

# A geographic gradient in small rodent density fluctuations: a statistical modelling approach

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## SUMMARY

The patterns of density dependence in Fennoscandian rodents are investigated statistically using a linear autoregressive scheme. Nineteen time series of microtine abundances along a latitudinal gradient in Fennoscandia from 60° N to 69° N are analysed. We provide statistical evidence that there exists a latitudinal gradient in density dependence in Fennoscandian microtines. Southern populations experience significantly stronger direct density dependence than northern populations. Delayed density dependence was significantly negative throughout the region and appeared constant across the latitudinal gradient. The populations consistently exhibit dynamics of second order throughout the region. Together, the clinal direct density dependence and constant delayed density dependence give rise to a cline in cycle period from 3 to 4.5 years. The statistical results are compared to assumptions and predictions made in previous studies on the geographic gradient in the population dynamics of these rodents. The results are in agreement with the predictions of the 'generalist predator hypothesis'.

## 1. INTRODUCTION

Over the past decade several authors have documented existence of geographic gradients in amplitude and periodicity of population fluctuations in microtine rodents (for examples, see Hansson & Henttonen 1985, 1988; Henttonen *et al.* 1985; Hansson 1987; Hanski *et al.* 1991; Turchin 1993 for a review see Stenseth & Ims 1993). To account for changes in the periodicity of the population fluctuations of Fennoscandian microtines, Hansson (1987) and Hanski *et al.* (1991) invoked changing abundance and diversity of generalist predators as an explanatory factor. Hanski *et al.* (1991) found, on the basis of a model-analysis, that increased abundance of generalist predators tend to decrease the cycle length and stabilize the dynamics of a vole cycle. The cyclicity, as such, was assumed driven by specialist predators such as mustelids: without the specialist predator there would be no cycles in the first place. Hanski *et al.* concluded that the latitudinal gradient observed in Fennoscandia is caused by the increase in abundance and diversity of generalist predators in Southern Fennoscandia. This hypothesis, as well as other hypotheses involving trophic interactions, can be interpreted in terms of altered patterns of statistical density dependence (DD) experienced by the populations (see Royama 1981). If a gradient in dynamics is present, we should find the strength of direct or delayed DD to correlate smoothly with latitude. Here, we report an analysis based on 19 time series from the Fennoscandian peninsula.

## 2. SOME HYPOTHESES

The ecological literature contains a bewildering diversity of hypotheses pertaining to the multi-annual fluctuations of small rodents (for recent reviews see Batzli 1992; Stenseth & Ims 1993). From the point of view of our statistical modelling approach, we highlight some assumptions and predictions of a small subset of the hypotheses. We make no attempt to undertake a full evaluation of all hypotheses, nor do we wish to advocate that the selected hypotheses have more merit than others in explaining the rodent cycles. We have, rather, selected the hypotheses which we consider to be reasonable candidates for explaining the differences between various cyclic populations in Fennoscandia.

1. The specialist predator hypothesis. The abundance of specialist predators are by definition linked to the abundance of the prey through a numerical, rather than functional, response (Murdoch & Oaten 1975). That is, the predator respond to increased prey density by increased reproductive effort. Changes in the interaction between a specialist predator and its prey may come about through changes in predator efficiency of catching prey or changes in converting prey biomass into predator offspring biomass. Because specialist predators respond to prey densities through reproductive output, any changes in the interaction is likely to affect the delayed component of DD (Butler 1953): it will always take some time to reproduce. A more efficient specialist predator may be expected to lead to more negative delayed DD. In short, this hypothesis predicts that a second order model (the simplest model that includes delayed DD) is necessary

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to describe the data. Any changes seen in the patterns of  $\mathbf{DD}$  should largely be in the delayed component.

2. The generalist predator hypothesis. Hansson (1987) and Hanski *et al.* (1991) observe that generalist predators are more abundant in the south of Fennoscandia. Generalist predation is characterized by a functional or migratory response to altered prey densities (Murdoch & Oaten 1975; Korpimäki 1994). The response of these predators to altered prey abundance is nearly instantaneous (Korpimäki 1994). Thus, increased generalist predator abundance will largely affect the direct component of  $\mathbf{DD}$ . If only generalist predators were present, we would expect that a simple first order model (only direct  $\mathbf{DD}$ ) would be sufficient to describe the dynamics. However, the hypothesis explicitly incorporates the presence of specialist predators, such as mustelids, throughout the region. These omnipresent specialists are assumed responsible for the underlying multi-annual rhythms observed. The predictions are, therefore, that a second order model (both direct and delayed  $\mathbf{DD}$ ) is necessary to describe the fluctuations. Consistent geographic variation is largely expected to be associated with the direct component of  $\mathbf{DD}$  (N. C. Stenseth *et al.* unpublished results).

3. The snow cover hypothesis. Hansson & Henttonen (1985) argue that the patterns of fluctuation correlate with winter snow cover. Steen (1995) demonstrate that survival is much higher during the winter than during the summer. It appears that snow may give some protection from predators. In which case, increased duration and depth of the snow cover will separate the dynamics of the prey and, at least parts, of the predator community. The dynamics is separated in the sense that the predators have limited access to the prey, whereas the prey, at least occasionally undertake winter reproduction (Kaikusalo & Tast 1984). This will make the predator-prey dynamics more discretized and, hence, enhance the delayed component of  $\mathbf{DD}$ , possibly 'at the expense', so to speak, of the direct  $\mathbf{DD}$ . A second order model will be necessary to describe the data.

### 3. THE DATA

Time series of abundances of 19 populations of Fennoscandian rodents (including a population on Kola) were studied (table 1). These time series represent five species from nine geographic locations, extending from 60.5° N (Finse) to 69° N (Kilpisjärvi). Only autumn counts have been considered (cf. Henttonen *et al.* 1985). The series were log-transformed. Population abundances are governed by birth and death processes which operate in a multiplicative manner. Such multiplicative process will be additive on a log scale, allowing the application of additive statistical models. Because of zeros in some series, a constant of 0.1 was added to all series before transformation. Conspicuous changes in abundance has been noticed for some of the time series during the late 1980s (see, for example, Small *et al.* 1993). Such non-stationarities cause problems for many statistical methods. To remove any trends, all time

series were detrended (after log-transformation) using a locally weighted regression (LOWESS; Statistical Sciences Inc. 1993; Trexler & Travis 1993). A six-year window width was chosen because this is just larger than the maximum period reported for the fluctuations of the Fennoscandian rodents (see, for example, Henttonen *et al.* 1985). The estimated period lengths (dominant period in the periodogram; see, for example, Priestley 1981) for the detrended data are given in table 1.

### 4. STATISTICAL MODELS FOR TEMPORAL FLUCTUATIONS

The patterns of  $\mathbf{DD}$  experienced by a population will create a certain signature in the autocovariance structure of a time series. We will use this in the reconstruction of the patterns of  $\mathbf{DD}$ . Because we examine correlates, we are not able to infer strict causality (Royama 1981, 1992). To emphasize that the estimated  $\mathbf{DD}$  may possibly be spurious (just like in any correlation analyses), we make inference about 'statistical  $\mathbf{DD}$ ' (Royama 1981). However, 'statistical direct  $\mathbf{DD}$ ' and 'statistical delayed  $\mathbf{DD}$ ' will just be denoted by direct  $\mathbf{DD}$  and delayed  $\mathbf{DD}$  to ease readability.

Temporal changes in population density may be described using stochastic difference equations (for examples see Dennis 1989). A general starting point is:

$$N_{t+1} = N_t f(N_t, N_{t-1}, \dots, N_{t-k(k-1)}, v_t), \quad (1a)$$

where  $N_t$  is the abundance at time  $t$ , and  $v_t$  is some stochastic term (possibly time or state dependent) affecting the population growth rate. The function  $f(N_t, N_{t-1}, \dots, N_{t-k(k-1)})$  is some function of past abundances determining the pattern of direct and delayed  $\mathbf{DD}$ . The maximal lag of  $\mathbf{DD}$  is determined by  $k+1$ .

Writing  $\log(N_t) = X_t$ ,  $\log(f(\mathbf{N})) = g(\mathbf{X})$  and the corresponding stochastic term as  $u_t$  we obtain:

$$R_t = X_{t+1} - X_t = g(X_t, X_{t-1}, \dots, X_{t-k(k-1)}, u_t), \quad (1b)$$

where  $R_t$  is the population growth at time  $t$ , and  $g(\bullet)$  is the function describing how the population growth rate depend on previous densities. From the literature on theoretical population ecology, it is clear that the choice of  $g(\downarrow)$  is not trivial; numerous functional forms have been suggested (for example see May & Oster 1976). For ease of comparison, it is necessary to settle for one. A useful simplification for the estimation of statistical  $\mathbf{DD}$  is to assume  $g(\downarrow)$  to be linear in  $u_t$  and  $\mathbf{X}_t$ s. That is, the growth rate changes linearly with log-abundances: the Gompertz assumption (for examples, see Reddingius 1990; Dennis & Taper 1994). This will not be strictly true for population dynamics in general (for examples, see May 1986). Specifically, the assumption of linearity is false for some of the populations investigated here (Falck *et al.* 1995; unpublished results). We stress, therefore, that this assumption is made to estimate the strength of  $\mathbf{DD}$ . Linear models appear to give fair approximations to some real population with non-linear dynamics (Subba Rao & Gabr 1980; Haggan *et al.* 1984; Royama 1992). Presently, we require the much weaker property that a linear model may recreate the autocovariance signa-

Table 1. Latitude North, location and taxon (genera: *L* = Lemmus, *M* = Microtus, *C* = Clethrionomys) for the 19 time series

(The period is the cycle period (years; see text). *n* is the number of annual observations. AICc(min) is the minimum of the AICc-profile. Order indicates the order corresponding to this minimum. Whenever the optimal dimension does not correspond to 2, the difference between the AICc for dimension 2 and the AICc(min) is indicated by ΔAICc; A difference of unity is considered not significant (Sakamoto *et al.* 1986). Order 2 indicates (Y = yes, N = no) whether the dynamics are consistent with a 2nd order model. All series but two are consistent with dimension 2. The columns  $(1 + \beta_1) \pm \text{s.e.}$  and  $\beta_2 \pm \text{s.e.}$  give the parameter estimates of the 2nd order autoregression and their standard errors.  $\sigma$  signifies the estimated standard deviation of the gaussian noise.)

latitude	location	species	period	<i>n</i>	AICc(min)	H	order	ΔAICc	order2	$(1 + \beta_1) \pm \text{s.e.}$	$\beta_2 \pm \text{s.e.}$	$\sigma$
60.5°	Finse	<i>L. lemmus</i> <sup>a</sup>	3.6	25	96.88		2	—	Y	$-0.47 \pm 0.18$	$-0.59 \pm 0.17$	1.50
60.5°	Finse	<i>L. lemmus</i> <sup>a</sup>	3.6	25	103.58		2	—	Y	$-0.32 \pm 0.19$	$-0.54 \pm 0.19$	1.72
60.5°	Finse	<i>Microtus</i> spp <sup>a</sup>	3.6	25	86.35		2	—	Y	$-0.24 \pm 0.16$	$-0.63 \pm 0.16$	1.21
60.5°	Finse	<i>Microtus</i> spp <sup>a</sup>	3.6	25	25.42		3	4.47	N	$-0.59 \pm 0.16$	$-0.67 \pm 0.15$	0.39
61.5°	Boda	<i>C. glareolus</i> <sup>b</sup>	3.5	28	101.01		2	—	Y	$-0.08 \pm 0.17$	$-0.55 \pm 0.17$	1.34
63°	Ruotsala	<i>Microtus</i> spp <sup>c</sup>	2.9	20	58.98		2	—	Y	$-0.58 \pm 0.16$	$-0.71 \pm 0.17$	0.89
63°	Alajoki	<i>Microtus</i> spp <sup>c</sup>	3.2	16	57.41		2	—	Y	$-0.57 \pm 0.21$	$-0.63 \pm 0.25$	1.15
64°	Umeå	<i>C. glareolus</i> <sup>d</sup>	3.4	24	67.72		2	—	Y	$-0.21 \pm 0.17$	$-0.64 \pm 0.16$	0.88
64°	Umeå	<i>C. rufocanus</i> <sup>d</sup>	3.4	24	52.05		2	—	Y	$-0.18 \pm 0.14$	$-0.73 \pm 0.13$	0.63
64°	Umea	<i>M. agrestis</i> <sup>d</sup>	3.4	24	53.45		2	—	Y	$-0.20 \pm 0.14$	$-0.76 \pm 0.13$	0.64
64°	Sotkamo	<i>M. agrestis</i> <sup>e</sup>	3.9	27	84.82		3	0.79	Y	$-0.38 \pm 0.17$	$-0.56 \pm 0.17$	1.07
64°	Sotkamo	<i>C. glareolus</i> <sup>e</sup>	3.9	27	76.59		0	0.09	Y	$-0.19 \pm 0.19$	$-0.39 \pm 0.19$	0.91
67°	Kola	<i>C. glareolus</i> <sup>f</sup>	4.80	19	72.90		2	—	Y	$0.14 \pm 0.21$	$-0.52 \pm 0.21$	1.40
67°	Kola	<i>C. rufocanus</i> <sup>f</sup>	4.80	19	68.91		2	—	Y	$0.05 \pm 0.20$	$-0.61 \pm 0.18$	1.25
68°	Pallasjärvi	<i>C. glareolus</i> <sup>g</sup>	4.60	23	75.21		2	—	Y	$0.12 \pm 0.17$	$-0.59 \pm 0.17$	1.09
68°	Pallasjärvi	<i>C. rufocanus</i> <sup>g</sup>	4.60	23	71.39		2	—	Y	$0.10 \pm 0.17$	$-0.60 \pm 0.17$	0.98
68°	Pallasjärvi	<i>C. rutilus</i> <sup>g</sup>	4.60	23	70.21		2	—	Y	$0.34 \pm 0.16$	$-0.63 \pm 0.16$	1.00
69°	Kilpisjärvi <sup>1</sup>	<i>C. rufocanus</i> <sup>h</sup>	4.4	22	65.69		3	1.14	N	$0.21 \pm 0.17$	$-0.65 \pm 0.17$	0.96
69°	Kilpisjärvi <sup>1</sup>	<i>C. rufocanus</i> <sup>h</sup>	4.8	24	86.04		2	—	Y	$0.10 \pm 0.18$	$-0.63 \pm 0.16$	1.28

<sup>a</sup> Framstad *et al.* (1993) and Erik Framstad (personal comm.).  
<sup>b</sup> Small *et al.* (1993).  
<sup>c</sup> Korpimäki & Norrdahl (1991) and Korpimäki (1994).  
<sup>d</sup> Hörnfeldt (1994) and Birger Hörnfeldt (personal comm.).  
<sup>e</sup> Henttonen *et al.* (1977) and Asko Kaikusalo & Hekki Henttonen (personal comm.).  
<sup>f</sup> Koshkina (1966; cited from Turchin 1993).  
<sup>g</sup> Henttonen *et al.* (1977), Henttonen *et al.* (1987) and H. Henttonen (personal comm.); old forest population only.  
<sup>h</sup> Kalela (1957), Laine & Henttonen (1983, 1987) and H. Henttonen (personal comm.).  
<sup>1</sup> The two time series from Kilpisjärvi is from a single population in which the dynamics is believed to have changed (Hekki Henttonen, personal comm.) associated with an altered variance. The series is therefore divided in two.

ture of a possibly nonlinear time series (Theiler *et al.* 1992). If the process is extremely nonlinear, we may over-estimate the number of lags required (i.e. the order). But we will not underestimate the dimension (cf. Takens theorem; Broomhead & Jones 1989).

Under the linear approximation, equation (1*b*) simplifies to (see, for example, Royama 1992, chapter 2):

$$R_t = X_{t+1} - X_t = \beta_0 + \beta_1 X_t + \beta_2 X_{t-1} + \dots + \beta_k X_{t-k+1} + u_t.$$

(2)

Rewriting and setting  $t = t - 1$  we obtain,

$$X_t = \beta_0 + (1 + \beta_1) X_{t-1} + \beta_2 X_{t-2} + \dots + \beta_k X_{t-k} + u_t.$$

(3)

Whenever we are willing to assume the  $u_t$ s to be independent and from an identical symmetric distribution, (3) is the autoregressive model of order  $k$ , AR( $k$ ) (see, for example, Priestley 1981). Ecologically speaking,  $\beta_1$  is an estimate of the strength of direct DD in the population growth, and  $\beta_2$  through  $\beta_k$  are estimates of the strength of delayed DD at various time lags.

The assumption of linearity is an important approximation to facilitate the comparison of the dy-

namics of different populations; there is only one restricted class of time series models which are linear, whereas nonlinearity may take several incomparable forms (nonlinearity in mean, nonlinearity in variance, threshold nonlinear, exponential nonlinear; see, for example, Tong 1990). A further simplification necessary for the comparison is to find an acceptable value for  $k$  for the time series. An appropriate approach for selecting a value for  $k$  is to use the AICc of Hurvich & Tsai (1989):  $AIC_c = -2 \log \text{likelihood} + 2p + 2[p + 1][p + 2]/[n - p - 2]$ , where,  $p$  is the number of model parameters and  $n$  is the sample size. The appropriate autoregressive model is that with the smallest AICc value among all the models considered. The rule of thumb in AIC-based selection is that a difference of unity in the AICc value is insignificant (Sakamoto *et al.* 1986).

(a) Dynamics of the second order autoregressive model

The dynamics of the AR(2) model varies greatly with the values of  $(1 + \beta_1)$  and  $\beta_2$ . The constant term,  $\beta_0$ , determines the average, and it does not affect the



astic perturbations are simulated by normally distributed noise with variance equal to the average estimated variances. The dominant periods of these simulated time series are summarized and compared to the largely independent periodicities reported by Hanski *et al.* (1991).

## 5. RESULTS

Using the  $AIC_c$  criterion to select the appropriate order of the processes reveals that the second order model is the most appropriate for describing the dynamics (table 1). The estimated coefficients of the second order autoregressive model are given in table 1. By examining the approximate confidence intervals (generated by two times the standard errors printed in table 1), it is clear that all coefficients for delayed DD ( $\beta_2$ ) are significantly different from zero and all the coefficient for direct DD ( $1 + \beta_1$ ) are significantly different from 1. Thus, all populations exhibit both direct and delayed DD which are significantly different from no regulation (cf. equation 3; Reddingius 1990).

The estimates of the latitudinal clines in statistical DD are summarized in figure 2. The best predictor for the direct DD ( $1 + \beta_1$ ) was linear in latitude (see figure 2a). This first order coefficient increase with latitude. Latitude explains as much as 66% of the observed variability ( $p < 0.01$ ). For the delayed DD ( $\beta_2$ ), there was no evidence of a latitudinal cline (figure 2b). Latitude explained less than 1% of the variation ( $p = 0.95$ ). Figure 2c is the scatter plot of  $\beta_2$  against ( $1 + \beta_1$ ). Superimposed on this is the arrow representing the simultaneous change of the two coefficients with latitude. The base of the arrow represents the southern limit of the data sets ( $60.5^\circ$ ) and the arrow head represents the northern ( $69^\circ$ ).

To examine the predictive power of our statistical model, coefficients of delayed and direct DD were predicted for each latitudinal degree ( $60^\circ$  N– $69^\circ$  N) from the models in figure 2. Time series of length 25 were simulated and the dominant periodicity calculated. The 'within-degree' variability and the overall trend are compared to the periodicities reported by Hanski *et al.* (1991) in figure 3. The fit is satisfactory. The average periodicity increases smoothly from 3.3 to 4.5 years.

## 6. DISCUSSION

The statistical pattern demonstrated in this study is consistent with the hypothesis put forth by Hansson (1987) and Hanski *et al.* (1991). They postulate that the greater abundances of generalist predators in Southern Fennoscandia is the reason for the shortening of the periodicity. Generalist predators are characterized by a switching type of functional response (Murdoch & Oaten 1975), or by a migratory response (Ydenberg 1987; Korpimäki 1994). These predators should therefore enhance the direct negative DD. Obviously, the omnipresence of specialist predators (or some other agent with lagged response) across the region is essential to explain the basal delayed DD. The snow cover hypothesis and the specialist predator

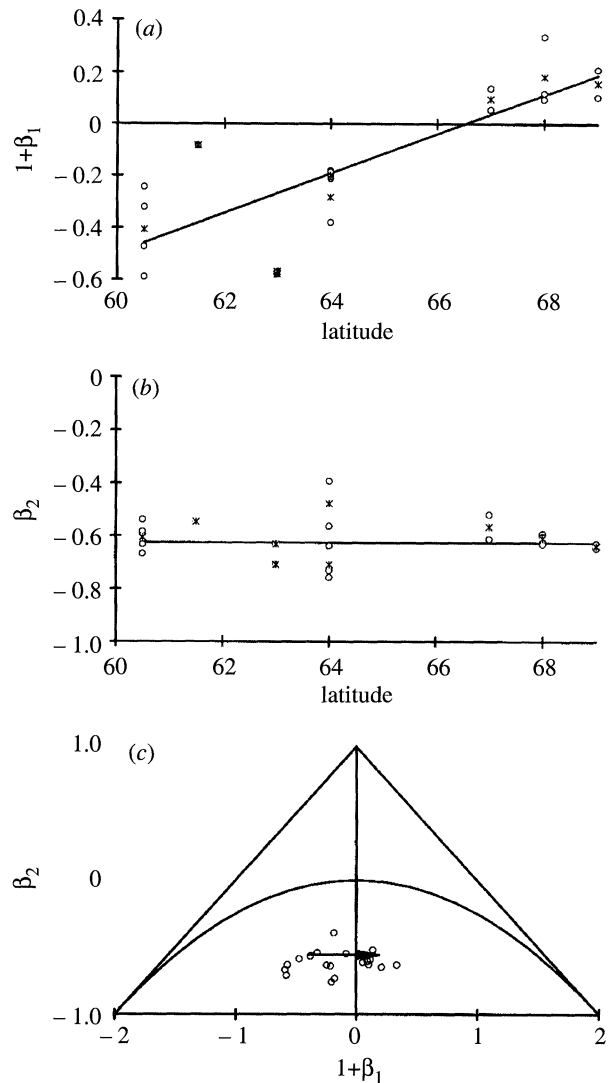


Figure 2. (a) The scatter plot of ( $1 + \beta_1$ ) against latitude. Circles represent the estimates (table 1), stars represent the mean of the estimates. The line depicts the optimal predictor of the coefficients (see text); ALL:  $-5.06$  (s.e. =  $0.81$ ,  $p < 0.01$ ) +  $0.08 \times \text{latitude}$  (s.e. =  $0.01$ ,  $p < 0.01$ ,  $R^2_{\text{adj}} = 0.66$ ); MEAN:  $-5.19$  (s.e. =  $1.58$ ,  $p = 0.01$ ) +  $0.08 \times \text{latitude}$  (s.e. =  $0.02$ ,  $p = 0.02$ ,  $R^2_{\text{adj}} = 0.53$ ). (b) The scatter plot of  $\beta_2$  against latitude. Symbols are the same as in (a). The line depicts the optimal predictor of the coefficients (see text); ALL:  $-0.63$  (s.e. =  $0.02$ ,  $p < 0.01$ ); MEAN:  $-0.61$  (s.e. =  $0.02$ ,  $p < 0.01$ ). (c) The scatter plot of ( $1 + \beta_1$ ) against  $\beta_2$  plotted like in figure 1. Clearly all populations exhibit cyclic dynamics (see legend figure 1). Superimposed is the arrow representing the simultaneous evolution of the two coefficients with latitude. The base of the arrow represents the southern limit of the data ( $60.5^\circ$ ) and the arrowhead represents the northern limit ( $69^\circ$ ).

hypothesis predict changes in delayed DD. The predictions of these hypotheses, therefore, disagrees with the statistical patterns in the data. They are not supported empirically. Note, however, that the study of Hansson & Henttonen (1985) invoking snow cover had a broader latitudinal scope than the present.

The correlation between geographic latitude and aspects of population dynamics is intriguing in its clarity. Many ecological factors are correlated with

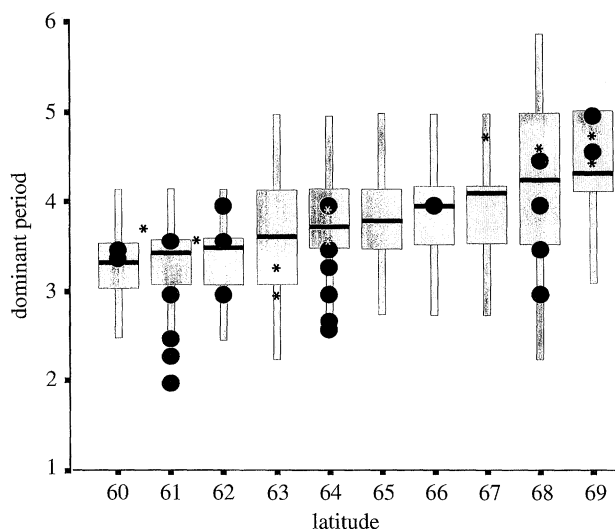


Figure 3. Box plots of the periodicity predicted by the estimated gradient in  $(1 + \beta_1)$  and  $\beta_2$ . For each latitudinal degree the parameters of the 2nd order autoregressive model was predicted using the model in figure 2. The stochastic term was assumed to be  $N(0, 1)$ . Each box plot summarizes the dominant period of 500 simulated time series of length 25. The central bars represents the mean, the box represents the observed inter-quartile range, and the bars represents the upper and lower five-percentile. Superimposed on the plot is the data collected by Hanski *et al.* (1991) (solid black circles) and the periodicity estimated from the present detrended time series (both black and white stars). Note, that the stars represents the same data as used to predict the gradient.

latitude, but the correlation is often indirect, through various environmental factors (see, for example, Pianka 1989). We rely on a correlation between latitude and predator fauna documented by Hansson (1987) and Hanski *et al.* (1991) in our statistical evaluation of the differences along a north-south gradient in Fennoscandia. Latitude must be used, with care, as a surrogate of underlying ecological parameters.

A fundamental question is whether our linear autoregressive model is an appropriate one. One constraint of the linear model is that it cannot exhibit stable limit cycles (nor low dimensional chaos; see, for example, Tong 1990). Any cyclic fluctuations exhibited will be of the phase-forgetting type (*sensu* Nisbet & Gurney 1982). Sustained fluctuations will require external forcing or perturbation. The present methodology will not be useful in the quest for clines in complexity of population dynamics (such as those sought by Turchin 1993). One way of evaluating the appropriateness of the linear autoregressive framework, is to test for nonlinearities using a piece-wise linear model (STAR model; see, for example, Tong 1990). Preliminary tests for nonlinearities has provided evidence of such (and thereby for the possibility of more complex dynamics) in several of the time series (Falck *et al.* 1995; unpublished results). It is, however, not clear how the few tests available behave in small sample situation considered here. Further work is urgently needed.

The above analyses have revealed a consistent geographic pattern of density dependency in a variety of microtine species. Table 1 suggests tentatively

(despite the scarcity of data) that the pattern of statistical DD experienced by any population is more of a biogeographical than a taxonomic property. This lays at the heart of the concept of interspecific synchrony in cyclic rodents (reviewed in Stenseth & Ims 1993). This is furthermore consistent with Hansson & Henttonen's (1988) interpretation of the microtine cycle as a community process. Certainly, it is easy to envisage that external agents (density dependent or density independent) can synchronize population fluctuations (see, for example, Moran 1953; Ims & Steen 1990; Royama 1992). It is, however, difficult to see how such external agents can tune the patterns of DD in all the species of the microtine community.

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