A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan*

NILS CHR. STENSETH[1], OTTAR N. BJØRNSTAD[1] AND TAKASHI SAITOH[2]

[1] *Division of Zoology, Department of Biology, University of Oslo, P.O. Box 1050, Blindern, N-0316, Oslo, Norway*
[2] *Wildlife Management Laboratory, Hokkaido Research Centre, Forestry and Forest Products Research Institute, Hitsujigaoka 7, Toyohira, Sapporo, Japan 062*

SUMMARY

A total of 31 years of abundance data from 90 populations of the grey-sided vole (*Clethrionomys rufocanus*) in northern Hokkaido (Japan) were analysed with respect to population dynamic characteristics. Both non-periodic and multi-annually periodic fluctuations occur among the studied populations. The length of the period varies from 2 to 5 years. The dynamics appear approximately linear on a logarithmic scale, and a log-linear stochastic difference model with one time-lag is found to recreate the periodograms of the time series. The deterministic (log-linear) component of these models determines the periodicity while stochasticity sustains the cycles. The dynamics of the Hokkaidian vole populations are found to vary clinally from the western coast eastwards and towards the interior of the study area. This gradient corresponds superficially to the latitudinal gradient seen in microtine populations in Fennoscandia. However, under close scrutiny, these gradients differ greatly: the Hokkaidian gradient is caused by a cline in delayed density dependence. Statistical delayed density dependence is more negative towards the east and the interior.

1. INTRODUCTION

Microtine rodents are well known for their multi-annual periodic density fluctuations (for examples, see Elton 1924, 1942; Krebs & Myers 1974; Stenseth & Ims 1993*a*, *b*), commonly referred to as the 'microtine density cycle' (see, for example, Stenseth 1985*a*). A central set of issues in the study of these density cycles relates to the geographic variation in dynamic features of any given species. The multi-annual density cycles occur only in parts of the species' range, and the period and amplitude vary within the region in which the cycles occur (Henttonen *et al.* 1985; Warkowska-Dratnal & Stenseth 1985; Hansson & Henttonen 1988; for review, see Stenseth & Ims 1993*b*). The northern red-backed vole (*Clethrionomys rutilus*), for instance, exhibits regular multi-annual cycles in Northern Europe, whereas, at the same latitude in North America, it does not (Henttonen *et al.* 1985; Gilbert & Krebs 1991). Within Europe, most microtines are cyclic north of 60° N and non-cyclic in the southern parts (Hansson 1971; Hansson & Henttonen 1985, 1988; Henttonen *et al.* 1985; Stenseth *et al.* 1985). North of 60° N, there is furthermore a latitudinal gradient in the periodicity and amplitude of the cycles (see, for example, Hanski *et al.* 1991; Bjørnstad *et al.* 1995). The gradient has been shown to be predom-

inately caused by an underlying gradient in the strength of direct density dependence (Bjørnstad *et al.* 1995).

Recently, Bjørnstad *et al.* (1996) documented the existence of geographic variation in the periodicity of fluctuations of the grey-sided vole (*Clethrionomys rufocanus* (Sundevall 1846)) in Hokkaido, Japan. Here we report on time series modelling of these data. We demonstrate that there is primarily a clinal gradient in delayed density dependence as going from the western coast to the eastern and interior part of Hokkaido. Our analysis suggests that the observed diversity of dynamics may adequately be accounted for by a log-linear model with a time delay.

2. MATERIALS AND METHODS

(*a*) Study area and data

The data discussed in this paper were collected in forested regions of northern Hokkaido (figure 1; 41° 24′–45° 31′ N, 139° 50′–145° 49′ E). Biogeographically, Hokkaido resembles the neighbouring Asian mainland more than the other Japanese islands (Tatewaki 1958; Kondo 1993) (figure 1*a*). Hokkaido belongs broadly to the coniferous taiga forest extending large parts of the Palaearctic, while the southern islands of Japan belong to temperate and subtropical biomes (see, for example, Walters 1984). The average temperature in August (the warmest month) in north-eastern Hokkaido (figure 2) is 20.8 °C (averaged over the survey years from 1962 to 1992); the average temperature in February (the coldest month) is −7.6 °C (SDMO 1991, 1992; see also Saitoh *et al.* 1996). Snow is abundant during 3–4.5 months

---

* Dedicated to the late Kashio Ota for his scientific leadership in rodent research and for profoundly contributing to the initiation of the monitoring programme in Hokkaido upon which data this paper rests.

Proc. R. Soc. Lond. B (1996) **263**, 1117–1126
Printed in Great Britain
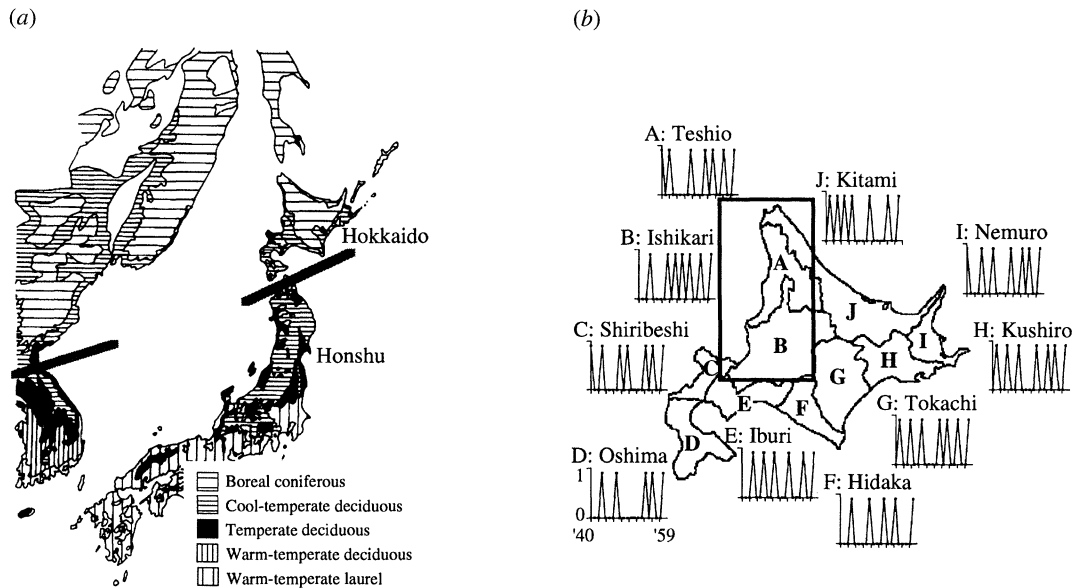
1117

© 1996 The Royal Society

(a)

(b)

Figure 1. The study sites are located on Hokkaido, the northernmost island of Japan, close to the Asian mainland (a). The grey-sided vole (*Clethrionomys rufocanus*) is found north of the grey bar between Hokkaido and Honshu (which coincide with the so-called 'Blakiston's Line' (cf. Blakiston & Pryer 1880; see also Kuroda 1939; Smith 1983; Dobson 1994)), and north of the corresponding bar on the Asian mainland (Kondo 1982; Kaneko 1990). The principal vegetation types of this region is indicated (after Kondo 1990). As can be seen, the boreal forest dominates in Hokkaido. (b) A close-up of Hokkaido with an indication of the occurrence of outbreak densities of the grey-sided vole (given in binary form) in the various regions of Hokkaido (adopted from: Ota 1984). The rectangle indicates the crude demarcation of the study area.

each winter, with more snow in the eastern part than in the western part (SDMO 1991, 1992).

The forests in which the data were collected are managed by the Forestry Agency of the Japanese Government and cover altogether an area of 2 830 885 ha (as of 1990) of which 76% is indigenous forests and 24% is planted forest. (Forest plantations were started in Hokkaido in 1896 but were not very common before mid 1950s (Ueda *et al.* 1966).) The forests are managerially divided into District Offices (76 as of 1992). Each District Office is further divided into Ranger Offices (altogether 436 Ranger Offices within the 76 District Offices in 1992).

The grey-sided vole (*Clethrionomys rufocanus*) is typically found in forested habitats (Stenseth 1985*b*; Corbet & Hill 1991). This is also the case in Hokkaido where the species is found in both the indigenous and the planted forests. The species also extends its habitat to open fields, which may be because of the absence of *Microtus* in Hokkaido (Ota 1984; Kondo 1993; Dobson 1994). As is the case elsewhere (Hansson 1987), voles may reach pest like abundances, particularly on larch (*Larix leptolepis*) and todo-fir (*Abies sachalinensis*) (Ota 1984). Rodent damage in forest plantations has periodically been observed from the beginning of the century (Ueda *et al.* 1966). According to the records (Ueda *et al.* 1966; Ota 1984), severe damage occurred in 1937, 1943, 1946, 1951, 1956, 1959, 1964, 1967, 1969 (figure 1*b*). It has been suggested that outbreak years are preceded by mast years of bamboograss (*Sasa* spp.) (Ota 1984). During the outbreak years, more than one million trees in plantations are commonly damaged (and killed) by voles (Forestry Division of Hokkaidian Government, unpublished data).

After preliminary rodent censuses in 1951, annual censuses were made permanent in 1954, after which the Forestry Agency did censuses of vole populations for management purposes at about 1000 grids within the 436 Ranger Offices all over Hokkaido (Fujimaki 1977). Here we analyse a subset of these monitoring data corresponding to 151 Ranger

Offices in the northernmost part of Hokkaido (approximately 10% of Hokkaido). From these 151 series, we focus on 90 series having complete fall censuses for the 31 years (figure 2). The average distance between these 90 locations is 85.8 km (s.d. (= standard deviation) = 49.7; min. = 3.3 km and max. = 272.1 km). The average distance to the nearest neighbouring population is 8.6 km (s.d. = 3.6; min. = 3.3 km and max. = 15.7 km) (figure 2). The trapping grids are located from the sea level to an altitude of 1 720 m. The mountainous regions are found towards the eastern and interior of the study area.

The censuses were done by the individual Ranger Offices. Trappings was done three times a year on 0.5 ha (50 × 100 m²) grids: Spring (May–June), Summer (July–August) and Autumn (September–October). On each grid 50 snap traps were suitably placed at approximately 10 m intervals. Personnel of the Ranger Offices identified the animals caught (see Saitoh *et al.* 1996). As abundances reach their maximum level in the fall in Hokkaido (Saitoh 1987), fall censuses were used in our analyses (see Henttonen *et al.* 1985).

The total number of grey-sided voles caught per 150 trap night is used as an index of abundance. From 1962 to 1976 each grid was trapped for five nights (giving a total of 250 trap nights); from 1977 to 1992 each grid was run for three nights. Data from the first 15 years were standardised to three-night equivalents by the empirically derived relation $y = 0.68x + 0.18$ (for $x > 0$), otherwise 0 ($r^2 = 0.94$), where y is the three-night equivalent and x is the number of animals caught over a five-night period (see Saitoh *et al.* 1996). A total of 45 890 specimens of *C. rufocanus* were caught at the 90 stations from 1962 to 1992. This species constitute 52.3% of the total number of all rodents caught. A total of three other microtine and murine species were recorded in the material: *Clethrionomys rutilus* (Pallas 1779) (1.1%), *Apodemus speciosus* (Temminck 1844) (18.1%) and *A. argenteus* (Temminck 1844) (28.5%).
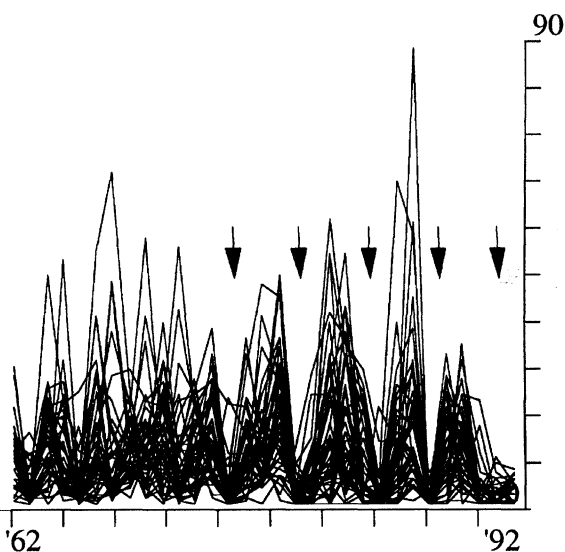
(a)

Okuchikubetsu

Ebishima

Heian

Asahiyama
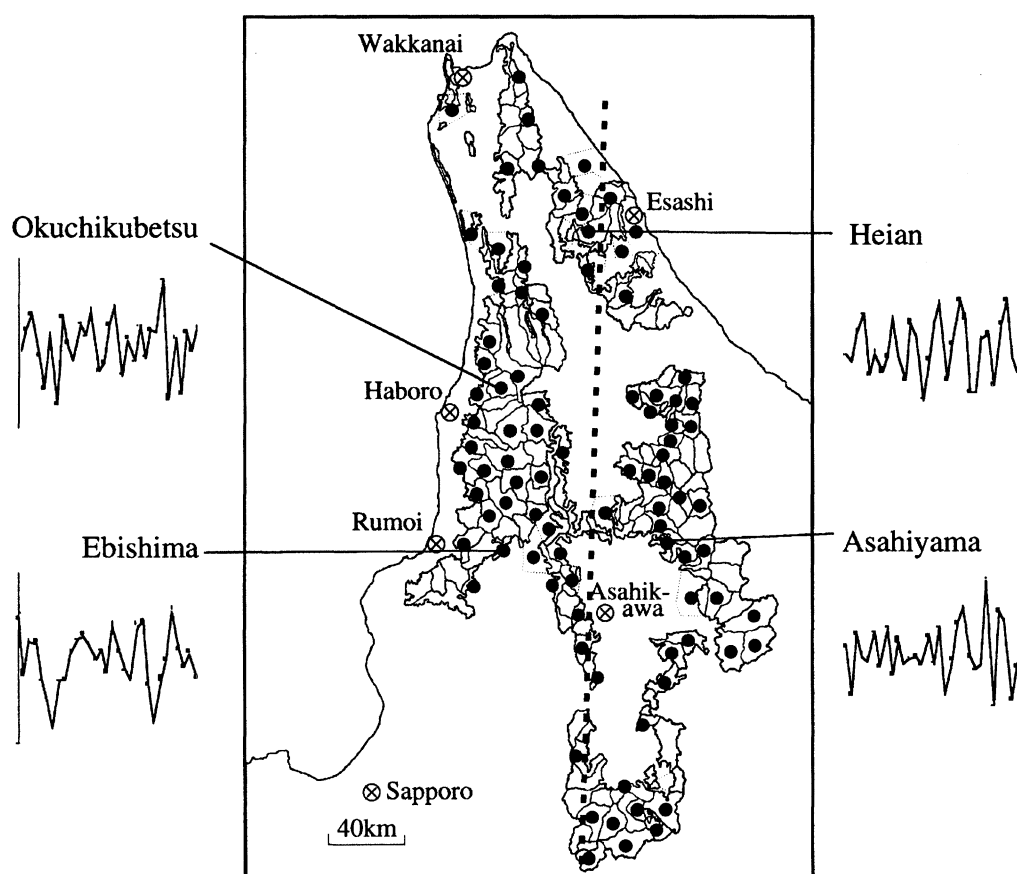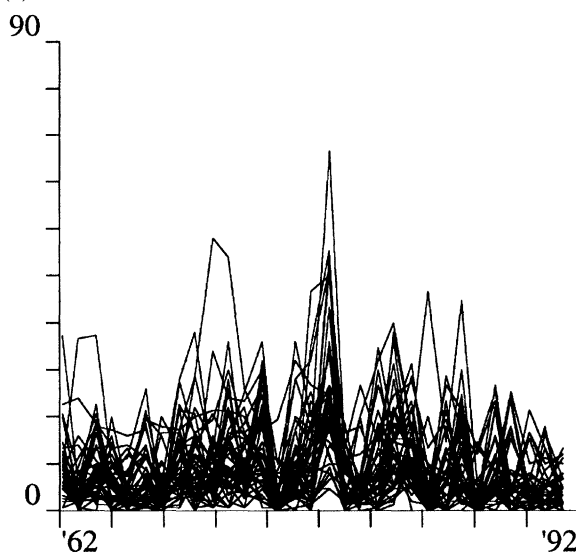
Figure 2. (a) The north-eastern part of Hokkaido from where the analysed material derives. Of the 151 Ranger Offices within this region (demarcated by thin lines), the 90 complete for fall samples are indicated by black dots. For four sites, the observed time trajectory of the abundances (in the fall) are shown: two for the western more stable region and two for the eastern and cyclic region. The yearly abundances (fall) within the coastal region within which negligible multi-annual fluctuations are found are given in (b); and the yearly abundances (fall) within the interior region in which significant multi-annual periodic fluctuations are found are given in (c) these regions are indicated by a broken line in (a)). The five arrow heads emphasise the great spatial synchrony in the cycle in the eastern region. In (a) log transformed and detrended data are plotted.

Table 1. *A preliminary Monte Carlo study to investigate the power of the non-parametric test for nonlinearity developed by Hjellvik & Tjøstheim* (1995)

(The percentage rejection of the null hypothesis is in each case based on simulation of 1000 time series of length 30. The number of replicates (1000) is too low to estimate type 1 and type 2 errors fully. They do, however, give an indication of the level. 'Henon' represent chaotic time series generated from the Henon map $(X_{t+1} = 1 - 1.4X_t^2 + 0.3X_{t-1})$ (see, for example, Cheng & Tong 1992), 'Logistic' represent time series generated from the logistic map $(X_{t+1} = 3.7X_t(1 - X_t)$ (May 1976, 1986), and 'Turchin-Hanski' are time series generated from the model for vole dynamics of Turchin & Hanski (unpublished data). The columns 0%, 33% and 50% indicate the percentage of measurement error the time series have been contaminated with before the test. 'Linear' represents surrogate data (Theiler *et al.* 1992) of the different nonlinear models; That is, they are linear analogues with identical autocovariance structure to the nonlinear time series. In this way, they reflect the type 2 error rates for the tests. The other entries indicate the power of the test against various types of nonlinearity.)

| | measurement error | | | |
model	0%	33%	50%	linear[a]
Henon	99.9	76.5	30.5	11.3
Logistic	99.0	54.6	17.2	5.4
Turchin-Hanski	72.2	33.3	27.8	11.9

[a] Order 2 is used for all tests, except for those on surrogate data (Linear) where order 5 is used.

The general ecology of the grey-sided vole in Hokkaido is summarized by Ota (1984), Bjørnstad *et al.* (1996) and Saitoh *et al.* (1996).

(*b*) *Analyses of the data*

The abundance index (plus one) in the fall of a year t is denoted by N_t. The constant of unity was added to permit log-transformation. Crude variability of each population was quantified using the *s*-index (= s.d. $(\log_{10} N_t)$; cf. Stenseth & Framstad 1980; Henttonen *et al.* 1985).

To apply Gaussian statistical models, data must be transformed to stabilize the variance (see, for example, Sen & Srivastava 1990). Commonly the most appropriate transformation of biological counts is either the square-root transformation (when the variance is proportional to the mean) or the logarithm (when the standard deviation is proportional to the mean) (see, for example, Sen & Srivastava 1990). By investigating the class of Box-Cox transformations (PROC BOXCOXAR; SAS Institute, Inc. 1990) the log-transformation was found to be the better one (the 95% confidence interval of the Box-Cox parameter included zero for all series; Atkin *et al.* 1989). Here we denote the log-transformed abundance index by X_t. To remove long-term temporal trends, all time series were detrended (after log-transformation) using a locally weighted smoother (LOWESS; see for example, Trexler & Travis 1993; Statistical Sciences Inc. 1993). A 6-year-wide window was chosen because this is just larger than the maximum period reported for the fluctuations of these rodents (Bjørnstad *et al.* 1996).

To apply population models to the data, the functional form of the density dependence must be evaluated. This implies both an identification of the order of the process, and

the extent of nonlinearity (on the log-scale). The issue of non-linearity in the dynamics of natural populations have become central in ecology (see, for example, May 1986). There are, however, few methods available for quantifying nonlinearity (see, for example, Falck *et al.* 1995*a*, *b*). An important problem is the specification of the alternative to linearity: there is only one type of linearity, but an endless array of types of non linearity. Testing for linearity against some particular form of nonlinearity may, thus, always be criticised as being caused by mis-specification of the alternative. To circumvent this problem, we apply the non-parametric method of Hjellvik & Tjøstheim (1995) employing recent advances in non-parametric regression for time series (Cheng & Tong 1992; Chen *et al.* 1995). The central idea is to estimate the function $X_t = F(X_{t-1}, ..., X_{t-d}) + \epsilon_t$ (where ϵ_t is a sequence of random numbers drawn independently from a symmetric distribution with zero mean and constant variance, σ^2) using a non-parametric local kernel estimator (Härdle 1990; Hastie & Tibshirani 1990). In this way F is determined by the data and may take on any linear or nonlinear form (including interactions between the lags). The goodness-of-fit of the non-parametric model is then compared to that of the linear alternative. The observed difference in the fit is compared to the null-distribution generated using Monte Carlo methods assuming linearity. The method is analogous to nonlinear prediction methods used in physics (Kennel & Isabelle 1992). This test is both non-parametric as well as having reasonable power in the small sample situation (Hjellvik & Tjøstheim 1995). However, because our sample size $(n = 31)$ is at the lower range of what may be considered appropriate, we report (table 1) preliminary results from a simulation of known models with various degrees of measurement contamination. As is clear, the power range between approximately 20–100% (the exact rates should not be taken too literally because of the low number of runs) with as much as 50% contamination for the highly nonlinear models being simulated. The test was done in S-plus version 3.2 (Statistical Sciences Inc. 1993), interfaced with a kernel conditional expectation estimator programmed in Borland Pascal version 7.0 (Borland International, Inc. 1992) to improve speed of calculation.

To investigate the patterns of density dependence, we used a linear autoregressive model (see for example Wei 1990; Royama 1992; Bjørnstad *et al.* 1995):

$$X_t = a_0 + (1 + a_1) X_{t-1} + \cdots + a_d X_{t-d} + \epsilon. \tag{1}$$

The coefficients $a_i (i = 1, 2, ..., d)$ characterise the pattern of autocovariance in the time series and may be interpreted as the strengths of the statistical density dependencies in the growth rate at the various lags (Royama 1981, 1992; Bjørnstad *et al.* 1995):

$$R_t = a_0 + a_1 X_{t-1} + \cdots + a_d X_{t-d} + \epsilon_t. \tag{2}$$

where $R_t = X_t - X_{t-1} = \log (N_t/N_{t-1})$ is the annual specific growth rate. (The log-linear relation corresponds to the classical Gompertz model (Gompertz 1825).)

We consider four alternative models (d equal to 0, 1, 2 and 3). A d equal to zero encompasses the hypothesis that the data is approximately a sequence of random numbers. A d equal to one embraces both the hypothesis that the population exhibits density independent growth ($a_1 = 0$) and negatively density dependent growth ($a_1 < 0$) (Dennis & Taper 1994). A d equal to two and a d equal to three represent different complexities of the delayed density dependence (see Bjørnstad *et al.* 1996; Stenseth *et al.* 1996*b*).

Comparing the fit of different models is a central statistical issue (see, for example, Miller 1990). A critical aspect is that

a more complicated model will give better fit to the data than a simpler one because of the larger number of free parameters. This is always the case when the data is first used to estimate the model parameters and subsequently to calculate the goodness-of-fit (Hjorth 1994). Because of this, statistics like the coefficient of determination, R^2, cannot be used as a measure of the various models' appropriateness. Several alternative methods have been developed. Here, we use the information theoretic criterion, $AIC_c = 2LL + 2p + 2(p+1)$ $(p+2)/(n-p-2)$ where LL is the log likelihood of the fitted model, p is the number of parameters and n is the sample size (Hurvich & Tsai 1989). By convention, a difference of unity or less in the value of AIC_c is considered insignificant (Sakamoto et al. 1986).

To validate the fit of an autoregressive model, the spectral density of the original series may be compared to those of simulations of the stochastic model (Tsay 1992; Bjørnstad et al. 1995; Falck et al. 1995a). We simulated time series of length 31 using the estimated coefficients $(\hat{a}_0, \hat{a}_1, ..., \hat{a}_d, \sigma)$ of the model for each series. A total of 1000 pseudo-series were generated for each series. The simulated periodograms were compared with those of the original series. A good fit was concluded if the estimated periodogram was contained within the 95% envelope as well as having the same general shape as the simulated series. The latter was scored by considering the Spearman rank correlation between the original spectral density and the median of the simulations. A correlation coefficient larger than 0.5 was considered acceptable.

For populations with geographically varying population dynamics, such as the grey-sided vole in Hokkaido (Bjørnstad et al. 1996), the analysis of the geographic pattern in the direct and delay statistical density dependence (i.e. in the a_i-coefficients) are generally of interest (Bjørnstad et al. 1995). We mapped the autoregressive coefficients. To investigate any gradient in patterns of statistical density dependence, the estimated coefficients of the optimal autoregressive model were regressed on a polynomial in distance from the Sea of Japan (see below). The polynomial was initially taken to be of order two, and superfluous terms were removed by backwards elimination $(p_{crit} = 0.1)$. The linear autoregressive models were fitted using PROC ARIMA (SAS Institute 1990).

3. RESULTS

The crude variability in the 90 time series, quantified by the s-index, varied between 0.28 and 0.52. Mapping the values, a geographically consistent pattern emerges (figure 3a). Along the western coast, there is less variability than in the eastern interior part of the study area (see also figure 2a). The distance from the Sea of Japan was found to be a correlate (figure 3b); specifically, this was a better 'predictor' than latitude or longitude. This reflects the fact that within the study area, climate is more influenced by sea currents and dominant wind directions than latitude (see below).

The null-hypothesis of linearity was rejected (5% level) for four out of 90 time series using the Hjellvik & Tjøstheim (1995) test. Four rejections at the 5% level is, however, to be expected by chance alone. The rejection rate is very low compared with that reported for synthetic data in table 1 even when a high degree of contamination is introduced. Hence, it is reasonable to consider the dynamics of the grey-sided vole in Hokkaido to be approximately linear on the log-scale.

Applying linear models of different complexity, the AIC_c criterion gave, for the 90 time series, the following distribution of the optimal order $(d$; see equations (1) and (2)): $d = 0$ for 41 series, $d = 1$ for 10 series, $d = 2$ for 33 series and $d = 3$ for six series. There is a clear indication of bimodality, but 84 series (93%) were consistent with d being less than or equal to two. A second-order autoregressive model, therefore, appear to provide a parsimonious model for the series:

$$R_t = a_0 + a_1 X_{t-1} + a_2 X_{t-2} + \epsilon_t. \tag{3}$$

where a_0 is the mean, a_1 is a measure of the strength of the statistical direct density dependence, and a_2 is a measure of the strength of the statistical delayed density dependence (Royama 1992; Bjørnstad et al. 1995). The dynamic properties as a function of a_1 and a_2 for the deterministic model (i.e. the skeleton) are well understood (Royama 1992; Bjørnstad et al. 1995) and outlined in figure 4. Parameter combinations outside the triangle lead to extinction, and are of no biological interest for stationary populations. Inside, moving counter-clockwise from the upper and right-most of figure 4 through the remaining regions within the triangle, oscillatory (dampened) dynamics with progressively longer periods result. The skeleton model for the upper part of the triangle give rise to either stable dynamics or a 2-year dampened oscillations, whereas in the lower part multi-annual dampened oscillations result (with longer periods as moving towards the right; see Bjørnstad et al. 1995).

To understand the regional patterns of population dynamics of the grey-sided vole, we studied the geographic variation of the magnitude of the autoregressive parameters in the second order autoregressive model. Estimated coefficients $(a_1$ and $a_2)$ are plotted in figure 4. The estimates of statistical direct density dependence, a_1, did not vary consistently with distance from the Sea of Japan. Neither the linear $(p = 0.39)$ nor the 2nd order term $(p = 0.11)$ was significant at the 10% critical level (nor functions of latitude or longitude). A constant for all populations were, thus, reasonable $\hat{a}_1 = -0.13$ $(\pm 0.02$; $pr(a_1 < 1$; i.e. no regulation) $< 0.001)$. In contrast the estimate of delayed density dependence decreased significantly as moving eastwards and towards the interior (away from the Sea of Japan, J, albeit with a slight increase towards the end: $\hat{a}_2 = -0.27$ $(\pm 0.2, p < 0.001) - 0.59$ $(\pm 0.18, p = 0.002) J + 0.41$ $(\pm 0.18, p = 0.03) J^2$ $(R^2 = 0.15, F = 7.57, $ d.f. $= 2, 87, p < 0.001)$. Note, though, that much variation remains to be explained, and further investigation is needed before a fairly complete description is obtained.

Simulating the second order autoregressive skeleton models for each of the 90 populations shows that the model gave good fit for 83 populations (92%) as judged by the confidence envelop criterion and 64 (71%) using the median criterion (see figure 4 for examples). Altogether, the models for 63 of the populations (70%) must be considered very good in the sense of recreating the spectral densities using only three parameters $(a_1, a_2$ and $\sigma^2)$. For comparison, Falck et al. (1995a) found that 47% (16 out of 34) the investigated European microtine time series fitted
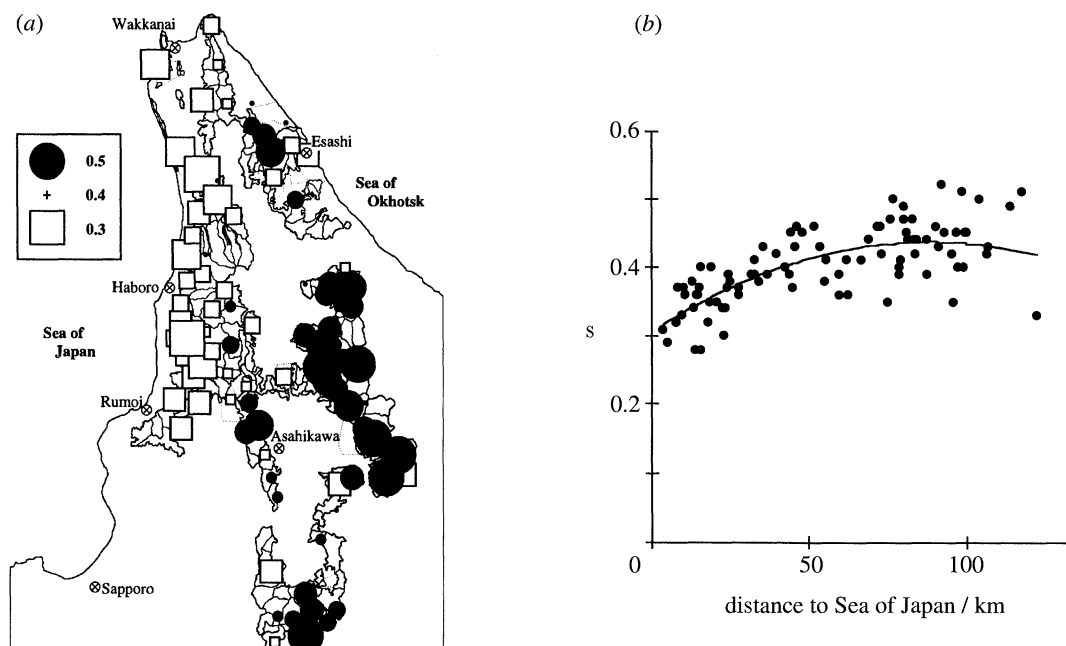
Figure 3. The temporal variability, s, of the 90 Hokkaidian time series on grey-sided voles within the study area. (a) The spatial structure of the variability within the study region. Black circles represent values larger than the average. Open squares represent values smaller than the average. The size of the symbols are proportional to the deviation from the average. (b) The relation between the crude temporal variability and the distance from the Sea of Japan, J (in km) (being a correlate of the gradient): estimated coefficients and standard deviations are given: $s = (0.308 \pm 0.011) + (0.003 \pm 0.001) \, J - (1.6 \times 10^{-5} \pm 4.8 \times 10^{-6}) \, J^2$ (adj. $R^2 = 0.55$; $p = 0.05$).

the response surface model (a nonlinear model with up to ten parameters; cf. Turchin & Millstein 1993).

4. DISCUSSION

Previously, it has been shown that both non-periodic and multi-annual periodic fluctuations are found in the studied populations of the grey-sided vole (*Clethrionomys rufocanus*) in northern Hokkaido (Bjørnstad *et al.* 1996). Along the coast of the north-western part of Hokkaido the species exhibits primarily non-cyclic fluctuations whereas in the interior and East the populations exhibit fluctuations with periods of 3.5–4 years. In this study, we have shown that: (i) the dynamics appear to have order two or lower; (ii) approximate linearity exists for the log-transformed abundances; (iii) a stochastic log-linear second order autoregressive model recreates the spectral densities satisfactorily; and (iv) the clinal gradient in the population dynamics as going inland from the north-eastern coast, is primarily caused by more negative delayed density dependence.

The geographic differences in the temporal variability in the Hokkaidian voles (see figure 2) is similar to that seen in cyclic and semi-stable microtine populations (Henttonen *et al.* 1985; Stenseth *et al.* 1985; Ostfeld 1988; Stenseth & Ims 1993*b*). For instance, Swedish populations of *C. glareolus* approximately 550 km apart at approximately 55° N and 60° N give $\bar{s} = 0.22$ for the former $(n = 7)$ and $\bar{s} = 0.47$ for the latter $(n = 7)$ (Hansson & Henttonen 1985, 1988). Observed changes in population dynamic characteristics as going from the coast to the mountainous

interior of Norway (Myrberget 1973; Hansson *et al.* 1978; Christiansen 1983) represent gradients as sharp as that seen in Hokkaido.

As in the case for the Fennoscandian system (Bjørnstad *et al.* 1995), a second order autoregressive model appears to describes the various populations in Hokkaido appropriately. The first order coefficient (a_1) is negative throughout the entire study area. This indicates significant statistical direct density dependence. (For the same set of data Saitoh *et al.* (1996) used several tests for density dependence and found that direct density dependence occurs in all studied populations.) To find strong density dependence in this species is not surprising in light of the very strong spatial- or social organization in *Clethrionomys* (see, for example, Bondrup-Nielsen 1985; Bondrup-Nielsen & Karlsson 1985; Bujalska 1985; Gipps 1985; Viitala & Hoffmeyer 1985; Kawata 1987; Saitoh 1991).

Both in Fennoscandia and in Hokkaido, a clear clinal structure in the autoregressive coefficients are found. However, as opposed to the gradient in Fennoscandia north of 60° N (cf. Hanski *et al.* 1991; Bjørnstad *et al.* 1995), which is primarily a gradient in the direct density dependence (a_1), the gradient in Hokkaido is largely a gradient in the delayed density dependence (a_2) (figure 3). The Fennoscandia gradient has been explained as a result of changes in the occurrence of generalist predators (both number and abundance of species; Hanski *et al.* 1991). A possible candidate for explaining the gradient in Hokkaido may be through changes in presence and effect of specialist predators (Hassell & May 1986). Environmental factors such as snow cover may be a possible proxy
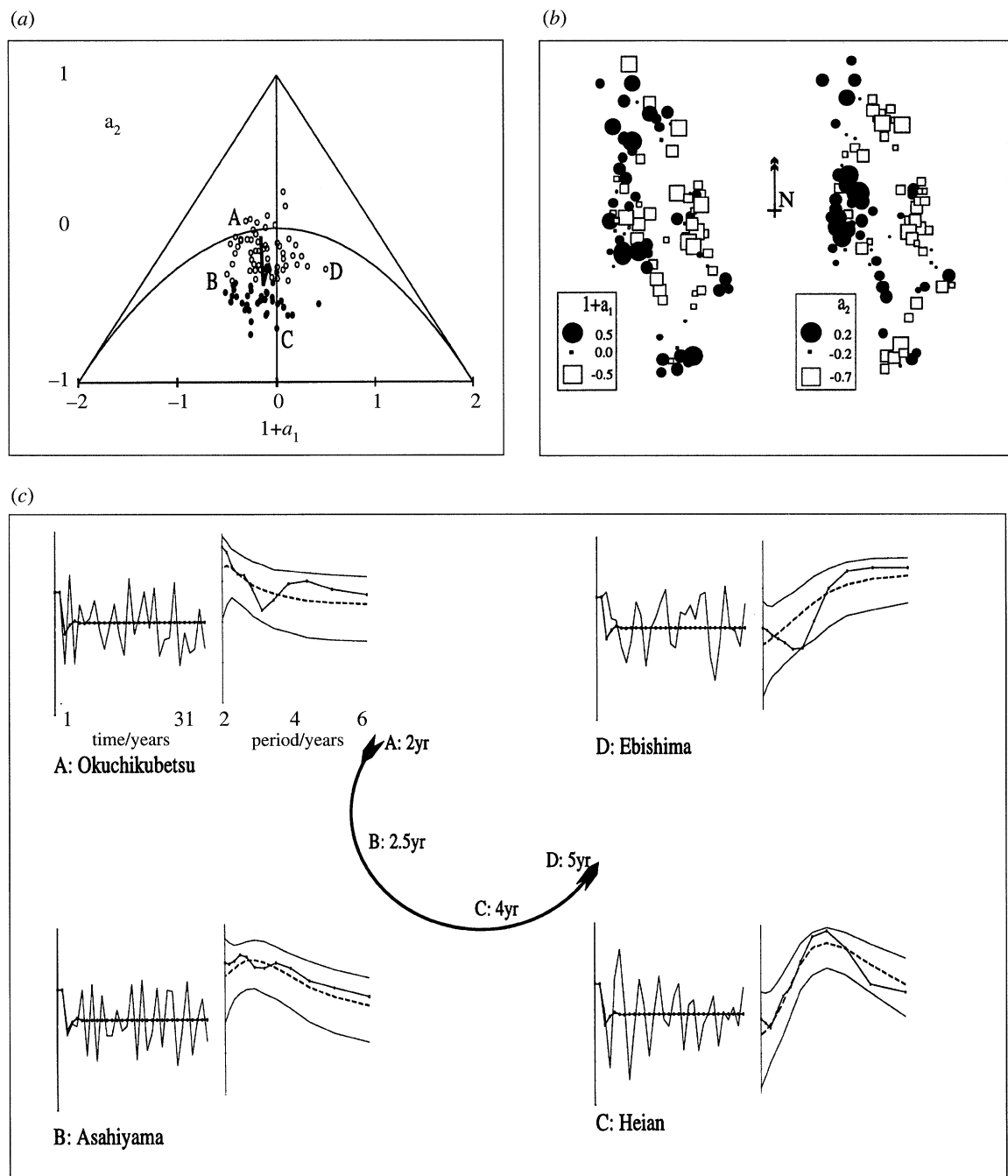
Figure 4. Detailed representation of the grey-sided vole population dynamics in Hokkaido: (*a*) Scatter plot of first order $(1 + a_1)$ versus second order (a_2) autoregressive coefficients for each of the 90 populations. All populations have a_1's significantly smaller than zero. Closed circles signify populations with a_2 significantly different from zero and thus significant delayed density dependence. The arrow indicates the average change in the parameters as moving eastwards. Of the two autoregressive coefficients, only a_2 was found to be related significantly to the distance from the Sea of Japan (hence, the vertical arrow). (*b*) The two coefficients are mapped on the study area. The regional pattern is particularly clear for a_2 (cf. figure 3). The capital letters inside the triangle denote location within the autoregressive parameter space of populations whose dynamical properties are illustrated in the panels marked A to D in (*c*) (see also figure 2, lower right and left). The counter-clockwise arrow in the centre of the lower part of the diagram moves through the various regions of the parameter space producing cycles of increasing period. In each panel A to D, the first graph indicate the predicted trajectory of each model in a noise-free deterministic world (damped trajectories) and an arbitrary realization in the presence of stochasticities. The second graph depicts the spectral density of the original time series (solid bold line) as well as the median (dotted line) and 95 % confidence envelope of simulations of the models (see the main text). See Royama (1992) and Bjørnstad *et al.* (1995) for a discussion of the periodicity of the second order autoregressive model.

creating such variation (Hansson 1987). Table 2 summarises available meteorological data for our study region. The second autoregressive parameter (a_2) as well as the snow depth and the duration of the snow appear to change in a systematic way as going east or towards the interior. Hansson (1987) argued that snow factors interact with predation rates such that mustelids (being specialist predators capable of finding rodent

Table 2. *Meteorological data for six principal towns and cities in northern Hokkaido, Japan (see figure 1)*

(Temperatures are given as monthly averages Centigrade during 1962–1992 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 1962–1992 (source: Sapporo District Meterological Office 1991, 1992).)

| city (or town) | temperature/°C | | | precipitation/ mm | snow | |
	February	August	average		depth/cm	days/10 cm
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

prey under the snow cover; Sittler 1995) may, on a relative scale, be more important than the large generalists predators where the snow cover last longer. This speculation may be worthy of further consideration.

The most common motivation for using linear time series models in population dynamics is to quantify density dependence (Royama 1981, 1992; Reddingius 1990; Hörnfeldt 1994; Bjørnstad *et al.* 1995). This is, to a certain extent, also our motivation (see also Saitoh *et al.* 1996). Until now the discussion of linearity versus nonlinearity has been troubled by the unresolved problems of quantifying degrees of nonlinearity (Falck *et al.* 1995 *a, b*). The problems arise when one is forced to rely on arbitrary specifications of the parametric form of the nonlinear alternative (such as a Ricker model or its derivatives; see, for example, Turchin 1993). In light of the current discussion within the field of ecology (see, for example, Turchin 1995), it is important to observe that the cyclic populations investigated in this study are approximately log-linear.

Model (1) is a so-called log-linear phase-forgetting model (*sensu* Nisbet & Gurney 1982). That is, these models have the 'forgetting' property that the dynamics is only state dependent. Hence, if the state changes through stochastic displacements, the dynamics proceeds according to the new state-vector. Such a linear model cannot – in the absence of stochasticity – sustain periodic oscillations (see, for example, Moran 1953; Royama 1992). Thus, it may appear paradoxical to find a log-linear model to represent our data appropriately, both along the coast and in the interior of the study area (where sustained density cycles occur). In the presence of environmental stochasticity (*sensu* May 1973; Goodman 1987), linear models will, however, give rise to sustained oscillations (Royama 1992; figure 3). Thus, the dampening inherent in approximately linear models is only problematic within an equilibrium view of the world (see, for example, Krebs 1995). We are lead to postulate that environmental stochasticity play a more important role in maintaining the 'microtine cycle'. This emphasis on the importance of environmental stochasticity is consistent with views earlier expressed by Moran (1953). In conclusion, we suggest that the periodic nature of dynamics is generated by the deterministic components of the system (possibly trophic interactions; cf. Stenseth *et al.* 1996*b*), while the oscillations are sustained by stochasticities keeping the populations in transience around the attractor. Our hypothesis is consistent with the general observation that many cyclic populations have a period that is less variable than the amplitude (cf. Warkowska-Dratnal & Stenseth 1985; Stenseth & Ims 1993*b*).

REFERENCES

Atkin, M., Anderson, D., Francis, B. & Hinde, J. 1989 *Statistical modelling in GLIM*. Oxford University Press.

Bjørnstad, O. N., Falck, W. & Stenseth, N. C. 1995 A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proc. R. Soc. Lond.* 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: evidence from spectral and principal components analysis. *Phil. Trans. R. Soc. Lond* B **351**, 867–873.

Blakiston, T. & Pryer, H. 1880 Catalogue of the birds of Japan. *Trans. Asiatic Soc. Japan* **7**, 172–241.

Bondrup-Nielsen, S. 1985 An evaluation of the effects of space use and habitat patterns on dispersal in small mammals. *Ann. Zool. Fenn.* **22**, 373–383.

Bondrup-Nielsen, S. & Karlsson, F. 1985 Movements and spatial patterns in populations of *Clethrionomys* species: a review. *Ann. Zool. Fenn.* **22**, 373–399.

Bujalska, G. 1985 Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*. *Ann. Zool. Fenn.* **22**, 331–342.

Borland International, Inc. 1992 *Borland Pascal version 7.0*. Borland International, Inc.

Chen, R., Liu, J. S. & Tsay, R. S. 1995 Additivity tests for nonlinear autoregression. *Biometrika* **82**, 369–383.

Cheng, B. & Tong, H. 1992 On consistent nonparametric

order determination and chaos. *J. R. Statist. Soc.* B **54**, 427–449.

Christiansen, E. 1983 Fluctuations in some small rodent populations in Norway 1971–1979. *Holarct. Ecol.* **6**, 24–31.

Corbet, G. B. & Hill, J. E. 1991 *A world list of mammalian species.* Oxford University Press.

Dennis, B. & Taper, M. L. 1994 Density dependence in time series observations of natural populations: estimation and testing. *Ecol. Monogr.* **64**, 205–224.

Dobson, M. 1994 Patterns of distribution in Japanese land mammals. *Mammal Rev.* **24**, 91–111.

Elton, C. S. 1924 Periodic fluctuations in the numbers of animals: their causes and effects. *Brit. J. exp. Biol.* **2**, 119–163.

Elton, C. S. 1942 *Voles, mice and lemmings.* Oxford: Clarendon Press.

Falck, W., Bjørnstad, O. N. & Stenseth, N. C. 1995*a* Bootstrap estimated uncertainty of the dominant Lyapunov exponent for Holarctic microtine rodents. *Proc. R. Soc. Lond.* B **261**, 159–165.

Falck, W., Bjørnstad, O. N. & Stenseth, N. C. 1995*b* Voles and lemmings: chaos and uncertainty in fluctuating populations. *Proc. R. Soc. Lond.* B **262**, 363–370.

Fujimaki, Y. 1977 Historical review on transformation of the census method of vole populations. *Vole* **142**, 74–75 (in Japanese).

Gilbert, B. S. & Krebs, C. J. 1991 Population dynamics of *Clethrionomys* and *Peromyscus* in southwestern Yukon 1973–1989. *Holarct. Ecol.* **14**, 250–259.

Gipps, J. H. W. 1985 Spacing behaviour and male reproductive ecology in voles of the genus *Clethrionomys.* *Ann. Zool. Fenn.* **22**, 343–351.

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. *Phil. Trans. R. Soc. Lond.* B **115**, 513–585.

Goodman, D. 1987 The demography of chance extinction. In *Viable populations for conservation.* (ed. M. E. Soulé) Cambridge University Press.

Hanski, I., Hansson, L. & Henttonen, H. 1991 Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**, 353–367.

Hansson, L. 1971 Small rodent food, feeding and population dynamics: a comparison between granivorous and herbivorous species in Scandinavia. *Oikos* **22**, 183–198.

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 Ecol. Evol.* **3**, 195–200.

Hansson, L., Löfquist, J. & Nilsson, A. 1978 Population fluctuations in insectivores and small rodents in northernmost Fennoscandia. *Z. Saugetier.* **43**, 75–92.

Hassell, M. P. & May, R. M. 1986 Generalist and specialist natural enemies in insect predator-prey interactions. *J. Anim. Ecol.* **55**, 923–940.

Hastie, T. & Tibshirani, R. 1990 *Generalized additive models.* London: Chapman and Hall.

Härdle, W. 1990 *Applied nonparametric regression.* Cambridge University Press.

Henttonen, H., McGuire, A. D. & Hansson, L. 1985 Comparisons of amplitude and frequencies (spectral analyses) of density variations in long-term data sets of *Clethrionomys* species. *Ann. Zool. Fenn.* **22**, 221–228.

Hjellvik, V. & Tjøstheim, D. 1995 Nonparametric tests of linearity for time series. *Biometrika* **82**, 351–368.

Hjorth, J. S. U. 1994 *Computer intensive statistical methods: validation, model selection and bootstrap.* London: Chapman & Hall.

Hurvich, C. M. & Tsai, C.-L. 1989 Regression and time series model selection in small samples. *Biometrika* **76**, 297–307.

Hörnfeldt, B. 1994 Delayed density dependence as a determinant of vole cycles. *Ecology* **75**, 791–806.

Kaneko, Y. 1990 Identification and some morphological characters of *Clethrionomys rufocanus* and *Eothenomys regulus* from USSR, Northeast China, and Korea in comparison with *C. rufocanus* from Finland. *J. Mammal. Soc. Japan* **14**, 129–148.

Kawata, M. 1987 Pregnancy failure and suppression by female-female interaction in enclosed populations of the red-backed vole, *Clethrionomys rufocanus bedfordiae. Behav. Ecol. Sociobiol.* **20**, 89–97.

Kennel, M. B. & Isabelle, S. 1992 Method to distinguish possible chaos from colored noise and determine embedding parameters. *Phys. Rev.* A **46**, 3111–3118.

Kondo, N. 1982 Mammal fauna of Japan, with special reference to the ecological property of species, Paleenvironment and the Tsugaru Strait. *Honyuurui-Kagaku. Mammal. Sci.* **43–44**, 131–144 (in Japanese).

Kondo, N. 1993 Mammal Fauna and Its Distribution in Hokkaido Biodiversity and Ecology in the Northernmost Japan. In *Biodiversity and ecology in the Northernmost Japan,* (pp. 76–87).

Krebs, C. J. 1995 Two paradigms of population regulation. *Wildl. Res.* **22**, 1–10.

Krebs, C. J. & Myers, J. H. 1974 Population cycles in small mammals. *Adv. Ecol. Res.* **8**, 267–299.

Kuroda, N. 1939 Distribution of mammals in the Japanese Empire. *J. Mammal.* **20**, 37–50.

May, R. M. 1973 *Stability and complexity in model ecosystems.* Princeton University Press.

May, R. M. 1976 Simple mathematical models with very complicated dynamics. *Nature, Lond.* **261**, 459–467.

May, R. M. 1986 When two and two do not make four: nonlinear phenomena in ecology. *Proc. R. Soc. Lond.* B **228**, 241–266.

Miller, A. J. 1990 *Subset selection in regression,* vol. 40. London: Chapman and Hall.

Moran, P. A. P. 1953 The statistical analysis of the Canadian lynx cycle. *Aust. J. Zool.* **1**, 163–173.

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

Nisbet, R. M. & Gurney, W. S. C. 1982 *Modelling fluctuating populations.* Chichester: Wiley.

Ostfeld, R. S. 1988 Fluctuations and constancy in populations of small rodents. *Am. Nat.* **131**, 445–452.

Ota, K. (ed.) 1984 *Study on wild murid rodents in Hokkaido.* Sapporo: Hokkaido University Press (in Japanese).

Reddingius, J. 1990 Models for testing: a secondary note. *Oecologia* **83**, 50–52.

Royama, T. 1981 Fundamental concepts and methodology for the analysis of animal population dynamics, with special reference to univoltine species. *Ecol. Monogr.* **51**, 473–493.

Royama, T. 1992 *Analytical population dynamics.* London: Chapman & Hall.

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. Res. pop. Ecol.* **33**, 367–386.

Saitoh, T., Stenseth, N. C. & Bjørnstad, O. N. 1996 Density-dependence in fluctuating grey-sided vole populations. *J. Anim. Ecol.* (In the press.)

Sakamoto, Y., Ishiguro, M. & Kitagawa, G. 1986 *Akaike information criterion statistics.* Tokyo: KTK Scientific Publishers.

SAS Institute. 1990 *SAS/ETS user guide,* version 6, 4th edn. Cary, North Carolina: SAS Institute Inc.

SDMO (Sapporo District Meteorological Office) 1991 & 1992 *The climate in Hokkaido.* Sapporo: Nihon Kisho-kyokai (in Japanese).

Sen, A. & Srivastava, M. 1990 *Regression analysis: theory, methods and applications.* New York: Springer-Verlag.

Sittler, B. 1995 Response of stoats (*Mustela arminea*) to a fluctuating lemming (*Dircrostonyx groenlandicus*) population in north east Greenland: preliminary results from a long-term study. *Ann. Zool. Fenn.* **32**, 79–92.

Smith, C. H. 1983 A system of world mammal faunal regions. I. Logical and statistical derivation of the regions. *J. Biogeog.* **10**, 455–466.

Statistical Sciences, Inc. 1993 *S-plus for windows version 3.2 supplement.* Seattle: Statistical Sciences Inc.

Stenseth, N. C. 1985a Models of bank vole and wood mice. *Symp. Zool. Soc. Lond.* **55**, 339–376.

Stenseth, N. C. 1985b Geographic distribution of *Clethrionomys* species. *Ann. Zool. Fenn.* **22**, 215–219.

Stenseth, N. C. & Framstad, E. 1980 Reproductive effort and optimal reproductive rates in small rodents. *Oikos* **34**, 23–43.

Stenseth, N. C. & Ims, R. A. 1993a The history of lemming research: from the Nordic Sagas to *The biology of lemmings.* In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims). London: Academic Press.

Stenseth, N. C. & Ims, R. A. 1993b Population dynamics of lemmings: temporal and spatial variation – an introduction. In *The biology of lemmings* (ed. N. C. Stenseth & R. A. Ims). London: Academic Press.

Stenseth, N. C., Bjørnstad, O. N. & Falck, W. 1996 Is spacing behaviour coupled with predation causing the microtine density cycle? Merging process-oriented studies and pattern-oriented studies. *Proc R. Soc. Lond.* B **263** (In the press).

Stenseth, N. C., Gustafsson, T. O., Hansson, L. & Ugland, K. I. 1985 On the evolution of reproductive rates in microtine rodents. *Ecology* **66**, 1795–1808.

Tatewaki, M. 1958 Forest ecology of the islands of the north pacific ocean. *J. facul. Agric. Hokkaido Univ.* **50**, 371–472.

Theiler, J., Eubank, S., Longtin, A., Galdrikian, B. & Farmer, J. D. 1992 Testing for non-linearity in time series: the method of surrogate data. *Physica* D **58**, 77–94.

Trexler, J. C. & Travis, J. 1993 Nontraditional regression analyses. *Ecology* **74**, 1629–1637.

Tsay, R. S. 1992 Model checking via parametric bootstraps in time series analysis. *Appl. Statist.* **41**, 1–15.

Turchin, P. 1993 Chaos and stability in rodent population dynamics: evidence from non-linear time-series analysis. *Oikos* **68**, 167–171.

Turchin, P. 1995 Chaos in microtine populations. *Proc. R. Soc. Lond.* B **262**, 357–361.

Turchin, P. & Millstein, J. A. 1993 *EcoDyn/RSM: response surface modelling of nonlinear ecological dynamics* (part I & II). New York: Applied Biomathematics, Setauket.

Ueda, M., S. Higuchi, B. Igarashi, M. Maeda *et al.* 1966 Historical review of studies on the Bedford's red-back vole, *Clethrionomys rufocanus bedfordiae* (Thomas). *Bull. Gov. For. Exp. Stat.* **191**, 1–100 (in Japanese).

Viitala, J. & Hoffmeyer, I. 1985 Social organisation in *Clethrionomys* compared with *Microtus* and *Apodemus*: social odour, chemistry and biological effects. *Ann. Zool. Fenn.* **22**, 359–371.

Walters, H. 1984 *Vegetation of the earth and ecological systems of the geobiosphere.* Berlin: Springer Verlag.

Warkowska-Dratnal, H. & Stenseth, N. C. 1985 Dispersal and the microtine cycle: comparison of two hypotheses. *Oecologia* **65**, 468–477.

Wei, W. W. 1990 *Time series analysis: univariate and multivariate methods.* New York: Addison-Wesley Publ. Co.