



Seasonal Forcing on the Dynamics of *Clethrionomys rufocanus*: Modeling Geographic Gradients in Population Dynamics

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Abstract. We interpret gradients in population dynamics of the gray-sided vole from the southwestern part of the island of Hokkaido to its northeastern part within the framework of a phenomenological model involving the relative length of summer and winter. In Hokkaido, as in other northern regions, both spring and fall is considered as short transition periods between the two main seasons – summer (the primary breeding season) and winter (the non-reproductive or secondary breeding season). We show that the geographic transition in dynamics may be understood as the combined consequence of different patterns of density-dependence during summer and winter, and geographically varying season lengths. Differences are shown to exist between summer and winter with respect to strength of density-dependence. Direct density-dependence, in particular, is stronger during winter than during summer. A model is presented to show how relative lengths of seasons can induce both stable and periodically fluctuating population dynamics. The results are compared and contrasted with what is otherwise known about the gradient in rodent dynamics in Fennoscandia.

Key words: density-dependence, length of summer and winter, phenomenological model, seasonal and annual dynamics, the gray-sided vole.

Introduction

Populations of the gray-sided vole (*Clethrionomys rufocanus* (Sundevall, 1846)) in the southern and western parts of Hokkaido exhibit only seasonal dynamics with population growth during summer and decline during winter. Populations in northern and eastern parts of Hokkaido exhibit multiannual periodic density fluctuations in addition to the seasonal dynamics (Bjørnstad et al. 1998a; Saitoh et al. 1998a; see also Saitoh 1987; Bjørnstad et al. 1996; Stenseth et al. 1996a; Saitoh et al. 1998b). The cycles in these northeastern parts resemble those found in microtine rodents in Fennoscandia (e.g. Hansson and Henttonen 1988; Hanski et al. 1991, 1993; Stenseth and Ims 1993; Bjørnstad et al. 1995; Stenseth et al. 1996b). The regional transition from pure seasonal to multiannually fluctuations is associated with an increase in population variability and a transition in the patterns of direct

and delayed density-dependence (Stenseth et al. 1996a; Saitoh et al. 1998a).

Various mechanisms have been suggested to explain the biogeographic transitions in dynamics of small rodents: changes in community composition (notably the predator guild; Erlinge 1987; Hansson and Henttonen 1988; Hanski et al. 1991; Bjørnstad et al. 1995; Turchin and Hanski 1997), changes in primary production (Jedrzejewski and Jedrzejewska 1996), and changes in climatic conditions (notably seasonality and extent of snowcover; Hansson and Henttonen 1985; Hansson 1987; Bjørnstad et al. 1998a). In Hokkaido, the main correlate to this transition appears to be the relative length of the summer (Kaneko et al. 1998). The most obvious difference between the seasons is with respect to reproduction (winter generally being a non-reproductive season; see, e.g. Ota 1984; Kaneko et al. 1998). A few recent studies on microtine rodents have, however, also indicated that patterns of density-dependence may differ between seasons (Mallorie and Flowerdew 1994; Hansen et al. 1998).

In this paper we explore the hypothesis that the relative lengths of seasons are responsible for the transition in

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dynamics. We propose that density-dependence differs between summer and winter, so that the overall strengths of direct and delayed density-dependence are shifted with the relative lengths of the seasons, which again affect the dynamical properties of the populations. For the purpose of providing background information, we first briefly summarize the difference in the growing season between southwestern and northeastern Hokkaido, and indicate how patterns of density-dependence differ between winter and summer. We then develop a phenomenological model that allows us to investigate the effect of relative lengths of summer and winter on annual patterns of density-dependence. Throughout we adopt the approach of Stenseth et al. (1996b) by asking what model (and mechanism) is compatible with the observed patterns. We close the paper with a general discussion on microtine rodent dynamics and dynamical effects of seasonal forcing.

Seasonal patterns of density-dependence

The climate in Hokkaido is affected by latitude and altitude as well as the direction of sea currents (see Kaneko et al. 1998). Warm currents run along the western shores of Hokkaido resulting in a milder climate for these regions (see Saitoh et al. 1998a). A northern cold current prevails along the northern and eastern shores resulting in a cooler climate for this region. The growing season for plants varies accordingly. In the southwest the growing season is long whereas in the northeast it is shorter (with a corresponding longer winter). An 'index of vegetative growth period' (also referred to as a 'warmth index'; *WI*) for the growing season of plants was presented and discussed by Kira (1949, 1971); it is defined as the sum of average monthly temperatures above 5°C within a year. Thus, $WI = \sum(T - 5)$, where T is average monthly temperature (excluding months of which the average temperature is lower than 5°C). The larger the value of the index, the longer is the growing season. This index correlates well with the forest distribution of Japan (Kira 1949, 1971). The 'geographic score index' (see Saitoh et al. 1998a) which correlates with the transition in dynamics from the southwestern to the northeastern part of Hokkaido (see Saitoh et al. 1998a) also correlates crudely with the 'index of vegetative growth period' (*WI*; Fig. 1b). In this paper we use the *WI*-index as a proxy for length of the breeding period of voles. This period is known to be around 7.5 months in the southwestern part of Hokkaido and around 6 months in the northeast (Fujimaki 1975; Kaneko et al. 1998).

The population dynamics of *C. rufocanus* has been studied on the basis of 225 time series on rodent abundance from the census conducted by the Forestry Agency of the

Japanese Government (FAJ) (Saitoh et al. 1998a; see also Kaneko et al. 1998; Bjørnstad et al. 1998a). (Most of the time series are between 20 and 31 years long; see Kaneko et al. (1998)). Populations were sampled (as described by Kaneko et al. (1998)) in both spring (May/June) and fall (September/October) as well as in the middle of the summer (July/August). Saitoh et al. (1998a) used the fall samples to estimate the annual structure of density-dependence in the 225 time series. The fall-samples are from the end of the breeding season (cf. Kaneko et al. 1998); hence, between two subsequent fall-samples there is only one continuous sequence of winter (non-reproductive season) and summer (reproductive season).

For characterizing the population growth from spring to fall and from fall to spring, we also use the spring samples.

The index of vegetative growing period (*WI*) is not yet available for all the 225 individual time series. As discussed by Saitoh et al. (1998a), the 225 time series were grouped into 11 groups, according to geographic and topographic characteristics (Fig. 1A). Figure 1B depicts the relation between *WI*-index and the geographic score, which is based on the 'diagonal' order along two directions (from south to north and from west to east) for each group (see also Saitoh et al. 1998a). The autoregressive analysis reported below is primarily based on the combined (i.e. mean) time series within each of the 11 groups (see Bjørnstad et al. 1998a). However, when analyzing winter and summer density-dependence (see *Discussion*) we use data from individual census points from the northern part of Hokkaido (roughly corresponding to the data used by Stenseth et al. (1996a)).

Saitoh et al. (1998a) demonstrate that several population dynamical descriptors correlate with the geographic score. The strength of density-dependence is, in particular, found to change with geographic position (Saitoh et al. 1998a; see also Stenseth et al. 1996a). This pattern remains when focusing on the descriptors of each of the mean time series for each group (see Bjørnstad et al. 1998a), although less clearly so.

We measure strength of direct and delayed density-dependence using the second order autoregressive model applied to the log-transformed series of fall abundance (Royama 1992; Bjørnstad et al. 1995):

$$x_t = b_0 + b_1 x_{t-1} + b_2 x_{t-2} + e_t \quad (1)$$

where x_t is the log-transformed fall abundance (really: abundance + 1) of year t , b_1 and b_2 are the first and second order autoregressive coefficients, b_0 is a scaling parameter, and $\{e_t\}$ is a sequence of independent and identically distributed random variables with zero mean and a constant variance (see also Stenseth et al. 1996a, b).

The first order autoregressive coefficient (b_1) increases with *WI*-index (Fig. 2A). There is a less clear relationship between the second order autoregressive coefficient (b_2)

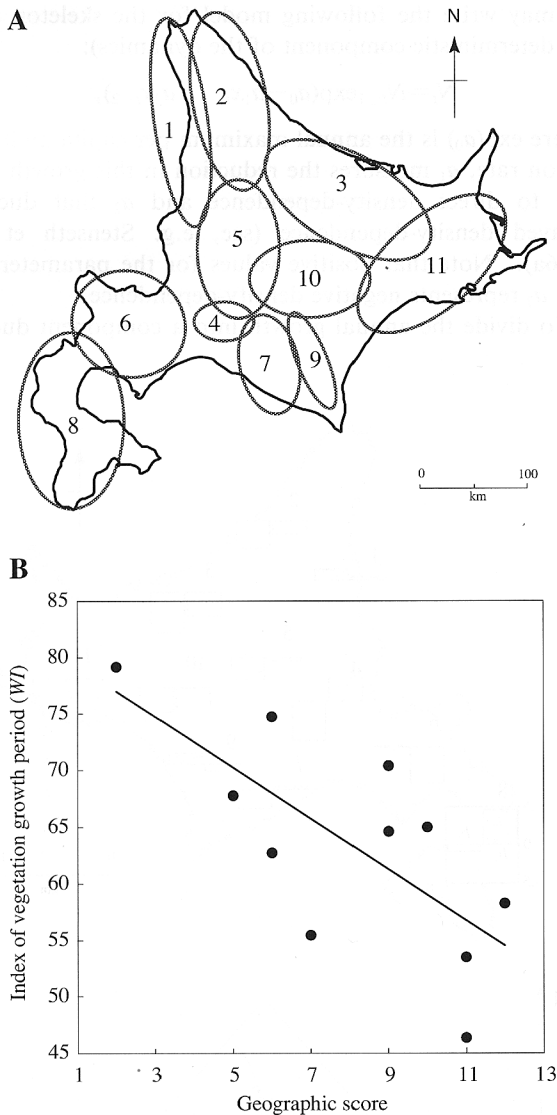


Fig. 1. (A) The geographic location of the 11 groups of *Clethrionomys rufocanus* populations, and (B) the relation between the 'index of vegetation growth period' (discussed in this paper) and the geographic score index (representing the 'northeasterness' and discussed by Saitoh et al. (1998a)). The line in B represents the linear regression; the Pearson correlation coefficient is -0.71 ($P=0.01$). The 225 time series were, as described by Saitoh et al. (1998a), grouped into the 11 groups according to geographic and climatic criteria: Group 1 (Teshio) consists of 31 time series; Group 2 (Kitami) consists of 31 time series; Group 3 (Abashiri) consists of 20 time series; Group 4 (Yubari) consists of 8 time series; Group 5 (Kamikawa-Taisetsu) consists of 27 time series; Group 6 (Shiribeshi) consists of 27 time series; Group 7 (West-Hidaka) consists of 20 time series; Group 8 (Oshima) consists of 30 time series; Group 9 (East-Hidaka) consists of 10 time series; Group 10 (Tokachi) consists of 13 time series; Group 11 (Kushiro-Nemuro) consists of 8 time series. The length of the time series are (depending on group) between 12 and 31 year (194 are longer than 23 years).

and *WI*-index (Fig. 2B). (Stenseth et al. (1996a) reported a slightly different gradient. This is, however, due to the fact that only the northern subset of the database was analyzed then, since only this part of the data was available at the time. Closer inspection show that the gradient observed by Stenseth et al. (1996a) may be seen as a part of the gradient when the entire island is considered as a whole).

Altogether it appears that the 'index of vegetative growth period' (*WI*) is a better correlate than the 'geographic scores'; unfortunately *WI*-index is not yet available for all individual time series where the 'geographic scores' are (see below).

In the following section we explore the hypothesis that the geographic gradient in the density-dependent structure of the time series may be understood as a result – direct or indirect – of relative season length. The present exposition should be considered a preliminary report only. We hope that the present study will stimulate further work on the issue of seasonal differences in density-dependence and the resulting dynamic effects.

A model of seasonal dynamics

The log-linear autoregressive model: a strategic preamble

The exact mechanism causing the microtine cycle is still in debate (see, e.g. Stenseth et al. 1998a). It is clear, though, that the mechanisms responsible for these periodic fluctuations lead to a rather specific signature of density-dependence (Stenseth et al 1996a,b, 1998b; see also Bjørnstad et al. 1995). The second order autoregressive log-linear model (Eq. (1)) has been found to be appropriate for the fall time series of *C. rufocanus* in northern Hokkaido (Stenseth et al. 1996a). A similar model structure has been successfully fitted to other microtine populations (see Bjørnstad et al. 1995; Stenseth et al. 1996b). The linear autoregressive model can arise (to some level of approximation) from a variety of more specific ecological (e.g. trophic) annual models, and can be interpreted in terms of such (see Stenseth et al. 1996a, 1997 for detailed examples). The general seasonal mechanism we propose does, however, not hinge on any specific ecological model. We therefore use the second order model as a starting point, and leave the issue of the exact mechanisms behind the density-dependence to be discussed elsewhere.

The estimated coefficients for the mean time series for each of the 11 groups are shown in Figs. 2 and 3. The distinct geographic pattern observed in the level of variability and periodicity (Bjørnstad et al. 1998a; Saitoh et al. 1998a) is reflected in the autoregressive coefficients. The gradient in the first order coefficient is very clear (Figs. 2

and 3). The patterns in the second order coefficient is less clear-cut, but the western groups (1, 6, 8) stand out by not exhibiting delayed density-dependence (Fig. 3). On the basis of the second order autoregressive model, the north-east areas are expected to exhibit from 3 to 4 year cycles (Fig. 3B; see also Bjørnstad et al. 1995).

Incorporating seasonality

Assume N_t to be the fall-abundance of year t resulting from net population growth during the preceding year,

we may write the following model for the skeleton (i.e. the deterministic component of the dynamics):

$$N_t = N_{t-1} \exp(a_0 - a_1 x_{t-1} - a_2 x_{t-2}), \quad (2)$$

where $\exp(a_0)$ is the annual maximum per capita multiplication rate, a_1 measures the reduction in this growth rate due to direct density-dependence and a_2 that due to delayed density-dependence (see, e.g. Stenseth et al. 1996a). Note that positive values for the parameters a_1 and a_2 represents negative density-dependence.

To divide the annual growth into a component due to

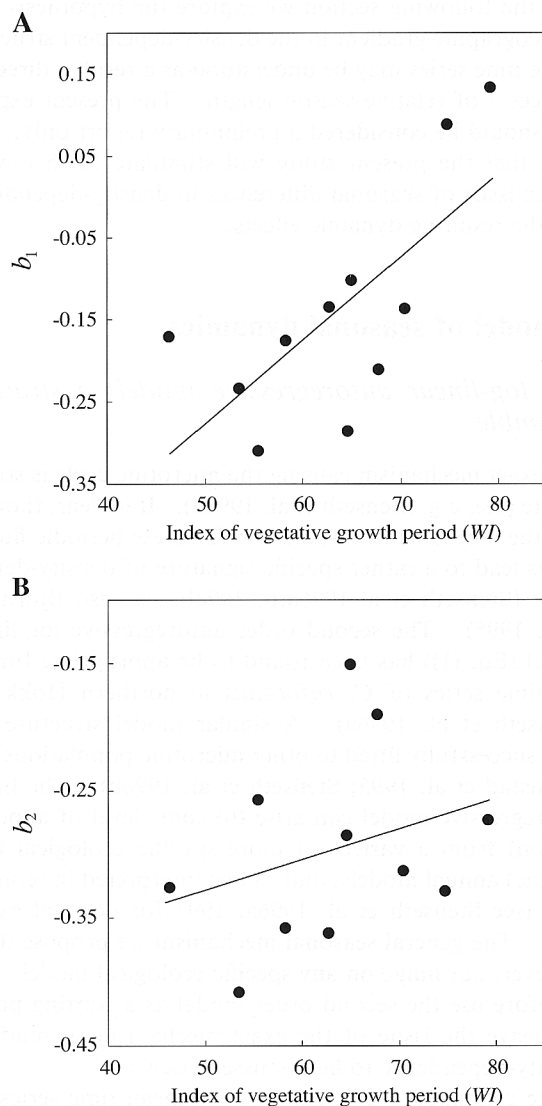


Fig. 2. The autoregressive coefficients (see Eq. (1)) estimated from the average time series from each group (see Fig. 1A; see also Bjørnstad et al. 1998a) plotted against the 'index of the vegetation growth period'. (A) The 1st order coefficient ($R^2=0.50$, $P=0.012$). (B) The 2nd order coefficient ($R^2=0.10$, $P=0.35$).

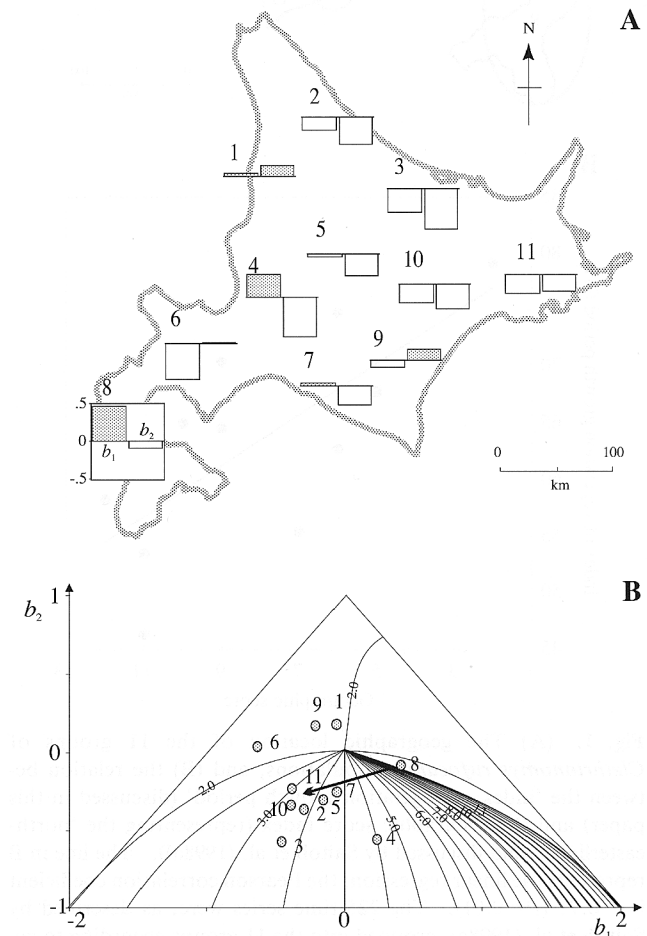


Fig. 3. (A) Map of the autoregressive coefficients for the time series of each of the 11 groups. The first column represent the 1st order coefficient, the second column represents the 2nd order coefficient. Positive values are shaded in gray. (B) A scatter plot of the coefficients for the 11 groups. The predicted dynamics based on the second order autoregressive model are given by the contour lines (see Royama 1992; Bjørnstad et al. 1995). Outside the triangle, the dynamics is divergent. Below the semicircle, dynamics is cyclic. The contour lines give the periodicity (measured in years) of the cycle. The arrow connects the groups with the highest WI to that of the lowest WI among the 11 groups.

winter dynamics and another due to summer dynamics, the model (2) may be split in a multiplicative manner (see Åström et al. 1996). Let τ ($0 < \tau < 1$) be the relative length of the summer defined as lasting from the initiation of spring reproduction until the end of the reproduction in fall. The annual model may approximately be seen as a sequence of density-dependent growths according to:

$$N_t = N_{t-1} \exp[(a_{w0} - a_{w1}x_{t-1} - a_{w2}x_{t-2})(1 - \tau)] \exp[(a_{s0} - a_{s1}x_{t-1} - a_{s2}x_{t-2})\tau], \quad (3)$$

where the parameters with the w -subscript refer to winter (expressed as per- τ units) and the parameters with the s -subscript refer to summer. This is an approximation not least due to the fact that the summer component should be a function of spring densities and not of the previous fall. However, since the model for the density-dependence is linear on the log-scale, the fall abundance can potentially be mapped to the spring data. The given formulation is thus a heuristic device for interpreting the

observed geographic patterns. Notice further that during the summer two demographic processes operate (survival and reproduction), whereas during the winter only one process operates (survival; winter reproduction is generally considered to be negligible for *C. rufocanus* in Hokkaido; see Ota 1984; Kaneko et al. 1998; Yoccoz et al. 1998).

Log-transforming both sides of Eq. (3) and collecting terms, we may write:

$$x_t = a_{w0}(1 - \tau) + a_{s0}\tau + (1 - a_{w1}(1 - \tau) - a_{s1}\tau)x_{t-1} - (a_{w2}(1 - \tau) + a_{s2}\tau)x_{t-2}. \quad (4)$$

The parameters in the model given by Eq. (4) may be directly related to the components of the autoregressive model given by Eq. (1):

$$b_0 = a_{w0}(1 - \tau) + a_{s0}\tau, \quad (5a)$$

$$b_1 = 1 - a_{w1} + (a_{w1} - a_{s1})\tau, \quad (5b)$$

$$b_2 = -a_{w2} + (a_{w2} - a_{s2})\tau. \quad (5c)$$

Changes in the length of the breeding season (τ) may

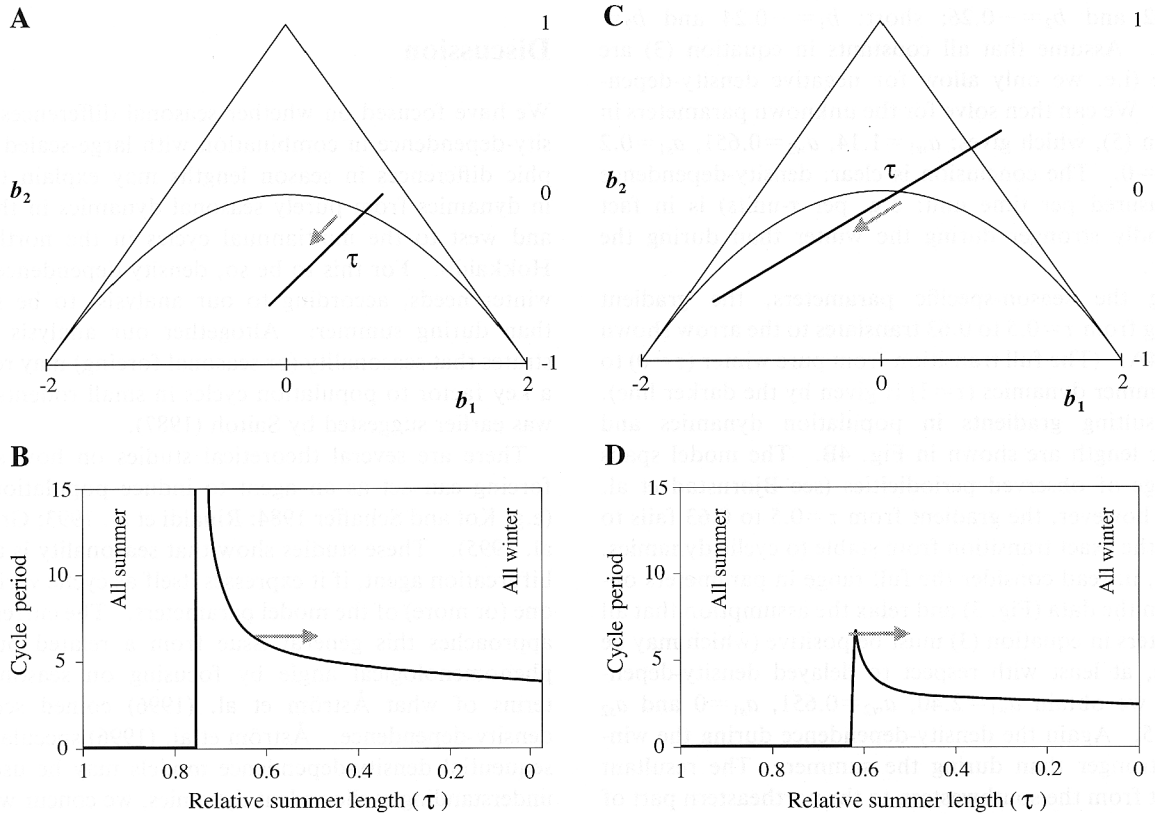


Fig. 4. Numerical examples to illustrate how changing the relative length of the summer (τ) changes the dynamics of a population when density-dependence differs between the seasons (see Eq. (4)). (A and B) We assume that the patterns of summer and winter density-dependence are $a_{w1} = 1.14$, $a_{w2} = 0.651$, $a_{s1} = 0.2$ and $a_{s2} = 0$. (A) Annual patterns of density dependence as a function of season length (the line spans $\tau = 0$ to $\tau = 1$). The arrow covers the distance from $\tau = 0.63$ to $\tau = 0.5$. (B) The resulting period length as a function of τ . A period length of zero corresponds to noncyclic dynamics. As can be seen, in a region with mainly summer, there is no cycles whereas cycles of length 3–4 years are expected in regions with short summers. Notice that after a short transition range, the period length is fairly insensitive to the relative length of the seasons. (C and D) The same as A and B but with $a_{w1} = 2.40$, $a_{w2} = 0.651$, $a_{s1} = 0$ and $a_{s2} = -0.35$.

induce a transition in the dynamics if the patterns of density-dependence differ between the seasons (see below).

The data on *Clethrionomys rufocanus*

We may compare equation (5) with the relations depicted in Fig. 2. Since the first order autoregressive coefficient increases with the length of the summer period, τ , we need to have $(a_{w1} - a_{s1}) > 0$ implying $a_{w1} > a_{s1}$. That is, the intra-specific interactions during the winter (measured per τ -units) needs to be stronger than during the summer.

To expand on this result and help interpret the implication of changing the relative length of the summer (τ), we have investigated a specific numerical example (Fig. 4). The length of the breeding (summer) period (for which the *WI*-index has been used as a proxy in this paper) in the southwestern and the northeastern part of Hokkaido corresponds to $\tau=0.625$ and $\tau=0.5$, respectively (see above). Consider a line in the autoregressive parameter space (Fig. 4A; defined by the regression lines shown in Fig. 2) connecting the longest and the shortest growth period (long: $b_1=0.02$ and $b_2=-0.26$; short: $b_1=-0.24$ and $b_2=-0.31$). Assume that all constants in equation (3) are positive (i.e. we only allow for negative density-dependence). We can then solve for the unknown parameters in equation (5), which gives: $a_{w1}=1.14$, $a_{w2}=0.651$, $a_{s1}=0.2$ and $a_{s2}=0$. The conclusion is clear: density-dependence (as measured per time unit; e.g. per τ -units) is in fact profoundly stronger during the winter than during the summer.

Using the season-specific parameters, the gradient resulting from $\tau=0.5$ to 0.63 translates to the arrow shown in Fig. 4A. (The full transition from pure winter ($\tau=0$) to pure summer dynamics ($\tau=1$) is given by the darker line). The resulting gradients in population dynamics and periodic length are shown in Fig. 4B. The model spans the range of observed periodicities (see Bjørnstad et al. 1998a); however, the gradient from $\tau=0.5$ to 0.63 fails to predict the exact transition from stable to cyclic dynamics.

If we, instead consider the full range in parameters observed in the data (Fig. 3) and relax the assumption that all parameters in equation (3) must be positive (which may be realistic, at least with respect to delayed density-dependence), we obtain $a_{w1}=2.40$, $a_{w2}=0.651$, $a_{s1}=0$ and $a_{s2}=-0.35$. Again the density-dependence during the winter is stronger than during the summer. The resultant gradient from the southwestern to the northeastern part of Hokkaido is represented by the arrow in Fig. 4C. (The full transition from pure winter ($\tau=0$) to pure summer dynamics ($\tau=1$) is given by the darker line.) This refined model predicts that southeastern populations (where the summer is the longest, $\tau=0.63$) should have no multi-annual periodicity (i.e. only exhibit seasonal fluctuations) and that northeastern populations (where the summer is

short, $\tau=0.5$) should have a 3–4 year cycle. The model is also able to capture the rather surprising effect that longer cyclic periods are observed at intermediate lengths of summer (between the areas with stable non-cyclic populations and the areas with 3–4 year cycles), as appears to be the case for the central part of Hokkaido (Group 4; see Bjørnstad et al. 1998a: Fig. 2).

The pattern of seasonal differences will certainly need future and more careful scrutiny. The present preliminary results do, however, demonstrate the viability of our basic hypothesis, namely that the relative lengths of the reproductive season may generate – directly or indirectly – the observed geographic pattern in population dynamics of *C. rufocanus* in Hokkaido. The intriguing finding is that we need not assume any particular clinal changes in the underlying density-dependent parameters (measured per time unit) to explain the transition in dynamics. It suffices to assume that the seasonal driver shifts the relative importance of the winter and summer components of the population dynamics.

Discussion

We have focused on whether seasonal differences in density-dependence in combination with large-scaled geographic differences in season lengths may explain the shift in dynamics from purely seasonal dynamics in the south and west to the multiannual cycles in the northeast of Hokkaido. For this to be so, density-dependence during winter needs, according to our analysis, to be stronger than during summer. Altogether our analysis demonstrates that seasonality (or seasonal forcing) may represent a key factor to population cycles in small rodents, which was earlier suggested by Saitoh (1987).

There are several theoretical studies on how seasonal forcing can act as an agent to induce population cycles (e.g. Kot and Schaffer 1984; Rinaldi et al. 1993; Grenfell et al. 1995). These studies show that seasonality is a potent bifurcation agent, if it expresses itself as cyclic variation in one (or more) of the model parameters. The current study approaches this general issue from a related but more phenomenological angle by focusing on seasonality in terms of what Åström et al. (1996) coined sequential density-dependence. Åström et al. (1996) speculated that sequential density-dependence models may be useful for understanding cyclic rodent dynamics; we concur with this.

In the following discussion we will first focus the seasonal difference, and provide some preliminary analyses showing that density-dependence indeed is stronger during winter. Then, we discuss possible mechanisms underlying the observed patterns. We finally discuss our findings in the more general context of gradients in rodent dynamics.

Seasonal differences in density-dependence

In order to explore the validity of our major conclusion of stronger density-dependence during the winter, we have undertaken an analysis to investigate differences in density-dependence between summer and winter in the gray-sided vole populations of Hokkaido. We used 73 time series from northern Hokkaido that have complete spring and fall censuses for all the 31 years of study (1963–1993). These results are preliminary, firstly, because some specific assumptions are needed to be made, and secondly because some methodological studies remain to be undertaken. The spring and fall censuses are roughly 6 months apart. By assuming that the reproductive season in northern Hokkaido is around 6 months (i.e. $\tau \approx 0.5$; see above) we may assess a_{w1} and a_{s1} from the census data (a_{w2} and a_{s2} may also be assessed; but for our preliminary exposition, a_{w1} and a_{s1} will suffice). In the absence of measurement error, estimates of a_{w1} and a_{s1} can be obtained through regressing $\log(\text{spring abundance})$ on $\log(\text{preceding autumn abundance})$ and *vice versa* (see Royama 1992). However, the rodent censuses is a count variable which does not provide exact estimates of abundance. Count variables typically harbour a Poisson or negative binomial error (e.g. Pielou 1977; Lebreton 1990). Measurement error bias estimates of density-dependence upwards (the density-dependence is concluded to be stronger than it really is) when using the 'log-regression' method (e.g. Itô 1972; see Bjørnstad et al. (1998b) for details when the error is of the Poisson-type). The key methodological problem for seasonal comparisons is that the variance of counts depends on the mean. For estimates based on annual counts (as those reported in Fig. 2), this bias is present: but it will be of the same magnitude for most populations. However, in seasonal estimation the bias may well differ between winter estimates (for which the initial abundance is relatively high) and summer estimates (for which the initial abundance is relatively low). In our analyses we estimate density-dependence assuming the dependent count has a Poisson error (e.g. Lebreton 1990; Bjørnstad et al. 1998b). We are in the process of developing methods that accommodates the Poisson error in independent counts (using Markov chain Monte Carlo methods; e.g. Gilks et al. 1996). Figure 5 depicts the winter and summer estimates of density-dependence for each of the 73 populations. The winter estimates are invariably greater than the summer estimates. With a *proviso* for any artefacts induced by differences in the magnitude of measurement error, we thus have some indications that winter density-dependence is stronger than summer density-dependence in these populations. Altogether then, these results support our basic assertion that density-dependence differs between seasons, and that it is strongest during winter.

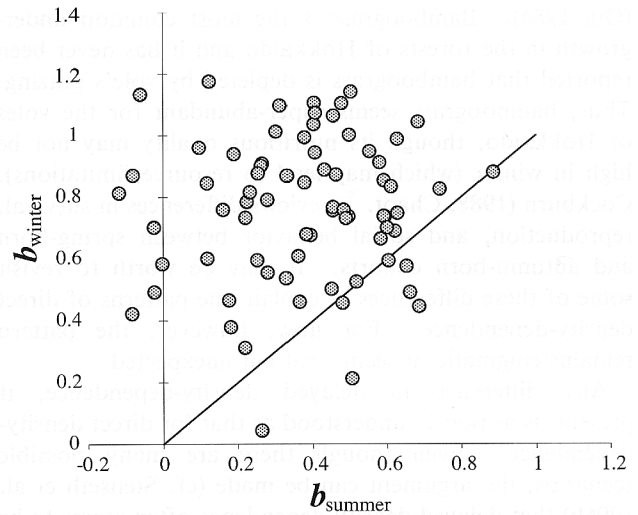


Fig. 5. Scatterplot of the estimates of winter density-dependence against summer density-dependence for each of the 73 time series from Northern Hokkaido that have complete spring and winter censuses for all the 31 years of the study (1963–1993). The estimates assume that the error in the dependent census count follows a Poisson error (see text). The basic model of winter growth is: $Nf_t = Ns_t \exp[c_s - b_{summer} \ln Ns_t]$, where Ns_t and Nf_t are spring and fall abundances (not log-transformed), b_{summer} is the density-dependence over the summer; c_s is the density-independent summer growth rate. The basic model for the winter growth is: $Ns_t = Nf_{t-1} \exp[c_w - b_{winter} \ln Nf_{t-1}]$, where b_{winter} is the density-dependence over the winter; c_w is the density-independent winter growth rate. Notice that the length of the winter and the summer in the particular region from which the data derive are about equal to each other ($b_{summer} \approx a_{s,1} 0.5$ and $b_{winter} \approx a_{w,1} 0.5$). The straight line represents identical strengths of density-dependence in the winter and in the summer. The scatter suggests that density-dependence is strongest in the winter. However a *proviso* must be made about the measurement error (see text).

Mechanisms for seasonal differences

Our discussion on mechanisms underlying the stronger winter density-dependence must necessarily remain speculative. The conclusion that winter regulation is the strongest is, in fact, surprising for a number of reasons: Reproduction is for one thing known to be density-dependent in these voles (e.g. Saitoh et al. 1997; Kaneko et al. 1998). Spacing behavior should, if anything, be expected to lead to stronger intraspecific interactions during the summer, since females defend exclusive territories during the breeding season, but have overlapping home ranges in winter (Ishibashi et al. 1998a, b). Food may be limiting in winter (Petrušewicz et al. 1971; Bujalska 1975; Viitala 1977). However, *C. rufocanus* of Hokkaido eat leaves and shoots of bamboograsses (*Sasa kurilensis*, *S. senanensis*, *S. nipponica* and others) for foods in winter

(Ota 1984). Bamboogras is the most common undergrowth in the forests of Hokkaido and it has never been reported that bamboogras is depleted by vole's grazing. Thus, bamboogras seems super-abundant for the voles of Hokkaido, though its nutritious quality may not be high in winter (which may lead to resource limitations). Cockburn (1988: Chapt. 5) reviews differences in survival, reproduction, and social behavior between spring-born and autumn-born cohorts. It may be worth to revisit some of these differences to explain the patterns of direct density-dependence. For now, however, the pattern remains enigmatic: it seems real but unexpected.

Any difference in delayed density-dependence, if present, is as poorly understood as that for direct density-dependence. Even though there are many possible scenarios, the argument can be made (cf. Stenseth et al. 1996b) that delayed density-dependence often seems to be induced by the trophic interaction between voles and some

specialized predators such as mustelids. The abundance of rodents in the proceeding year, can then be seen as a proxy for the abundance of specialist predators during the year in question. Hansson (1987) suggested that the interaction between rodents and their predator may be modified greatly by snow cover (see also Lindström and Hörnfeldt 1994; Saitoh and Takahashi 1998). If predation is the source of delayed density-dependence in rodents, any such effect could lead to seasonal differences. This is an important topic for future study, not least since delayed density-dependence is a critical component of the rodent cycles (Hörnfeldt 1994; Bjørnstad et al. 1995; Stenseth et al. 1996a, b).

Gradients in rodent dynamics

To complement the discussion on the dynamics in Hokkaido, we briefly revisit the dynamics of microtines in Fennoscandia (Hansson and Henttonen 1988; Hanski et al. 1991; Bjørnstad et al. 1995). In Fennoscandia there are pure seasonal fluctuations in the south and multianually periodic fluctuations in the north (see Hansson and Henttonen 1988). In addition, there is a clear latitudinal gradient in patterns of statistical density-dependence. Bjørnstad et al. (1995) specifically showed that the latitudinal gradient in the periodicity of the cyclic rodents of Fennoscandian (i.e. those north of 60°N) is associated with a decrease in the strength of direct density-dependence

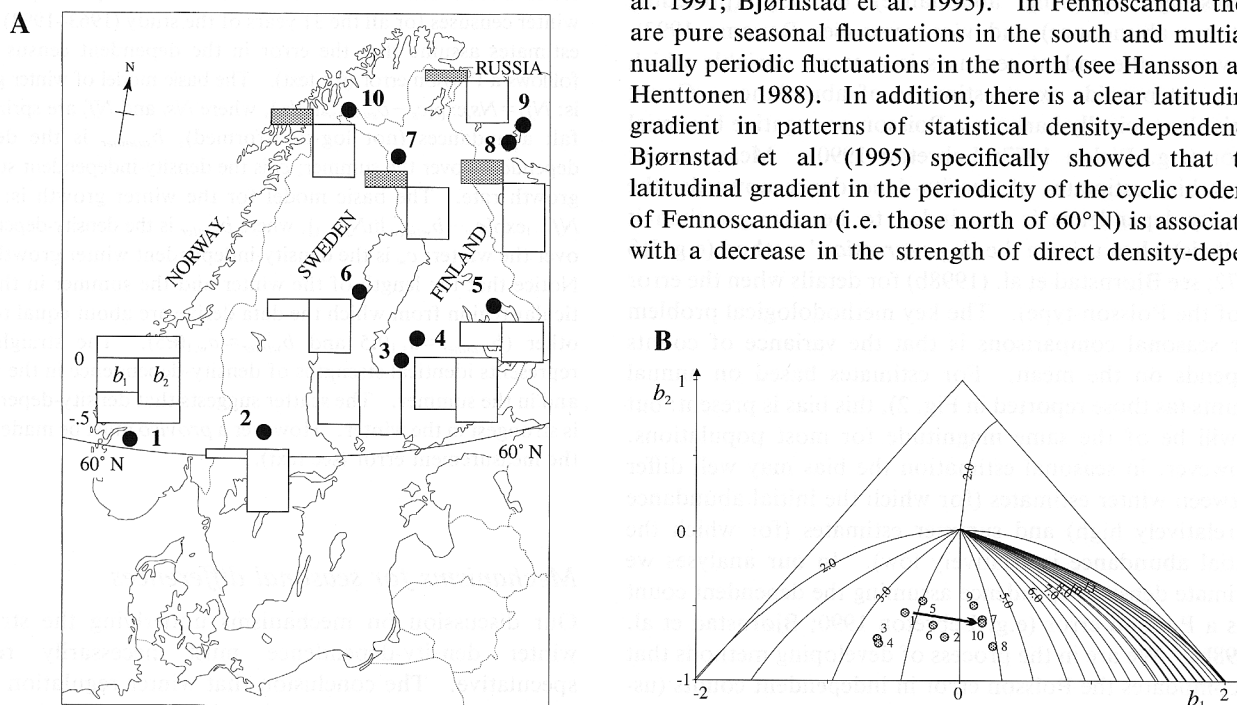


Fig. 6. (A) The map of the autoregressive coefficients for time series of various microtine rodents at 10 different locations in Fennoscandia (data as analyzed in Stenseth et al. 1996b: Table 1). When more than one species are present, the coefficients represent the averages. The first column represent the 1st order coefficient, the second column represents the 2nd order coefficient. Positive values are shade in grey. (B) A scatter plot of the coefficients for the 10 locations. The predicted dynamics are given by the contour lines (see Fig. 4). The arrow connects the southernmost and the northernmost location. The species, location and sources are as follows: 1) *Lemmus lemmus* and *Microtus oeconomus* at Finse from Framstad et al. (1993, 1997); 2) *Clethrionomys rufocanus* at Boda from Marcström et al. (1990); 3, 4) Both *Microtus* spp at Alajoki and Routsala from Korpimäki and Norrdahl (1991), Korpimäki (1993, 1994); 5) *C. glareolus* and *M. agrestis* at Sotkamo from Henttonen et al. (1977), A. Kaikusalo (personal communication); 6) *C. rufocanus*, *C. glareolus* and *M. agrestis* at Umeå Hörnfeldt (1994); 7) *C. rufocanus*, *C. glareolus* and *C. rutilus* at Pallasjärvi from Henttonen et al. (1977, 1987), Hanski and Henttonen (1996), H. Henttonen (personal communication); 8) *C. rufocanus* on Kola from Kataev et al. (1994); 9) *C. glareolus* on Kola from Koshkina (1966) (provided by P. Turchin); and 10) *C. rufocanus* at Kilpisjärvi from Kalela (1957), Laine and Henttonen (1983, 1987), H. Henttonen (personal communication).

dence (Fig. 6). A dominant hypothesis in the literature to explain this gradient is through changes in the predator community (Hanski et al. 1991; Bjørnstad et al. 1995; Turchin and Hanski 1997). Leaving aside the cyclicity itself, the analysis presented in this paper suggests an alternative explanation for the gradient north of approximately 60°N, namely that a shift in season length may change the annual pattern of density-dependence (see also Hansen et al. 1998). This may be a particularly fruitful line of inquiry for Fennoscandian rodents, since the length of the winter changes greatly with latitude. Figure 6 depicts the gradient in the autoregressive coefficients: in the southern part the first autoregressive coefficient is negative whereas in the northern part it is positive. This is in sharp contrast to the pattern of correlation between density-dependence and season length presented for Hokkaido. One possible difference could be that subnivean winter reproduction appears to be quite common in parts of Fennoscandia (cf. Stenseth 1978; Hansson 1984). The seasonal differences with respect to parameter values seem to be different from the Hokkaido case: within the framework of our model (Eq. (2)), we would need to assume that $a_{w1} < a_{s1}$ (incidentally, this may be consistent with assuming that generalist predators play an important role in Fennoscandia but that hunting success differs between seasons; cf. Hanski et al. 1991⁴).

This is not the place to enter into a detailed analysis of the Fennoscandian gradient. The above considerations do, however, demonstrate that our model (and hypothesis) may profitably be applied to other rodent populations. Above all it is a rather general phenomenological hypothesis pointing to the importance of the relative length of the seasons as well as detailed characteristics of the conditions during the different seasons.

Conclusion

The most important general conclusion of our analysis is that seasonal forcing and seasonal differences in density-dependence may represent a key to the understanding of microtine population dynamics. Within the field of microtine rodent ecology, there has been a disproportional focus on the summer season even though pioneers in the field (e.g. Elton 1924; Formozov 1946; Chitty 1952; Pitelka 1957; Kalela 1962; Schwarz 1963, 1977; Schwarz et al. 1964; Fuller 1967; Merritt 1984) all emphasized the importance of winter regulation and abrupt seasonality. In regions where multiannual fluctuations are most common, the winter covers a substantial portion of the year. It is

our hope that this paper will contribute to a renewed focus on seasonality and the winter ecology of rodents.

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⁴ Realizing that in Kilpisjärvi (northern Finland), the summer is very short (i.e. τ is small) and the winter is long (i.e. $1-\tau$ is large), we might easily obtain $a_{w1}(1-\tau) > a_{s1}\tau$ (as concluded by Hansen et al. 1998).

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