine waves of discrete frequencies with different amplitudes which describes the time series. Assuming that the amplitude of any sine wave is a continuous function of its frequency, the program then smooths out this function of amplitude vs frequency. This is done by choosing a bandwidth, a continuous range of frequencies of specified width, and computing the average squared amplitude of the sinusoids within that frequency band. The average squared amplitude is thus the spectral density, and the smoothed function is generated by going through the entire frequency range with overlapping band widths to calculate a series of spectral density points. It is the spectral density estimates which we compare to *s*, below.

Note that although narrow bandwidths preserve detail in the smoothed function, larger bandwidths are powerful in eliminating noise and may provide a better portrayal of the significant features of the observed time series. We have consistently used the larger bandwidth in this analysis. For a more detailed description and examples of this technique we advise the reader to consult Dixon (1981).

We performed the comparison of *s* and spectral analysis in two ways:

1) Since many data sets did not include both spring and autumn densities, we first performed the spectral analyses using only those data sets that included information on both spring and late summer/autumn densities. Using both density estimates, populations with predominantly seasonal fluctuations can be better distinguished from populations which are truly cyclic. In this comparison we calculated *s* using the late summer/autumn densities.

2) Then, we performed spectral analyses on all data sets using a single yearly density estimate. This was either the mean of spring and late summer/autumn densities, or the single yearly value given in a number of data sets. In this comparison we calculated each *s* from the density estimate used in the particular spectral analysis.

3. Results and discussion

3.1. Comparison of *s* and spectral analyses

In Tables 1 and 2 patterns of frequency contributions to density variation ("wavelength" contributions) have been divided into classes. The percentages indicate how great a proportion of the total spectral density belongs to each wave length range. Table 3 shows the advantage of using autumn densities when calculating *s* for comparative analyses.

We started our analyses with data sets including two seasonal estimates of density (Table 1). These data sets can be divided into two types: 1) data sets with low *s* have a density variation pattern showing predominantly only seasonal or short-term variation (dominant wavelength less than 2.5 or 1.5 years), and 2) data sets with high *s*-values have a density variation pattern where the classic 3–5-year cyclicity (dominant wave length 2.5–5.5 years) clearly dominates over seasonal variation.

Table 1. Comparison of *s* and spectral analysis on the basis of two seasonal values. Figures in each wavelength column give the contribution (%) of that range to the total spectral variance in the data set. Dominant pattern of density variation in italics. For more details, see text.

Species	*s*	Wavelength ranges (years)			
		< 1.5	1.5-2.5	2.5-5.5	> 5.5
1. *C. rutilus*	0.17	*30*	*32*	18	20
2. *C. rutilus*	0.17	*47*	29	23	0
3. *C. rutilus*	0.18	*40*	28	26	6
4. *C. rutilus*	0.22	*31*	23	28	18
5. *C. gapperi*	0.35	25	*39*	18	18
6. *C. glareolus*	0.33	16	*31*	24	29
7. *C. glareolus*	0.32	*46*	25	21	8
8. *C. glareolus*	0.26	*51*	36	12	2
9. *C. glareolus*	0.85	30	19	*39*	11
10. *C. rutilus*	0.78	23	19	*45*	12
11. *C. rufocanus*	0.77	9	29	*47*	15
12. *C. rufocanus*	0.74	19	24	*39*	18
13. *C. rutilus*	0.64	30	15	*39*	15

1. S Siberia (Okulova & Myskin 1973). 2-4. S Siberia (Koshkina & Korotkov 1975). 5. NW Canada (Mihok & Fuller 1981). 6. England (Southern & Lowe 1982). 7. Soviet Union, Moscow (From Bashenina 1981). 8. Denmark (Jensen 1982). 9-11. Finnish Lapland, Pallasjärvi (Henttonen et al. 1977, Henttonen, unpubl.). 12-13. Finnish Lapland, Kilpisjärvi (Tast 1984, Henttonen, unpubl.).

Thus, when seasonal information is available, *s* distinguishes between these two classes perfectly. All *Clethrionomys* data sets belonging to the latter group are from northern Fennoscandia; others are from Siberia, the European temperate zone and North America.

Table 2 shows the relationship between *s* and the pattern of density variations for cases where *s* is calculated on the basis of one annual density estimate. It should be remembered that the heterogeneity of data sets is much greater here than in Table 1. Generally, the lower *s*-values are connected with short-term density variations and higher ones with more typical (4-year) cyclic patterns. A Spearman's rank correlation between *s* and the wavelength class with the greatest percentage of spectral variance is significant ($r = 0.38$, $p < 0.05$; an index variable (1,2,3,4,5) for the dominant class was used). Much of the short term pattern is probably seasonal, as suggested in Table 1.

Table 2. Comparisons of *s* and spectral analysis on the basis of single annual density estimate. For more details, see text and Fig. 1.

Species	*s*	Wavelength ranges (years)				
		< 2.5	2.5-3.5	3.5-5.5	5.5-10	> 10
1. *C. rutilus*	0.19	*38*	11	11	30	11
2. *C. gapperi*	0.30	*27*	*25*	13	17	19
3. *C. gapperi*	0.54	1	7	*32*	*31*	29
4. *C. glareolus*	0.27	*41*	19	13	13	13
5. *C. glareolus*	0.39	*49*	41	8	3	0
6. *C. glareolus*	0.30	*46*	31	10	7	6
7. *C. glareolus*	0.29	*38*	*37*	21	4	1
8. *C. glareolus*	0.16	*63*	22	13	2	0
9. *C. glareolus*	0.32	*54*	23	16	7	1
10. *C. glareolus*	0.26	*36*	26	19	14	5
11. *C. glareolus*	0.47	*32*	*31*	26	8	3
12. *C. glareolus*	0.28	27	*35*	21	14	3
13. *C. glareolus*	0.49	22	*33*	30	10	5
14. *C. glareolus*	0.27	8	20	17	*27*	*28*
15. *C. glareolus*	0.34	16	*28*	*29*	19	8
16. *C. glareolus*	0.36	13	*37*	5	20	26
17. *C. glareolus*	0.37	14	*32*	4	20	30
18. *C. rufocanus*	0.20	3	*40*	28	21	8
19. *C. rufocanus*	0.25	18	*48*	21	12	1
20. *C. rufocanus*	0.24	16	*44*	23	15	3
21. *C. rufocanus*	0.30	11	*45*	21	14	9
22. *C. rufocanus*	0.22	15	*49*	25	10	1
23. *C. rufocanus*	0.30	6	*25*	20	*25*	*25*
24. *C. rutilus*	0.10	25	*32*	29	12	3
25. *C. rutilus*	0.20	32	21	*36*	10	2
26. *C. rutilus*	0.22	7	13	*44*	20	15
27. *C. glareolus*	0.63	21	21	*45*	13	1
28. *C. rutilus*	0.56	20	20	*45*	12	3
29. *C. rufocanus*	0.68	27	18	*43*	10	2
30. *C. rutilus*	0.54	12	*49*	19	13	7
31. *C. rufocanus*	0.69	16	18	*31*	20	17
32. *C. glareolus*	0.79	9	22	*33*	16	18
33. *C. rufocanus*	0.69	6	20	*39*	27	9
34. *C. rutilus*	0.36	7	20	*38*	13	23
35. *C. glareolus*	0.37	19	24	*38*	11	8

1. S Siberia (Okulova & Myskin 1973). 2. NW Canada (Mihok & Fuller 1981). 3. Quebec, E Canada (Grant 1976). 4-9. Soviet Union (from Bashenina 1981). 10. Denmark (Jensen 1982). 11-16. Soviet Union (from Bashenina 1981). 17. England (Southern & Lowe 1982). 18-23. Hokkaido, Japan (Nakatsu 1982). 24-26. S Siberia (Koshkina & Korotkov 1975). 27-29. Pallasjärvi, Finnish Lapland (Henttonen et al. 1977, Henttonen, unpubl.). 30-31. Kilpisjärvi, Finnish Lapland (Tast 1984, Henttonen, unpubl.). 32-34. Kola Peninsula, NW Soviet Union (= NE Fennoscandia, Koshkina 1966, Semenov-Tjan-Shanskij 1970). 35. Karelia, NW Soviet Union (Ivanter 1975).

Using an *s* less than 0.5 to classify populations as non-cyclic and *s* greater than 0.5 to classify populations as cyclic we performed a step-wise discriminant analysis with the wavelength classes of Table 2 as variables. The discriminant program chose the wavelength class 3.5-5.5 as the first variable to incorporate into the discriminant function. This variable is most indicative of 4-year cyclicity. The use of this single variable allowed the discriminant function to classify with 82.9% accuracy. After the incorporation of one more variable (2.5-3.5) the discriminant function classified with 91.4% accuracy. In other words, of the total of

35 data sets in Table 2, only three data sets (numbers 25, 26, 35) were misclassified on the basis of *s*-value only. Two (numbers 25 and 26 in Table 2) of these three showed predominantly seasonal variation in Table 1 (where they are numbers 3 and 4; for 35 there were no seasonal data). Thus, when seasonal variation in these two data sets was largely removed by using yearly mean densities (Table 2), longer-term trends obviously emerged.

We conclude that when a single index of "cyclicity" is needed, *s*, the standard deviation of logarithmic densities, is a suitable one. High *s*-values seem to characterize typically cyclic microtine populations where long-term trends clearly dominate over seasonal variation (see also Hansson & Henttonen 1985a, b).

3.2. Additional comments

There are a few data sets in Table 2 which require comments, even though they were classified correctly in the discriminant analysis. Study number 3 (Grant 1976) covers only 11 years, and is mostly characterized by very low densities. Study number 14 (from Bashenina 1981), on the other hand, covers 25 years and is characterized by high densities (mostly 10-35 animals per 100 trap-nights). However, another study (number 7) from the same region (Tulskaja Oblast, Soviet Union) fits the general trend.

Study numbers 34 and 35 in Table 2 fit the 4-year cyclic pattern but have only moderate *s*-values. The latter is from the southern part of Soviet Karelia, which belongs to the transition zone between cyclic populations of microtines in northern Fennoscandia and non-cyclic ones in southern Fennoscandia (Hansson & Henttonen 1985a). The first one is from NE Fennoscandia (Kola Peninsula), where the densities of *C. rutilus* are strongly influenced by *C. rufocanus*. This also applies to number 30 (Viitala 1984); in this case the spectral frequency point was situated at the wavelength corresponding to 3.5 years, but just at its lower side.

Japanese studies in Table 2 (number 18-23) have quite low *s*-values, but consistently a three year pattern. However, Japanese short term studies including seasonal information (Kuwahata 1962, Fujimaki 1969, Abe 1976) show that also in these cases seasonal variation might be the dominant pattern.

Table 3. Comparison of discrimination efficiency of seasonal *s*-values (mean±*SD*) between cyclic and non-cyclic *Clethrionomys*. In the cyclic data sets, *s*-values based on autumn indices gave higher mean than those based on spring or mean of the year indices ($p < 0.05$, Kruskall-Wallis one-way analysis of variance). In the non-cyclic data sets there was not a significant difference in the mean level among seasonal *s*-values ($p > 0.1$). Thus, *s*-values calculated from autumn indices better separate cyclic and non-cyclic populations. For details, see text.

	Cyclic	Non-cyclic
Spring	0.62±0.13	0.32±0.05
Mean of the year	0.62±0.07	0.24±0.08
Autumn	0.76±0.08	0.24±0.10

3.3. Why autumn densities?

As mentioned earlier, we prefer late summer/autumn density estimates when calculating *s*, because they better differentiate between the two groups emerging from Table 1. To demonstrate the advantage of using *s*-values based on autumn densities, we calculated *s*-values from the 13 data sets in Table 1 for spring, autumn and yearly mean densities each (Table 3). In cyclic populations autumn densities gave higher *s*-values than either spring densities or yearly mean ones ($H = 5.75$, $p < 0.05$; Kruskall-Wallis one-way analysis of variance based on *s*-values in the three groups in Table 3). On the contrary, there were no clear differences between seasonal *s*-values in non-cyclic populations ($H = 4.28$, $p \geq 0.1$). Thus, *s*-values derived from autumn density estimates more efficiently separate cyclic and non-cyclic *Clethrionomys* populations.

3.4. Other characteristics of cyclicity

Conclusions based on *s*-values can be supported by some other features of density variations. For example, a decline continuing through summer and leading to extremely low densities the following autumn and winter has been shown to be a typical feature for cyclic populations of *Clethrionomys glareolus* and *Microtus agrestis* (Hansson & Henttonen 1985b). The deepest crash phase is often characterized by densities of 1 animal/1000 trap nights or less (see e.g. Hansson 1969, Henttonen et al. 1977).

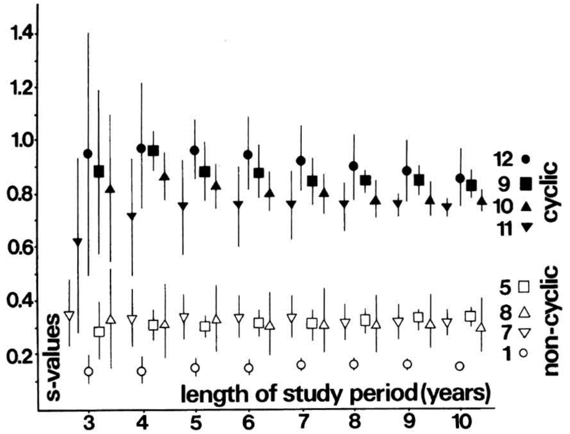

Fig. 1. Effect of the length of a theoretical study period on *s* (mean±*SD*). Calculations are based on data sets covering 15 years or more. For details, see text. Numbers to the right refer to data set numbers in Table 1.

In Table 1, all five data sets with high *s*-values and 4-year cyclic pattern are characterized by summer declines in the "crash" phase. In six (number 1-4, and 7-8) of the eight non-cyclic data sets there is no summer decline; these studies cover 96 years altogether. Number 6 (Whytham Wood, Southern & Lowe 1982) shows 8 summer declines in 30 years. However, in 6 of these 8 cases the density is still over 50 voles per hectare in early winter. In the other two cases densities are 5-15 voles per hectare. These densities of *C. glareolus* after "summer declines" differ by orders of magnitude from those in northern Fennoscandia. In addition, study number 5 in Table 1 (NW Canada, Mihok & Fuller 1981) included 3 summer declines in 15 years. Generally, the densities in that study were quite low, but none of the 3 summer declines lead to extremely low densities in relation to the normal ones. Thus, the occurrence of summer declines is probably a good qualitative attribute of true "cyclicity" (see also Hansson & Henttonen 1985a, b). The dependence of high *s*-value on summer declines and extreme lows rather than high peaks is interesting here since population models which are cyclic because of time delays and large negative feedbacks, exhibit much more extreme fluctuations than the same models having only environmental "white noise" (May 1975). Hansson (1979), Hansson & Henttonen (1985a), Oksanen & Oksanen (1981) and Laine & Henttonen (1983) have discussed the biological factors causing summer declines and extreme lows.

Another interesting feature characterizing microtine cyclicity is the degree of synchrony among sympatric microtines. In this respect we regard the synchronous or asynchronous occurrence of the deepest low phase as the most important aspect. Phase differences in the course of increase and peak years are well-known among sympatric microtines in northern Fennoscandia, while the deepest low is synchronous (Hansson 1969, Tast & Kalela 1971, Henttonen et al. 1977, Laine & Henttonen 1983, Hansson & Henttonen 1985a). Thus, density variation patterns within the entire microtine community can provide useful clues to the type of density regulation of an individual population.

3.5. Considerations of length of data sets

In the foregoing discussion we have used the term "cyclic" for the pattern found in northern Fennoscandia. We are well aware that our analysis is not a rigorous mathematical description of cyclicity. However, the primary purpose of this paper is to evaluate a measure for comparative analysis of density variations. The cyclic nature of microtine fluctuations in northern Fennoscandia has elsewhere been demonstrated by use of autocorrelation techniques (Finerty 1980, Kaikusalo & Hanski 1984, Oksanen et al. (in prep.)). The negative results of Garsd & Howard (1981) for autocorrelation analyses of northern Fennoscandian data sets in Henttonen et al. (1977), may be due to the fact that their technique is very sensitive to the number of study years in relation to the wavelength. Autocorrelation analysis by Oksanen et al. (in prep.), based on longer data set in Laine & Henttonen (1983) demonstrates significant periodicity as does the analysis by Kaikusalo & Hanski (1985) from the same locality.

When analyzing density patterns of microtines, the unavailability of long-term (over 10 or 15 years) studies is an ubiquitous problem, and therefore short-term studies have also had to be incorporated (Stenseth & Framstad 1980, Henttonen & Hansson 1985, Hansson & Henttonen 1985a, b). Consequently, it is important to know with confidence the necessary lower limit for the length of a study period to be included. In Fig. 1 we show the effect of the length of the study period on *s* (for clarity, only four data sets from both groups are shown in Fig. 1). Using long-term (15 years or more) data sets from Table 1 with late summer-autumn values, we computed *s*-values for combinations of theoretical study periods for sequential periods ranging from 3 to 10 years. For example, a 20 year data set contains 18 three-year study periods. If ten of these three-year study periods are randomly selected, and an *s*-value is calculated for each, then a mean *s*-value and standard deviation can be calculated. When possible, we calculated 10 random sets per period. Fig. 1 shows the means and standard deviations in relation to the computed length of each study period of every data set.

It is obvious that 3 years is too short a period to calculate *s* for strongly cyclic populations. However, when the study period is 4 years standard deviations have decreased considerably, and are almost levelled off at 5 years. For the lower range of *s* (non-cyclic populations), 3-year periods have somewhat greater standard deviations than 4-year periods, but the variation has clearly levelled off by the 4-year study periods.

In order to calculate *s*, we would recommend a minimum length of 5 subsequent years for cyclic populations and 4 years for non-cyclic ones. However, since this criterion would exclude a great number of studies, we are inclined to accept the minimum of 4 years for cyclic populations and 3 years for non-cyclic populations. This, we believe, should in most cases differentiate between cyclic and non-cyclic populations.

Acknowledgements. This study was made during HH's ASLA-Fulbright Scholarship at the Institute of Arctic Biology, University of Alaska in Fairbanks. Studies in Finnish Lapland have been supported by the Emil Aaltonen Foundation, the Research Council for the Natural Sciences of Finland and the Finnish Cultural Foundation. We thank the Institute of Arctic Biology and University of Alaska, Fairbanks, for use of their computer facilities, and John F. Fox for advice on computation and data analysis. We further thank Erkki Haukioja and Nils Christian Stenseth for comments on an earlier draft. Bill Fuller and Takashi Saitoh kindly provided some references.

References

Abe, H. 1976: Population structure and reproductive activity of Clethrionomys rufocanus bedfordiae (Thomas) in a wind shelter belt of the Ishikari Plain, Hokkaido. (In Japanese with English summary.) — J. Mammal. Soc. Japan 7:17-30.

Bashenina, N. V. (ed.) 1981: Evropejskaja ryžaja polevka. — Nauka, Moscow.

Bloomfield, P. 1976: Fourier analysis of time series: an introduction. — Wiley, New York.

Box, G. E. P. & Jenkins, G. M. 1976: Time series analysis, forecasting and control. — Holden-Day.

Brillinger, D. R. 1975: Time series: data analysis and theory. — Holt, Rinehart and Winston, New York.

Dixon, W. J. (ed.) 1981: BMDP Statistical Software. — Univ. California Press, Los Angeles.

Elton, C. 1942: Voles, mice and lemmings; problems in population dynamics. — Oxford Univ. Press, Oxford.

Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Jansson, G., Liberg, O., Nilsson, I.N., Nilsson, T., von Schantz, T. & Sylven, M. 1983: Predation as a regulating factor on small rodent populations in southern Sweden. — Oikos 40:36-52.

Finerty, J. P. 1980: The population ecology of cycles in small mammals: mathematical theory and biological fact. — Yale Univ. Press, New Haven.

Fujimaki, Y. 1969: The fluctuations in the numbers of small rodents. (In Japanese with English summary.) — Bull. Hokkaido Forest Exp. Station 7:62-77.

Grant, P. R. 1976: An 11-year study of small mammal populations at Mont St. Hilaire, Quebec. — Can. J. Zool. 54:2156-2173.

Garsd, A. & Howard, W. E. 1981: A 19-year study of microtine population fluctuations using time-series analysis. — Ecology 62:930-937.

Hansson, L. 1969: Spring populations of small mammals in central Swedish Lapland in 1964-1968. — Oikos 20:431-450.

—"— 1971: Small rodent food, feeding and population dynamics. A comparison between granivorous and herbivorous species in Scandinavia. — Oikos 22:183-198.

—"— 1979: Food as a limiting factor for small rodent numbers: tests of two hypotheses. — Oecologia 37:297-314.

Hansson, L. & Henttonen, H. 1985a: Gradients in density variations of small rodents: the importance of latitude and snow cover. — Oecologia (in press).

—"— 1985b: Regional differences in cyclicity and reproduction in Clethrionomys spp.: are they related? — Ann. Zool. Fennici 22:277-288.

Henttonen, H. & Hansson, L. 1985: Is litter size related to cyclicity or environmental conditions — a reexamination of data from the vole Clethrionomys rutilus. — Can. J. Zool. (in press).

Henttonen, H., Kaikusalo, A., Tast, J. & Viitala, J. 1977: Interspecific competition between small rodents in subarctic and boreal ecosystems. — Oikos 29:581-590.

Ivanter, E. V. 1975: Populjacionnaja ekologija melkih mlekopitajuščih taežnogo severo-zapada SSSR. — Nauka, Leningrad.

Jenkins, G. M. 1979: Practical experience with modeling and forecasting time series. — Gwilym Jenkins and Partners.

Jensen, T. S. 1982: Seed production and outbreaks of non-cyclic rodent population in deciduous forests. — Oecologia 54:184-192.

Kaikusalo, A. & Hanski, I. 1985: Population dynamics of Sorex araneus and Sorex caecutiens in Finnish Lapland. — Acta Zool. Fennica 173:283-285.

Kalela, O. 1962: On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. — Ann. Acad. Sci. Fennicae (A IV) 66:1-38.

Koshkina, T. V. 1966: O periodičeskih izmenenijah čislennosti polevok (na primere Kols'kogo poluostrova). — Bjull. M. o-va isp. prirody, otd. biol. 71:14-26.

Koshkina, T. V. & Korotkov, Yu. S. 1975: Regulative adaptations of the red vole Clethrionomys rutilus under optimum conditions of its range. (English translation by W. A. Fuller. — Fauna i ekologija gryzunov 12:5-61.

Kuwahata, T. 1962: Studies on population fluctuations of the red-backed vole Clethrionomys rufocanus bedfordiae (Thomas). I. An analysis of a process of the gradiation. — Bull. Governm. Forest. Exp. Station 143:14-37.

Laine, K. & Henttonen, H. 1983: The role of plant production in microtine cycles in northern Fennoscandia. — Oikos 40:407-418.

Lewontin, R. C. 1966: On the measurement of relative variability. — Syst. Zool. 15:141-142.

May, R. M. 1975: Stability and complexity in model ecosystems. 2nd. ed. — Princeton Univ. Press, Princeton.

Mihok, S. & Fuller, W. A. 1981: Morphometric variation in Clethrionomys gapperi: are all voles created equal? — Can. J. Zool. 59:2275-2283.

Nakatsu, A. 1982: The relationship between the population density of Clethrionomys rufocanus bedfordiae and the damage caused by these voles to forests. (In Japanese with English summary). — Ann. Rep. Hokkaido Branch, Forestry Forest Products Res. Inst.: 85-89.

Oksanen, L. & Oksanen, T. 1981: Lemmings (Lemmus lemmus) and grey-sided voles (Clethrionomys rufocanus) in interaction with their resources and predators on Finnmarksvidda, northern Norway. — Rep. Kevo Subarctic Res. Stat. 17:7-31.

Okulova, N. M. & Myskin, A. A. 1973: K ocenke značenija različnyh fačktorov v dinamike cislennosti sibirskoj krasnoj polevki. — Zool. Zhurnal 52:1849-1860.

Semenov-Tjan-Shanskij, O. E. 1970: Cikličnost'v populjacijah lesnyh polevok. — Bjull. Mv. o.-va isp. prirody, otd. biol. 75:11-26.

Southern, H. N. & Lowe, V. P. N. 1982: Predation by tawny owls (Strix aluco) and bank voles (Clethrionomys glareolus) and wood mice (Apodemus sylvaticus). — J. Zool. 1988:83-102.

Stenseth, N. C. 1977: Theoretical studies on fluctuating populations: an evolutionary approach. — Ph. D. Thesis, Univ. Oslo.

—"— 1978: Demographic strategies in fluctuating small rodent populations. — Oecologia 33:149-172.

Stenseth, N. C. & Framstad, E. 1980: Reproductive effort and optimal reproductive rates in small rodents. — Oikos 34:23-34.

Stenseth, N. C. & Gustafsson, T. 1985: Reproductive rates, survival, dispersal and cyclicity in Clethrionomys species: Some theoretical considerations. — Ann. Zool. Fennici 22:289-301.

Tast, J. 1984: Winter success of root voles, Microtus oeconomus, in relation to population density and food conditions at Kilpisjärvi, Finnish Lapland. — Spec. Publ. Carnegie Mus. Nat. Hist. 10:59-66.

Tast, J. & Kalela, O. 1971: Comparisons between rodent cycles and plant production in Finnish Lapland. — Ann. Acad. Sci. Fennicae (A IV) 186:1-14.

Viitala, J. 1984: The red vole, Clethrionomys rutilus (Pall.), as a subordinate member of the rodent community at Kilpisjärvi, Finnish Lapland. — Acta. Zool. Fennica 172:67-70.

Williamson, M. 1972: The analysis of biological populations. — Edward Arnold, London.

Received 11.II.1984
Printed 11.X.1985