

# Density dependence in fluctuating grey-sided vole populations

TAKASHI SAITOH\*, NILS CHR. STENSETH† and  
OTTAR N. BJØRNSTAD†

\*Hokkaido Research Centre, Forestry and Forest Products Research Institute, Hitsujigaoka 7, Toyohira, Sapporo, Japan 062; and †Division of Zoology, Department of Biology, University of Oslo, PO Box 1050 Blindern, N-0316 Oslo, Norway

## Summary

1. The presence of direct and delayed (1 year) density dependence in fluctuating grey-sided vole populations (*Clethrionomys rufocanus*) in Hokkaido, Japan, were tested using 90 time series spanning 31 years (1962–92).
2. The autocorrelation test of Bulmer, the randomization test of Pollard, Lakhani & Rothery, and the bootstrap test of Dennis & Taper using two different models (Ricker and Gompertz) detected direct density dependence in most of the time series (90.0–100%) at the 5% level (one-tailed test).
3. Plotting population growth rates as functions of abundance suggested that the Gompertz model is more appropriate than the Ricker model for the studied populations. The tests for direct density dependence using the Gompertz model also rejected the null hypothesis of density-independent growth more frequently than the tests using the Ricker model.
4. We extended the randomization and the bootstrap methods to investigate delayed density dependence by using partial correlation and partial regression, respectively. The extended tests detected delayed density dependence in 8–15 time series (8.9%–16.7%) at the 5% level (two-tailed test).
5. The high incidence of direct density dependence and the low, but significant, incidence of delayed density dependence in these vole populations are discussed. Delayed maturation at high densities by social interference and a rich generalist fauna are thought to represent plausible mechanisms generating direct density dependence. As a candidate mechanism for delayed density dependence, specialist predator and climate conditions (affecting the exposure to predators) are discussed.

*Key-words:* *Clethrionomys rufocanus*, direct and delayed density dependence, Gompertz model, population dynamics, Ricker model.

*Journal of Animal Ecology* (1997), **66**, 14–24

## Introduction

Even though extrinsic biotic and abiotic factors have had their proponents in the study of population fluctuations in microtine rodents at earlier stages (Kalela 1957; Pitelka 1958; Pearson 1964, 1966; Fuller 1969; Batzli 1985a,b; see Stenseth & Ims 1993a for review), there was for several decades a major emphasis on phenotypic and genotypic differences between individuals in different phases of the population cycle (Christian 1950, 1980; Chitty 1960, 1967; Krebs & Myers 1974; Stenseth 1977, 1981, 1986; Krebs 1978; Charnov & Finerty 1980; Hestbeck 1982). As a result of this emphasis, much interest was devoted to phase

dependency rather than density dependency in populations of small mammals. This is in sharp contrast to other animal groups, for instance insects, for which the question of population regulation through density dependence has been studied extensively (Itô 1980; Hanski 1990; Woiwod & Hanski 1992; Turchin 1995; see also Cappuccino & Price 1995).

Within microtine rodent ecology there has recently been a revival of the study of extrinsic factors, such as predator–prey interactions in determining the population dynamics (e.g. Hansson & Henttonen 1985, 1988; Hansson 1987; Hanski, Hansson, & Henttonen 1991; Hanski *et al.* 1993; Hanski & Korpiimäki 1995). This has led to an increased interest in

density dependence – both direct and delayed – in small rodent populations (e.g. Turchin 1993; Hörnfeldt 1994; Saucy 1994; Bjørnstad, Falck & Stenseth 1995).

Searching for density dependence has often been criticized. Krebs (1991), for instance, concluded that the 'density-dependence paradigm is bankrupt because it is descriptive and *a posteriori* [...] and because no mechanisms are specified'. However, density dependence is expected in species with strong social effects on demographic rates as found in many microtine rodents, such as *Clethrionomys* spp. For instance, territoriality is frequently observed in microtines (Bondrup-Nielsen & Karlsson 1985; Madison 1985; Cockburn 1988; Ostfeld 1990), as is delayed maturation during high densities (Kalela 1957; Bujalska 1970; Abe 1976; Saitoh 1981; Bondrup-Nielsen 1986; Gilbert *et al.* 1986; Nakata 1989). In addition, generalist predators with switching or migratory response to prey abundance, may induce direct density dependence (Hassell & May 1986; Bjørnstad *et al.* 1995). Specialist predators with numerical response is, on the other hand, expected to produce delayed density dependence (Hanski *et al.* 1991, 1993; Hörnfeldt 1994; Hanski & Korpimäki 1995).

The extent to which these mechanisms lead to observable density dependence in the dynamics of real rodent populations, is most easily investigated using time series data (Turchin 1993; Hörnfeldt 1994; Saucy 1994; Bjørnstad *et al.* 1995). This motivates an evaluation of the frequency of direct and delayed density dependence in time series of rodent populations. Fluctuating populations of small rodents are well suited for such an enterprise, not least because of their rather violent and sometimes fairly regular fluctuations, through which densities may span several orders of magnitude (e.g. Krebs 1993; Stenseth & Ims 1993a).

In this paper we analyse the density dependence (both direct and delayed) in fluctuating populations of the grey-sided voles (*Clethrionomys rufocanus* [Sundevall 1846]) in Hokkaido, Japan. Our data derives from monitoring 90 populations sampled at different locations across northern Hokkaido (an area of 8034 km<sup>2</sup>) over 31 years (1962–92). Both periodic and aperiodic density fluctuations are known to occur among these populations (Bjørnstad *et al.* 1996; Stenseth, Bjørnstad & Saitoh 1996).

## Material and methods

### STUDY AREA

Hokkaido is the northernmost island (41°24'–45°31'N, 139°50'–145°49'E) of Japan and covers 78 073 km<sup>2</sup>. The data analysed in this paper comes from the northern part of the island. The forests in this part cover an area corresponding to about 10% of the island's total area. Within the northern region the climate on the West coast (the Haboro and Rumoi

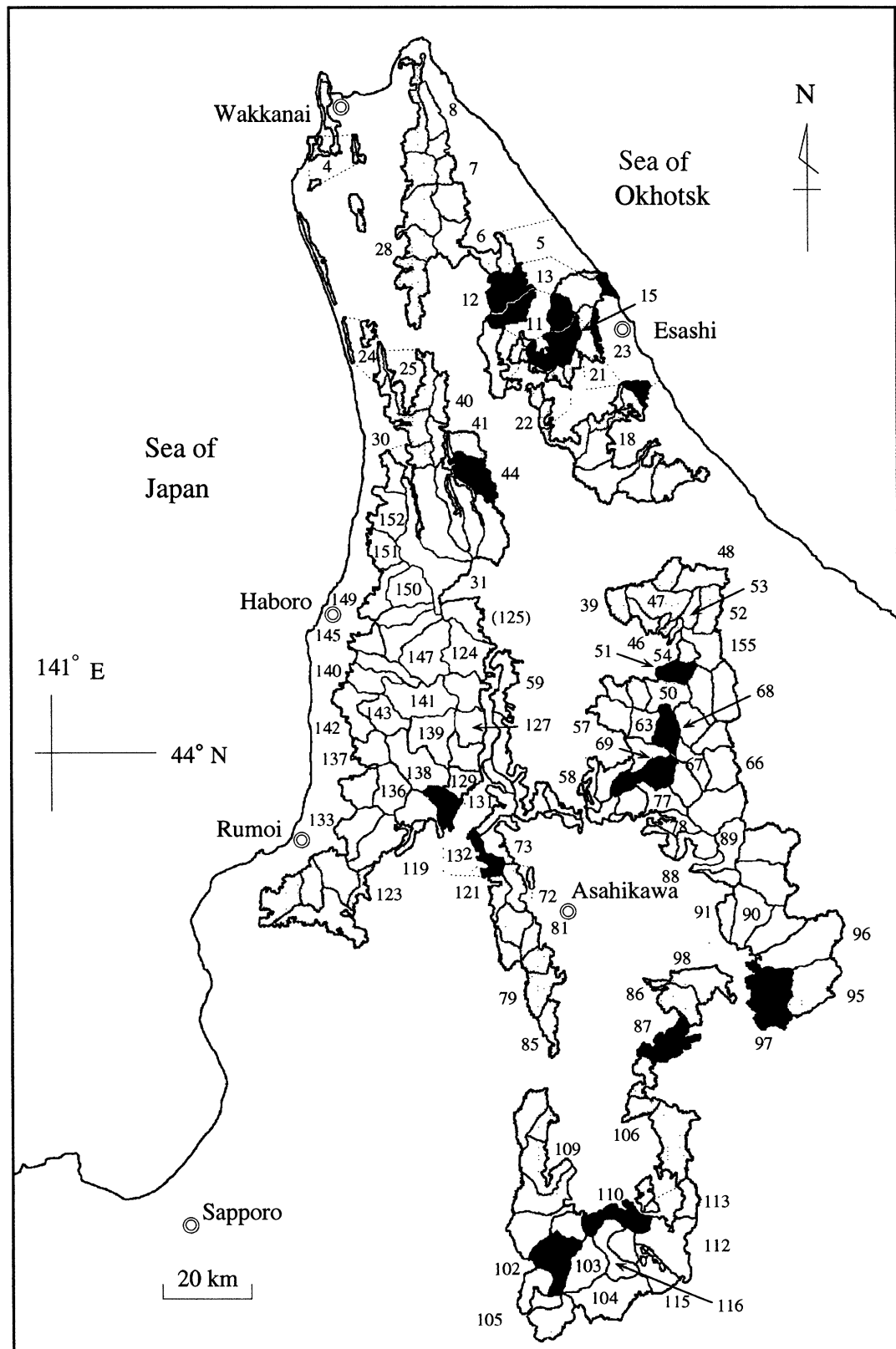
area towards the Sea of Japan; Fig. 1 and Table 1) is somewhat warmer than that of the inland and the East coast (Asahikawa and Esashi). The winters are snowy throughout.

In Hokkaido the grey-sided vole is a pest species on plantations of larch (*Larix kaempferi* [Lambert]) and todo-fir (*Abies sachalinensis* Fr. Schmidt). It is also abundant in natural forests (Ota 1984). Most of the natural forests in this area is classified as the 'pan mixed forest' with needle and broad-leaved trees, which is regarded as a transition between the temperate and the subarctic zones (Tatewaki 1958). The dominant tree genera are *Abies*, *Acer*, *Betula*, *Picea* and *Quercus* (Tatewaki 1958). A similar zone is also found in Scandinavia (Tatewaki 1958). However, the flora of Hokkaido is richer than in Scandinavia. The predator community is also rich in Hokkaido, but has few nomadic predators (Henttonen, Hansson & Saitoh 1992); *Mustela nivalis* L., *M. itatsi* Temminck, *Vulpes vulpes* (L.), and *Elaphe* spp. (snakes) dominate the predator community. Even though the main predators (*M. nivalis* and *V. vulpes*) are the same as those in northern Fennoscandia, more generalist predators are found in Hokkaido (Henttonen *et al.* 1992). A rich alternative prey community (hares, grouse and frogs) also characterizes Hokkaido (Henttonen *et al.* 1992). With respect to flora and fauna, Hokkaido bears some resemblance to the southern transition zone in Fennoscandia (Hansson & Henttonen 1988). Notice, however, that no *Microtus* is found in Hokkaido (for details on rodent community, see next section).

### CENSUS METHODS AND DATA ARRANGEMENT

The Forestry Agency of the Japanese Government has since 1954 carried out censuses of vole populations for management purposes at *c.* 1000 sampling locations in forests all over Hokkaido. The forests managed by the Forestry Agency cover 28 300 km<sup>2</sup> (21 500 km<sup>2</sup> natural forests, and 6800 km<sup>2</sup> planted forests, 1990 figures). These forests were in 1990 managed by 81 District Offices. Every District Office is further divided into several Ranger Offices. The censuses were carried out by the individual Ranger Offices which therefore represent our basic unit of analysis.

Trapping was carried out three times a year in spring (May/June), summer (July/August) and autumn (September/October) on 0.5 ha (50 × 100 m) grids, where 50 snap traps were set at 10-m intervals for five or three nights (below). Since abundance reaches their maximum in autumn in Hokkaido (Saitoh 1987), autumn censuses were used in our analyses to maximize the power of the tests. Ninety Ranger Offices provided complete autumn-series for 31 years (1962–92; Fig. 1). The total number of *C. rufocanus* caught in the 90 Ranger Offices over the 31 years was 45 890; this constitutes 52.3% of the small rodents captured. Three other microtine and murine rodent species were frequently recorded in the material: *C. rutilus* (Pallas),



**Fig. 1.** The study region in the northern part of Hokkaido, Japan. Shaded areas represent the forests managed by the Forestry Agency of the Japanese Government. Numbers indicate the 90 analysed populations. The 13 time series exhibiting significantly negative delayed density dependence according to the bootstrap test based on the Gompertz model using detrended data, are indicated by solid black area. The one time series with significant positive delayed density dependence (No. 125) is given in parentheses. Towns and cities referred to in Table 1 are indicated by double circles.

**Table 1.** Meteorological data for six major towns and cities in northern Hokkaido, Japan (see Fig. 1; SDMO 1991, 1992). Temperatures are given as monthly averages degrees centigrade during 1962–92 in each category. The lowest and highest temperatures in a year are usually recorded in February and August, respectively. The total precipitation (mm), the maximum snow depth (cm), and the number of days with snow cover over 10 cm in a year are also given as averages during 1962–92

City (or town)	Temperature (°C)			Precipitation (mm)	Snow Depth (cm)	Days ( $\geq 10$ cm)
	February	August	Average			
Wakkanai	5.7	19.1	6.4	1180	96.5	115.8
Esashi	7.1	18.6	5.6	1301	115.8	137.7
Haboro	5.3	20.4	7.2	1319	108.3	120.4
Rumoi	4.9	20.6	7.4	1238	107.5	117.5
Asahikawa*	7.6	20.8	6.4	1093	93.5	128.0
Sapporo	3.9	21.7	8.3	1120	99.7	109.0

\* Asahikawa is located in a basin whereas the neighbouring populations are located in mountainous areas. Hence, these measures may be of limited relevance with respect to the neighbouring area.

*Apodemus speciosus* (Temminck), and *A. argenteus* (Temminck). Their percentage in the total number caught in the 90 Ranger Offices was 1.1%, 18.1%, and 28.5%, respectively. In addition, *C. rex* Imaizumi, *A. peninsulae* (Thomas), and shrews (*Sorex* spp.) were occasionally caught. Personnel of the Forestry Agency identified the specimens. *Clethrionomys* is easily distinguished from other rodents. Distinguishing *C. rufocanus* from other *Clethrionomys* species may be more difficult. The number of other *Clethrionomys* species is, however, very low in Hokkaido (Ota 1984), reducing the impact of any misclassification.

Each Ranger Office censused 2–6 separate grids. Census grids were usually located in selected habitats (a planted forest with a neighbouring natural forests) which together constitute a unit. Census grids were sometimes relocated within the area of a given Ranger Office. In this study only samples from the natural forests were analysed, since pesticides were occasionally applied to the plantations.

From 1962 to 1976 traps were set for five nights. From 1977 to 1992 a three day trapping scheme was employed. Census data for the first 15 years were transformed to three-night equivalents, using an empirical regression relation of the three-night ( $N$ ) on the five-night ( $x$ ) captures ( $N = 0.681x + 0.18$ ;  $r^2 = 0.935$ ); when the five-night count was zero the three-night equivalent was also set to zero. This relation was determined from a subset of the five-night data where details on the daily captures were recorded. Although this introduces some unavoidable uncertainty in our analyses, the correspondence (as measured by the  $r^2$ ) is high.

Average census-values for the three-night captures over all grids (sometimes more than one grid was trapped; above) in natural forests within a Ranger Office were used as the abundance index. In order to avoid numerical problems associated with zeros, a fixed number of unity was, following standard practice (Stenseth & Ims 1993b), added to all abundance indices.

Non-stationarity in the form of trends in the mean or non-constant variance is nontrivial in most types

of time series analysis (e.g. Priestley 1981). A trend in the mean is often associated with a trend in the variance. Because of this, detrending the mean by subtracting a regression line of abundance on time, will not alleviate all problems. Furthermore, in the presence of non-constant variance (heteroscedacity), the estimation of any trend in time series will be difficult due to the heteroscedacity in combination with the temporal autocorrelation (Sen & Srivastava 1990). In the present data sets the majority of time series did not entertain any significant trends. However, nine time series did. Pollard, Lakhani & Rothery (1987) and Wolda & Dennis (1993) ascertain that their tests for direct density dependence are very robust to trends in the mean (see also Fox & Ridsdill-Smith 1995). All tests for direct density dependence are therefore conducted on non-detrended data. Our experience is that tests for delayed density dependence is far less robust to trends in the series. Apparently (more on this below), trends often turn up as spurious positive delayed density dependence. Hence, for delayed density dependence, we used linearly detrended data whenever necessary.

For comparison with previous investigations of rodent time series, we calculated the  $s$ -values [the standard deviation of the  $\log_{10}(N + 1)$ ] as a crude index of variability in abundance for each population (Stenseth & Framstad 1980; Henttonen, McGuire & Hansson 1985).

#### THE GREY-SIDED VOLE

The grey-sided vole is the most common rodent in Hokkaido with populations exhibiting a wide spectrum of population dynamics ranging from stable to cyclic (Bjørnstad *et al.* 1996). Even though the between-year variation is extensive, the seasonal pattern is rather predictable. Populations usually increase from spring to autumn and decrease through the winter (Saitoh 1987). The basic biology of this species in Hokkaido is summarized by Ota (1984: Chapter 3): The breeding season lasts from spring (April) to autumn

(October) with a summer pause in August. Winter breeding is sometimes observed. Overwintered populations consist mainly of voles born in the previous autumn. Autumn-born voles usually do not breed in the year they are born, while many of spring-born individuals do. Breeding females usually produce two or three litters during the main breeding season. Litter size usually range from four to six.

In most of its range of distribution, the grey-sided vole is a specialist on the dwarf shrub *Vaccinium myrtillus* L. (Hansson 1985). However, even though *Vaccinium* is common in Hokkaido, the grey-sided vole appears to have a wider diet. The grey-sided vole is more folivorous than the other *Clethrionomys* species (Hansson 1985). This feeding habit is particularly prevalent in Hokkaido – possibly due to the absence of *Microtus*. Leaves and shoots of bamboo grass dominate the food during winter, while various forbs and grasses are eaten during summer. Acorns are also, to some extent, eaten in the autumn while bark are taken during winter (Ota 1984).

Reproducing females of the grey-sided vole are territorial (Saitoh 1985) but flexible (Ims 1987). Maturation of young females is suppressed in populations with high densities (Saitoh 1981; Nakata 1989). However, territory sizes of breeding females are negatively related to female density (Saitoh 1991). Females whose home ranges overlap greatly with other females, appear to fail to become pregnant (Kawata 1987).

#### TESTING FOR DENSITY DEPENDENCE

Denoting the abundance index at time  $t$  by  $N_t$ , and writing the log-transformed abundance as  $X_t$  [ $= \ln(N_t + 1)$ ], density-independent population growth (the null-hypothesis) is represented by  $d_t = X_{t+1} - X_t = e_t$ , where  $e_t$  is a realization of a sequence of independent, identically distributed random variables. In contrast to this null-model, direct density-dependent population growth is represented by  $d_t = F(X_t) + e_t$ , and  $F(X_t)$  is some monotonically decreasing function. Two different models is commonly used to describe density dependence; the Gompertz population model (Gompertz 1825) where a log-linear function of abundance (i.e.  $d_t = a - bX_t$ ) is assumed, or the Ricker population model (Ricker 1954) where a linear function of abundance (i.e.  $d_t = a - bN_t$ ) is assumed.

To visualize the functional relationship between the population growth rate and the abundance,  $d_t$  was plotted against both  $N_t$  and  $X_t$  (Fig. 2). As can be seen, the data suggest log-linearity of the kind assumed in the Gompertz model (Fig. 2b).

We employed four tests for direct density dependence and three tests for delayed density dependence. Even though several authors recommend a specific test (Vickery & Nudds 1991; Holyoak & Crowley 1993; Turchin 1995), different tests may differ with respect

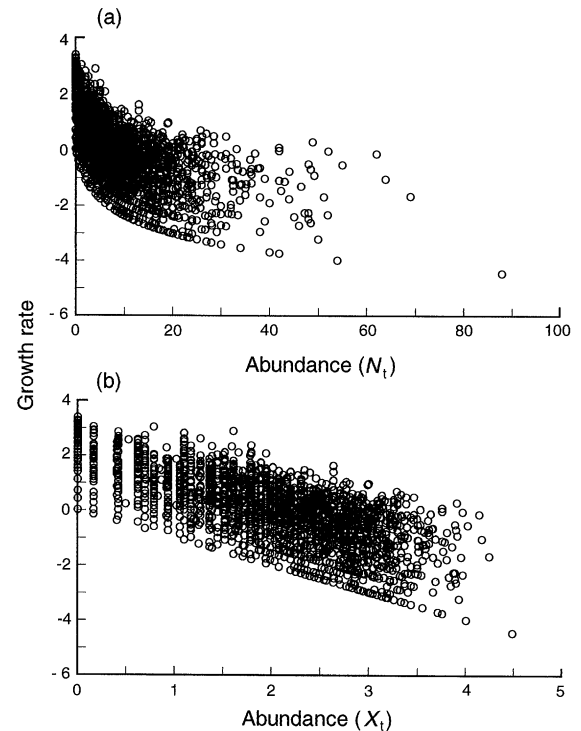


Fig. 2. Relationship between the population growth rate ( $d_t = X_{t+1} - X_t$ ) and abundance index: (a) using  $N_t$  on the abscissa, and (b) using  $X_t = \ln(N_t + 1)$  on the abscissa.

to sensitivity to particular patterns in the data (Holyoak & Lawton 1992; Holyoak 1993; Fox & Ridsdill-Smith 1995). Therefore we apply several techniques. This also facilitates comparison with other studies.

For details of the methods used, the original sources should be consulted. Below we give a synoptic presentation. In addition to the tests in focus we report on the test results based on the first and second order autoregressive coefficients in the autoregressive model (Reddingius 1990). The latter model is the focus of the study by Stenseth *et al.* (1996).

#### Direct density dependence

##### (i) The autocorrelation method of Bulmer (1975)

The test statistic proposed by Bulmer (1975) is given by  $R = V/U$ , where

$$V = \sum_{t=1}^n (X_t - \bar{X})^2, \quad U = \sum_{t=1}^{n-1} (X_{t+1} - X_t)^2,$$

and  $n$  ( $= 31$ ) is the number of years in the time series. Critical values of  $R$  are given in Bulmer (1975). This test statistic is the reciprocal of the Geary's ratio (or the scaled semivariance; Cressie 1991) used to test for spatial dependency in geostatistics, and the Schoener's ratio (Schoener 1981) used to test for autocorrelation in home range analysis. It is thus a measure of wide applicability in the quantification of non-randomness.

*(ii) The randomization test of Pollard et al. (1987)*

Under the null-hypothesis of density-independent growth, the sequence of the  $d_t$  values may be randomized, as each ordering of the sequence is equally likely. The Pearson correlation coefficient between  $d_t$  and  $X_t$  is used as the test statistic; Thus, the Gompertz model is used as the alternative hypothesis. This statistic was calculated for the original as well as for 10 000 randomized sequences. The null-hypothesis was rejected, whenever less than 5% of the test statistics for the randomized series were smaller than or equal to that for the real series (the one-tailed test).

*(iii) The bootstrap test of Dennis & Taper (1994) based on the Ricker model*

The original bootstrap test of Dennis & Taper (1994) uses the Ricker model as the alternative hypothesis (see also Kemp & Dennis 1993; Wolda & Dennis 1993). The test statistic, which is identical to the one used in linear regression of  $d_t$  on  $N_t$  was compared with the null-distribution based on 10 000 time series derived through a computer-intensive method under the null-hypothesis. Rejection of the null-hypothesis was done at a nominal 5% level (as in *ii* above).

*(iv) The bootstrap test of Dennis & Taper (1994) based on the Gompertz model*

We further performed the procedure originally suggested by Dennis & Taper (1994) with the Gompertz model as the alternative. That is, the linear regression of  $d_t$  on  $X_t$  was investigated.

*Delayed density dependence*

A crucial aspect in testing for delayed density dependence is that strong direct density dependence will contaminate the relationship between  $d_t (= X_{t+1} - X_t)$  and  $X_{t-1}$  (or  $N_{t-1}$ ). To correct for such effects, the effect of the direct dependence was 'partialled out', both in the test statistic and in the computer-intensive generation of the null-distribution for the test statistic (Holyoak 1994). This is in exact analogy to the partial autocorrelation function (PACF, e.g. Royama 1992).

*(v) The extended randomization test of Pollard et al. (1987)*

Density-independent time series were generated by the procedure described by Pollard *et al.* (1987). By analogy to test (*ii*), the test statistic is the partial correlation coefficient (e.g. Sokal & Rohlf 1981) between  $d_t$  and  $X_{t-1}$  given  $X_t$ . This was done for the observed and the 10 000 randomized sequences.

*(vi) & (vii) The extended bootstrap test of Dennis & Taper (1994) based on the Ricker as well as the Gompertz model*

Density-independent time series were generated by the procedure in Dennis & Taper (1994), modified as described above (see *iii*). The test statistic is the partial regression coefficient (e.g. Sokal & Rohlf 1981).

**Results**

## GENERAL FEATURES

The distribution of the  $s$ -values was symmetric around the mean of  $0.40 \pm 0.05$  ( $\pm$  SD; Fig. 3). The observed range of  $s$ -values covers the major part of the values reported in the literature for other microtine populations, except for a lack of the extreme values (Henttonen *et al.* 1985; Ostfeld 1988).

## DIRECT DENSITY DEPENDENCE

Bulmer's test ( $R$ ) detected direct density dependence in all 90 time series at a nominal 5% (Table 2). The randomization test of Pollard *et al.* (1987) gave consistent results with these. All but one time series (98.9%) exhibited strong evidence of density dependence. The bootstrap test of Dennis & Taper (1994) using the Ricker model detected density dependence in 81 series (90.0%), while that using the Gompertz model detected density dependence in all but three time series (96.7%). The higher detection rate, using the Gompertz model, is likely to reflect the closer fit of that model to the time series (Fig. 2). There was no clear relationship between the detection rates and the trend in abundance (Table 2). A typical direct density-dependent population without delayed density dependence (No. 39) is shown in Fig. 4.

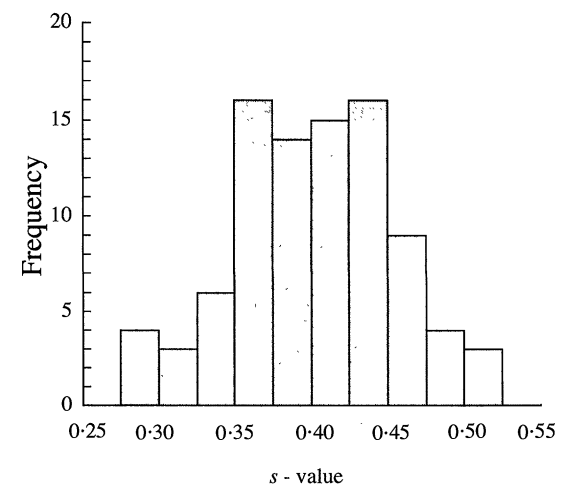


Fig. 3. Frequency distribution of  $s$ -value in the 90 time series.

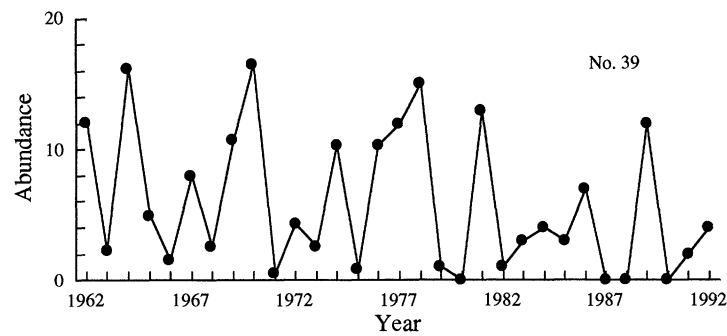


Fig. 4. The density fluctuations in a population with strong direct density dependence without any significant delayed density dependence (No. 39).

#### DELAYED DENSITY DEPENDENCE

The results of delayed density dependence (1 year lag) are summarized in Table 2. For non-detrended series the extended randomization test and the extended bootstrap test using the Gompertz model detected delayed density dependence in similar percentage of time series (14.4% and 16.7%, respectively). The extended bootstrap test using the Ricker model detected delayed density dependence less frequently (11.1%).

Using the detrended data, the extended randomization test, the extended bootstrap test using the Gompertz model, and that test using the Ricker model detected delayed density dependence in 15.6%, 15.6% and 8.9% of time series, respectively (Table 2). Detrending the series eliminated most apparent incidences of positive delayed density dependence. The results were consistent with those of the autoregressive analyses carried out by Stenseth *et al.* (1996).

A typical population (No. 15) with negatively

delayed density dependence is shown in Fig. 5. This population exhibited significant delayed density dependence according to two of the three tests (the extended randomization test and the extended bootstrap test using the Gompertz model) both in non-detrended and detrended data. This series also showed strong direct density dependence according to all tests. It oscillates with a 3–5-year interval with high amplitude ( $s$ -value = 0.46). No populations exhibiting negatively delayed density dependence were found on the Haboro-Rumoi region; they were all scattered around the eastern or more interior areas (Fig. 1).

#### Discussion

The great consistency across the methods is a striking feature in our analysis. This is particularly so in the case of direct density dependence. All tests essentially gave the same results; namely, strong negative density dependence in the growth rates. We interpret this to

Table 2. Results from the testing for direct density dependence using four methods, and the testing for delayed density dependence using three methods on 90 time-series covering 31 years. The number of populations which exhibited density dependence are shown for detrended and non-detrended populations. Figures in parentheses indicates the numbers of positive delayed density-dependent populations. Results of the autoregressive analysis are further described by Stenseth *et al.* (1996)

	Direct density dependence					Delayed density dependence			
	Bulmer <sup>a</sup>	Pollard <sup>b</sup>	Dennis & Taper <sup>c</sup> Ricker	Gompertz	AR(1) <sup>d</sup>	Pollard <sup>e</sup>	Dennis & Taper <sup>f</sup> Ricker	Gompertz	AR(2) <sup>g</sup>
9 populations with trends									
Not detrended	9	8	8	8	9	2(2)	2(2)	2(2)	1(1)
Detrended	–	–	–	–	9	0	0	0	1(1)
81 populations without trend									
Not detrended	81	81	73	79	81	11(5)	8(6)	13(3)	15(1)
Detrended	–	–	–	–	81	14(3)	8(6)	14(1)	15(1)

<sup>a</sup> Autocorrelation test of Bulmer (1975).

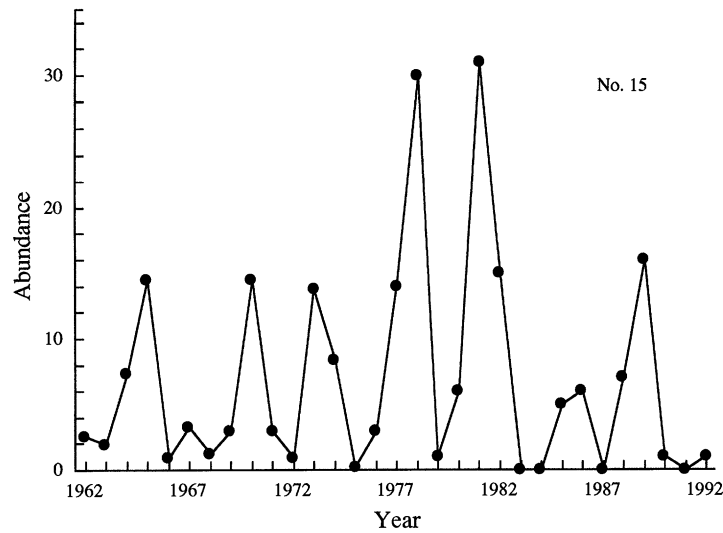
<sup>b</sup> The randomization test of Pollard *et al.* (1987).

<sup>c</sup> The boot-strapping test of Dennis & Taper (1994).

<sup>d</sup> First order autoregressive process (AR(1)) was used for direct density dependence. Delayed density dependence was tested by the second order autoregressive model (AR(2)). This statistical model is discussed in detail by Stenseth *et al.* (1996).

<sup>e</sup> The extended randomization test of Pollard *et al.* (1987).

<sup>f</sup> The extended boot-strapping test of Dennis & Taper (1994).



**Fig. 5.** The density fluctuations in a population with strong negative delayed density dependence (No. 15). This population exhibit significant delayed density dependence according to both the extended randomization test and the extended bootstrap test using the Gompertz model.

say that the abundance of the grey-sided vole in Hokkaido are governed by factors leading to strong density dependence.

Small mammals such as microtine rodents, and in particular the genus *Clethrionomys*, often show strong spatial and social organization (Bondrup-Nielsen & Karlsson 1985; Bujalska 1985; Gipps 1985; Ims 1987; see also Cockburn 1988). *Clethrionomys* species are therefore prime candidates for the detection of density dependence. Female grey-sided voles are often seen to establish territories as well as to exhibit delayed maturation at high densities (see Introduction and The grey-sided vole), both of which may cause direct density dependence in the population growth rate. In Hokkaido, territoriality in the grey-sided vole is commonly observed (Saitoh 1985); maturation rates are furthermore known to be reduced at high densities (Abe 1976; Saitoh 1981; Nakata 1989; but see Saitoh 1991). Our study thus links earlier studies on spacing behaviour and density dependence in life-history parameters (e.g. Abe 1976; Gaines & McClenaghan 1980; Bujalska 1988; Nakata 1989; Saitoh 1991; Ostfeld, Canham & Pugh 1993; Ostfeld & Canham 1995) with regulation at the population level. The presence of density dependence in life-history parameters as well as population growth rates have previously been demonstrated for other mammalian herbivores (e.g. Fowler 1981; Clutton-Brock & Albon 1985, 1989; Messier 1994; for a review, see Fowler 1987).

The patterns of delayed density dependence in *C. rufocanus* in Hokkaido is less clear-cut than that of direct density dependence. The test results based on the Ricker model diverged markedly from those obtained by the other tests. The Ricker bootstrap test suggests several instances of positive delayed density dependence. We suspect that this is an artefact of the inappropriateness of the Ricker model for these series. Another notable problem is that trends in abundance

appear to induce instances of spurious positive delayed density dependence (Table 2).

The two tests employing the Gompertz model as the alternative detected negative delayed density dependence more frequently than expected by chance alone. Although the number of populations exhibiting negative delayed density dependence was relatively small compared to similar time series in Fennoscandia (where all cyclic series exhibit significant negative delayed density dependence; Bjørnstad *et al.* 1995). In a separate analysis of the same time series as those analysed here, Bjørnstad *et al.* (1996) reported that interior and eastern populations had clear 3–4-year rhythms, whereas western coastal populations did not exhibit multiannual cycles. In light of that result, and of the results from recent Fennoscandian studies (Hörnfeld 1994; Saucy 1994; Bjørnstad *et al.* 1995), one would anticipate a somewhat higher incidence of delayed density dependence than found in this study. The deviation between these expectations and our results remains unclear. Further progress on this issue must await the collection and analyses on data of different types of fluctuation.

Predation by generalists is commonly assumed to increase in response to rodent density without lag, while specialist predators are believed to track rodent densities with a time delay (Hassell & May 1986; Hanski *et al.* 1991; Hanski and Korpimäki 1995). Such predator–prey interactions are often invoked to explain geographic variation in patterns of fluctuations in rodents (Hansson & Henttonen 1985; Henttonen *et al.* 1985, 1992; Hansson 1987; Hansson & Henttonen 1988; Hanski *et al.* 1993). It is hypothesized that specialist predators generate multiannual cycles in northern Fennoscandia and that abundant generalist predators modify the dynamics into noncyclic and more stable in the south.

The predator–prey community in northern Fen-



noscandia is dominated by specialist predators with few alternative prey species, whereas a multitude of alternative prey for a variety of generalist predators exists in Hokkaido (Henttonen *et al.* 1992). Thus, the present result that most time series showed direct density dependence may also be the result of the action of generalist predators. It seems though that self-regulation through spacing behaviour and social interaction is the simplest explanation for the high incidence of direct density dependence.

The predator-prey hypothesis of biogeographic differences in dynamics has been suggested to be related to local climatic conditions (Hansson 1987). In a mild climate with short winters voles have no subnivean refuge from generalist predators. In areas with long snow-rich winters, in contrast, there will be a general scarcity of prey for generalist predators because these rarely probe under deep snow. Thus, small specialist predators with subnivean hunting habits are likely to be more dominant in such climatic conditions. The interior and eastern parts of our study area have winters that are more severe (cold and heavy snow; Table 1) than the western coastal area. The interior and eastern parts correspond to that in which most populations are known to exhibit multiannual rhythms (Bjørnstad *et al.* 1996), and in which we, presently, observed some evidence of negative delayed density dependence. The western Haboro-Rumoi region, where no negatively delayed density-dependent populations were found, is warmer and has shorter periods with snow-cover than other areas (Table 1). Further speculations on this issue must await more detailed data on the ecological communities and local climatic conditions. The meteorological data from the interior Asahikawa indicate little snow (Table 1). This does not reflect the real climatic conditions for these areas, however, since Asahikawa is located in a basin whereas the studied populations are located in mountainous areas.

A key feature emerging from our analyses is the clear tendency for the Ricker based model to be less indicative of density dependence. This, we believe, relates to the growth rates of our populations being approximately log-linearly, rather than linearly, related to abundance (Fig. 2). Altogether our analyses suggest that the Gompertz model represents a more appropriate model for the population dynamics of the grey-sided vole in Hokkaido than the Ricker model. This might be a more generally valid conclusion, not least because a change of one density unit at low density is generally likely to have a much larger effect on the population growth than a change of one density unit at a higher density level.

As a concluding footnote we need to comment briefly on the possible influence of density-independent factors in the determination of observed population fluctuation pattern. It is well known that the Gompertz model cannot give rise to sustained density cycles in the absence of environmental noise (Royama 1992;

Bjørnstad *et al.* 1995). However, with environmental stochasticity, the Gompertz model may easily give rise to sustained cycles of similar periodicity as those observed both in Fennoscandia (Bjørnstad *et al.* 1995) and in Hokkaido (Stenseth *et al.* 1996). Our analyses bring us back to a long-lasting controversy in ecology; namely, the role of determinism and density dependence on the one hand, and stochasticity and density independence (such as weather) on the other hand (for reviews, see Itô 1980; Krebs 1985; Cappuccino & Price 1995; Turchin 1995). In order to bridge the gap between these views, it is important not only to test for density dependence, but to quantify the strength and relative contribution of the density-dependent and the density-independent factors (such as demographic and environmental stochasticity) when studying population variability (Reddingius 1990; Royama 1992; Wolda 1995).

### Acknowledgements

We are indebted to the Forestry Agency of the Japanese Government for providing the material analysed in this paper. A grant from Japan Society for Promotion Science, given to H. Abe for bringing N.C.S. to Japan, made it possible to start the analyses reported in this paper; a follow-up grant from the Norwegian Research Council, given to N.C.S. for bring T.S. to Norway, facilitated our analyses; a travel grant from the Norwegian Research Council to N.C.S. was instrumental in completing the final revision of the present paper. We are also indebted to Zelalem Mengistu and Masakado Kawata for their kind help with computer programming. Peter Turchin is thanked for valuable comments on an earlier version of this paper. Comments by two anonymous referees are also greatly appreciated.

### References

- Abe, H. (1976) Population structure and reproductive activity of *Clethrionomys rufocanus bedfordiae* (Thomas) in a wind shelter-belt of the Ishikari Plain, Hokkaido. *Journal of the Mammalogical Society of Japan*, **7**, 17–30. (In Japanese with English summary.)
- Batzli, G.O. (1985a) The role of nutrition in population cycles of microtine rodents. *Acta Zoologica Fennica*, **173**, 13–17.
- Batzli, G.O. (1985b) Nutrition. *Biology of New World Microtus* (ed. R. H. Tamarin), Special Publication of the American Society of Mammalogists, **8**, 778–811.
- Bjørnstad, O.N., Falck & Stenseth, N.C. (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proceedings of the Royal Society of London B*, **262**, 127–133.
- Bjørnstad, O.N., Champely, S., Stenseth, N.C. & Saitoh, T. (1996) Cyclicity and stability of grey-sided voles, *Clethrionomys rufocanus*, of Hokkaido: spectral and principal components analyses. *Philosophical Transactions of the Royal Society of London B*, **351**, 867–875.
- Bondrup-Nielsen, S. (1986) Investigation of spacing behaviour

- of *Clethrionomys gapperi* by experimentation. *Journal of Animal Ecology*, **55**, 269–280.
- Bondrup-Nielsen, S & Karlsson, F. (1985) Movements and spatial patterns in populations of *Clethrionomys* species: a review. *Annales Zoologici Fennici*, **22**, 373–399.
- Bujalska, G. (1970) Reproduction stabilizing elements in an island populations of *Clethrionomys glareolus* (Schreber, 1780). *Acta Theriologica*, **15**, 381–412.
- Bujalska, G. (1985) Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. *Annales Zoologici Fennici*, **22**, 331–342.
- Bujalska, G. (1988) Life history consequences of territoriality in the bank vole. *Evolution of Life Histories of Mammals* (ed. M. S. Boyce), pp. 75–90. Yale University Press, New Haven.
- Bulmer, M. (1975) The statistical analysis of density dependence. *Biometrics*, **31**, 901–911.
- Cappuccino, N. & Price, P. (eds) (1995) *Population Dynamics*. Academic Press, New York.
- Charnov, E.L. & Finerty, J.P. (1980) Vole population cycles: a case for kin-selection? *Oecologia*, **45**, 1–2.
- Chitty, D. (1960) Population processes in the vole and the relevance to general theory. *Canadian Journal of Zoology*, **38**, 99–113.
- Chitty, D. (1967) The natural selection of self-regulatory behaviour in animal populations. *Proceedings of the Ecological Society of Australia*, **2**, 51–78.
- Christian, J.J. (1950) The andro-pituitary system and population cycles in small mammals. *Journal of Mammalogy*, **31**, 247–259.
- Christian, J.J. (1980) Endocrine factors in population regulation. *Biosocial Mechanism in Population Regulation* (eds M. N. Cohen, R. S. Malpass & H. G. Klein), pp. 55–115. Yale University Press, New Haven.
- Clutton-Brock, T.H. & Albon, S.D. (1985) Competition and population regulation in social mammals. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (eds R. M. Sibly & R. H. Smith), pp. 557–575. Blackwell Scientific Publications, Oxford.
- Clutton-Brock, T.H. & Albon, S.D. (1989) *Red Deer in the Highlands*. Blackwell Scientific Publications, Oxford.
- Cockburn, A. (1988) *Social Behaviour in Fluctuating Populations*. Croom Helm, London.
- Cressie, N. (1991) *Statistics for Spatial Data*. Wiley, New York.
- Dennis, B. & Taper, M.L. (1994) Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs*, **64**, 205–224.
- Fowler, C.W. (1981) Density dependence as related to life history strategy. *Ecology*, **62**, 602–610.
- Fowler, C.W. (1987) A review of density dependence in populations of large mammals. *Current Mammalogy*, Vol. 1 (ed. H. H. Genoways), pp. 401–441. Plenum, New York.
- Fox, E.R. & Ridsdill-Smith, J. (1995) Tests for density dependence revisited. *Oecologia*, **103**, 435–443.
- Fuller, W.A. (1969) Changes in numbers of three species of small rodent near Great Slave Lake, N.W.T. Canada, 1964–1967, and their significance for general population theory. *Annales Zoologici Fennici*, **6**, 113–144.
- Gaines, M.S. & McClenaghan, L.R. Jr (1980) Dispersal in small mammals. *Annual Review of Ecology and Systematics*, **11**, 163–196.
- Gilbert, B.S., Krebs, C.J., Talarico, D. & Cichowski, D.B. (1986) Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology*, **55**, 543–552.
- Gipps, J.H.W. (1985) The behaviour of bank voles. *The Ecology of Woodland Rodents: Bank Voles and Wood Mice* (eds J. R. Flowerdew, J. Gurnell & J. H. W. Gipps), Oxford Science Publications, Oxford, *Symposia of the Zoological Society of London*, **55**, 61–87.
- Gompertz, B. (1825) On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philosophical Transactions of the Royal Society of London*, **115**, 513–585.
- Hanski, I. (1990) Density dependence, regulation and variability in animal populations. *Regulation and Relative Abundance of Plants and Animals* (eds R. M. May & M. P. Hassell), pp. 140–150. The Royal Society, London.
- Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, **60**, 353–367.
- Hanski, I., L. Turchin, P., Korpimäki, E. & Henttonen, H. (1993) Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, **364**, 232–235.
- Hanski, I. & Korpimäki, E. (1995) Microtine rodent dynamics in northern Europe: parameterized models for the predator–prey interaction. *Ecology*, **76**, 840–850.
- Hansson, L. (1985) *Clethrionomys* food: genetic, specific and regional characteristics. *Annales Zoologici Fennici*, **22**, 315–318.
- Hansson, L. (1987) An interpretation of rodent dynamics as due to trophic interactions. *Oikos*, **50**, 308–318.
- 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 process. *Trends in Ecology and Evolution*, **3**, 195–200.
- Hassell, M.P. & May, R.M. (1986) Generalist and specialist natural enemies in insect predator–prey interactions. *Journal of Animal Ecology*, **55**, 923–940.
- 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. *Annales Zoologici Fennici*, **22**, 221–227.
- Henttonen, H., Hansson, L. & Saitoh, T. (1992) Rodent dynamics and community structure: *Clethrionomys rufocanus* in northern Fennoscandia and Hokkaido. *Annales Zoologici Fennici*, **29**, 1–6.
- Hestbeck, J. (1982) Population regulation of cyclic small mammals: the social fence hypothesis. *Oikos*, **39**, 157–163.
- Holyoak, M. (1993) New insights into testing for density dependence. *Oecologia*, **93**, 435–444.
- Holyoak, M. (1994) Identifying delayed density dependence in time series data. *Oikos*, **70**, 296–304.
- Holyoak, M. & Lawton, J.H. (1992) Detection of density dependence from annual censuses of bracken-feeding insects. *Oecologia*, **91**, 425–430.
- Holyoak, M. & Crowley, P.H. (1993) Avoiding erroneously high levels of detection in combinations of semi-independent tests. *Oecologia*, **95**, 103–114.
- Hörnfeldt, B. (1994) Delayed density dependence as a determinant of vole cycles. *Ecology*, **75**, 791–806.
- Ims, R.A. (1987) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *Journal of Animal Ecology*, **56**, 585–596.
- Itô, Y. (1980) *Comparative Ecology*. Cambridge University Press, Cambridge.
- Kalela, O. (1957) Regulation of reproductive rate in subarctic populations of the vole, *Clethrionomys rufocanus* (Sund.). *Annales Academiae Scientiarum Fennicae, Series A, IV Biologica*, **34**, 1–60.
- Kawata, M. (1987) Pregnancy failure and suppression by female–female interaction in enclosed populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Behavioural Ecology and Sociobiology*, **20**, 89–97.

- Kemp, W.P. & Dennis, B. (1993) Density dependence in rangeland grasshoppers (Orthoptera: Acrididae). *Oecologia*, **96**, 1–8.
- Krebs, C.J. (1978) A review of the Chitty hypothesis of population regulation. *Canadian Journal of Zoology*, **56**, 2463–2480.
- Krebs, C.J. (1985) *Ecology*, 3rd edn. Harper & Row, New York.
- Krebs, C.J. (1991) The experimental paradigm and long-term population studies. *Ibis*, **133** (suppl.), 3–8.
- Krebs, C.J. (1993) Are lemmings large *Microtus* or small reindeer? A review of lemming cycles after 25 years and recommendations for future work. *The Biology of Lemming* (eds N. C. Stenseth & R. A. Ims), pp. 248–260. Academic Press, London.
- Krebs, C.J. & Myers, J.H. (1974) Population cycles in small mammals. *Advances in Ecological Research*, **8**, 267–299.
- Madison, D.M. (1985) Activity rhythms and spacing. *Biology of New World Microtus* (ed. R. H. Tamarin), Special publication of the American society of Mammalogists, **8**, 567–620.
- Messier, F. (1994) Ungulate population models with predation: a case study with the North American moose. *Ecology*, **75**, 478–488.
- Nakata, K. (1989) Regulation of reproduction rate in a cyclic population of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Researches on Population Ecology*, **31**, 185–209.
- Ostfeld, R.S. (1988) Fluctuations and constancy in populations of small rodents. *American Naturalist*, **131**, 445–452.
- Ostfeld, R.S. (1990) The ecology of territoriality in small mammals. *Trends in Ecology and Evolution*, **5**, 411–415.
- Ostfeld, R. S., Canham, C.D. & Pugh, S.R. (1993) Intrinsic density-dependent regulation of vole populations. *Nature*, **366**, 259–261.
- Ostfeld, R. S. & Canham, C.D. (1995) Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76**, 521–532.
- Ota, K. (ed.) (1984) *Study on Wild Murid Rodents in Hokkaido*. Hokkaido University Press, Sapporo (in Japanese).
- Pearson, O.P. (1964) Carnivore–mouse predation: an example of its intensity and bioenergetics. *Journal of Mammalogy*, **45**, 177–188.
- Pearson, O.P. (1966) The prey of carnivores during one cycle of mouse abundance. *Journal of Animal Ecology*, **35**, 217–233.
- Pitelka, F.A. (1958) Some aspects of the populations structure in the short-term cycle of the brown lemming in northern Alaska. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 237–251.
- Pollard, E., Lakhani, K.H. & Rothery, P. (1987) The detection of density dependence from a series of annual censuses. *Ecology*, **68**, 2046–2055.
- Priestley, M.B. (1981) *Spectral Analysis and Time Series*. Academic Press, London.
- Reddingius, J. (1990) Models for testing: a secondary note. *Oecologia*, **83**, 50–52.
- Ricker, W.E. (1954) Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, **11**, 559–923.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, London.
- Saitoh, T. (1981) Control of female maturation in high density populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. *Journal of Animal Ecology*, **50**, 79–87.
- Saitoh, T. (1985) Practical definition of territory and its application to the spatial distribution of voles. *Journal of Ethology*, **3**, 143–149.
- Saitoh, T. (1987) A time series and geographical analysis of population dynamics of the red-backed vole in Hokkaido, Japan. *Oecologia*, **73**, 382–388.
- Saitoh, T. (1991) The effect and limits of territoriality on population regulation in grey red-backed voles, *Clethrionomys rufocanus bedfordiae*. *Researches on Population Ecology*, **33**, 367–386.
- SDMO (Sapporo District Meteorological Office) (1991, 1992) *The Climate In Hokkaido*. Nihon Kisho-kyokai, Sapporo (in Japanese).
- Saucy, F. (1994) Density dependence in time series of the fossorial form of the water vole, *Arvicola terrestris*. *Oikos*, **71**, 381–392.
- Schoener, T.W. (1981) An empirically based estimate of home range. *Theoretical Population Biology*, **20**, 281–325.
- Sen, A. & Srivastava, M. (1990) *Regression Analysis: Theory, Method and Applications*. Springer-Verlag, New York.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. Freeman, New York.
- Stenseth, N.C. (1977) Evolutionary aspects of demographic cycles: the relevance of some models of cycles for microtine fluctuations. *Oikos*, **29**, 525–538.
- Stenseth, N.C. (1981) On Chitty's theory for fluctuating populations: the importance of genetic polymorphism in the generation of regular cycles. *Journal of Theoretical Biology*, **90**, 9–39.
- Stenseth, N.C. (1986) On the interaction between stabilizing social factors and destabilizing trophic factors in small rodent populations. *Theoretical Population Biology*, **29**, 365–384.
- Stenseth, N.C. & Framstad (1980) Reproductive effort and optimal reproductive rates in small rodents. *Oikos*, **34**, 23–34.
- Stenseth, N.C. & Ims, R.A. (1993a) Population dynamics of lemmings: temporal and spatial variation – an introduction. *The Biology of Lemming* (eds N. C. Stenseth & R. A. Ims), pp. 61–96. Academic Press, London.
- Stenseth, N.C. & Ims, R.A. (1993b) Techniques for studying the population biology of lemmings – an introduction. *The Biology of Lemming* (eds N. C. Stenseth & R. A. Ims), pp. 535–546. Academic Press, London.
- Stenseth, N. C, Bjørnstad, O.N. & Saitoh, T. (1996) A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of the Royal Society of London B*, **263**, 1117–1126.
- Tatewaki, M. (1958) Forest ecology of the islands of the north pacific ocean. *Journal of the Faculty of Agriculture of Hokkaido University*, **50**, 371–472.
- Turchin, P. (1993) Chaos and stability in rodent population dynamics: evidence from non-linear time-series analysis. *Oikos*, **68**, 167–172.
- Turchin, P. (1995) Population regulation: old arguments and a new synthesis. *Population dynamics* (eds N. Cappuccino & P. Price), pp. 19–40. Academic Press, New York.
- Vickery, W.L. & Nudds, T.D. (1991) Testing for density-dependent effects in sequential censuses. *Oecologia*, **85**, 419–423.
- Woiwod, I.P. & Hanski, I. (1992) Patterns of density dependence in moths and aphids. *Journal of Animal Ecology*, **61**, 619–629.
- Wolda, H. & Dennis, B. (1993) Density dependence tests, are they? *Oecologia*, **95**, 581–591.
- Wolda, H. (1995) The demise of the population regulation controversy? *Researches on Population Ecology*, **37**, 91–93.

Received 13 July 1995; revision received 12 March 1996