Interaction between seasonal density-dependence structures and length of the seasons explain the geographical structure of the dynamics of voles in Hokkaido: an example of seasonal forcing

Nils Chr. Stenseth¹*, Marte O. Kittilsen¹, Dag Ø. Hjermann¹, Hildegunn Viljugrein¹ and Takashi Saitoh²

¹Division of Zoology, Department of Biology, University of Oslo, PO Box 1050, Blindern, N-0316 Oslo, Norway
²Field Science Centre, Hokkaido University, North 11, West 10, Sapporo 060-0811, Japan

The grey-sided vole (Clethrionomys rufocanus) is distributed over the entire island of Hokkaido, Japan, across which it exhibits multi-annual density cycles in only parts of the island (the north-eastern part); in the remaining part of the island, only seasonal density changes occur. Using annual sampling of 189 grey-sided vole populations, we deduced the geographical structure in their second-order density dependence. Building upon our earlier suggestion, we deduce the seasonal density-dependent structure for these populations. Strong direct and delayed density dependence is found to occur during winter, whereas no density dependence is seen during the summer period. The direct density dependence during winter may be seen as a result of food being limited during that season: the delayed density dependence during the winter is consistent with vole-specialized predators (e.g. the least weasel) responding to vole densities so as to have a negative effect on the net growth rate of voles in the following year. We conclude that the observed geographical structure of the population dynamics may be properly seen as a result of the length of the summer in interaction with the differential seasonal density-dependent structure. Altogether, this indicates that the geographical pattern in multi-annual density dynamics in the grey-sided vole may be a result of seasonal forcing.

Keywords: Clethrionomys rufocanus; state-space modelling; geographical gradient; winter food shortages; predation; predator-swamping

1. INTRODUCTION

Rodent species exhibiting periodic multi-annual density cycles typically do so only in parts of their distribution range (Hansson 1971; Hansson & Hettonen 1985, 1988, 1998; Stenseth 1999). For example, populations of the grey-sided vole, Clethrionomys rufocanus (named by Sundevall 1846) in northern and eastern parts of Hokkaido, Japan, exhibit multi-annual periodic density fluctuations superimposed upon a seasonal dynamic pattern, with population growth during summer and decline during winter (Saitoh 1987; Stenseth et al. 1996; Bjørnstad et al. 1998, 1999; Saitoh et al. 1998, 1999, 2002). In the southern and western parts of Hokkaido, populations of the species exhibit only seasonal dynamics.

Several mechanisms have been suggested to explain the geographical variability in dynamics of small rodents: differences in the predator guild (e.g. Hansson & Hettonen 1988; Hanski et al. 1991; Bjørnstad et al. 1995; Turchin & Hanski 1997; Korpimäki et al. 2002), primary productivity (e.g. Jedrzejewski & Jedrzejewska 1996) and/or in climatic conditions (such as seasonality and extent of snow-cover (e.g. Hansson & Hettonen 1985; Hansson 1987; Bjørnstad et al. 1998; Hansen et al. 1999)). Expanding on the latter idea, Åström et al. (1996) (see also Kot & Schaffer 1984; Rinaldi et al. 1993; Grenfell & Finkenstädt 1998; Lindström et al. 2001) suggested that different density-dependent structures within each of the seasons might represent a mechanism leading to multi-annual periodic cycles only in parts of a species’ range of distribution. The proposition that the relative length of the seasons determines whether a population is cyclic or not is referred to as ‘seasonal forcing’.

In this paper, we demonstrate that the estimated annual density dependencies exhibit a clear geographical structure, and that this geographical structure might be a result of the relative length of the summer season at different locations within Hokkaido. On this basis, we empirically strengthen the conclusion of Stenseth et al. (1998) that shortening the summer length will change the annual dynamics from no multi-annual density cycles to multi-annual density cycles. Here, we expand and improve on the earlier analysis reported by Stenseth et al. (1998) in four respects.

(i) We use estimates for the direct and delayed density dependencies obtained through a statistical model incorporating sampling variance. For this purpose, we explicitly model the sampling process by adopting a state-space modelling approach (cf. Fahrmeir & Tutz 1994) and by so doing reducing biases inherent in the more classical autoregressive approach (see Ludwig & Walters 1981; Reddingius & den Boer 1989; Rothery 1998; Shenk et al. 1998).
(ii) We document the geographical structure of the pattern of density-dependent dynamics, using geographical coordinates as predictors of the density-dependent coefficients in the autoregressive model.

(iii) We use a seasonal decomposition of the annual dynamics being improved compared with that used by Stenseth et al. (1998). By so doing, the estimated direct density dependencies during summer and winter are directly comparable.

(iv) We deduce (empirically) an index for the length of the summer season being a descriptor of the geographical structure of the annual direct and delayed density dependencies. This quantity (τ) is then used as an index for decomposing the seasonal structure of the annual density dependencies.

Although our focus on the seasonal density-dependent structure is similar, the approach taken in this paper is different from that of Hansen et al. (1999), Merritt et al. (2001) and Stenseth et al. (2002), who used data on both spring and autumn densities to assess the seasonal density-dependent structure of the same species. Whereas Hansen et al. (1999) and Stenseth et al. (2002) made the tacit assumption of the spring and autumn sampling coinciding with the termination of the winter and the summer seasons, we do in this study let the annual density-dependent structure ‘tell us’ how the year is most appropriately to be divided into two phases (which we will call ‘seasons’ and refer to as ‘summer’ and ‘winter’).

2. THE STUDY AREA AND THE VOLE DATA

Hokkaido is the northernmost island (41°24′–45°31′ N, 139°46′–145°49′ E) of Japan and covers an area of 78 073 km². This island neighbours the Asian continent and is surrounded by the Sea of Okhotsk, the Pacific and the Sea of Japan (figure 1). A southern warm current prevails in the Sea of Japan along the western shore of Hokkaido, whereas a northern cold current prevails in the Pacific along the northern and eastern shores. Mountain ridges run north-south through the middle of the island and in the southwestern part there is another mountain ridge. Except for the southwestern peninsula harbouring temperate deciduous forests, most of the natural forests in Hokkaido are characterized by a transition type of forest between the temperate and the subarctic zones (Tatetawki 1958). The dominant tree genera are Abies, Acer, Betula, Picea and Quercus.

Hokkaido represents the easternmost part of the grey-sided voles’ distribution, ranging from its westernmost edge in Fennoscandia (see Kaneko et al. 1998). The grey-sided vole (C. rufocanus) represents a pest on plantations of pine (Pinus sylvestris) and spruce (Picea spp.) (Ueda et al. 1966), which are quite abundant but nutritionally rather poor. Hokkaido is rich in predators such as snakes, birds and mammals (Henttonen et al. 1992); however, their activity under snow cover is rather restricted for most of these species, one exception being the least weasel (Mustela nivalis), which is the most important predator under snow cover (e.g. Hansson & Henttonen 1985; Hansson 1987).

In the present paper, we use, following what is typically done (e.g. Stenseth et al. 1998), only the autumn data. We used the total number of caught grey-sided voles, together with the corresponding trapping efforts, as our basic data. Trapping effort is defined by multiplying the number of traps by the number of nights and the number of census plots. For example, when three night censuses were carried out at three grids in a ranger office, the trapping efforts by the ranger office at the census was 450 (50 × 3 × 3). Trapping effort in year t is given as \( T_t \).

The studied populations include both multi-annual cyclic (groups 2, 3 and 5; see figure 1) and multi-annual non-cyclic (groups 1, 4, 7, 6 and 8) populations (e.g. Bjørnstad et al. 1998). Each site was assigned geographical coordinates (\( g_{sx} \) and \( g_{sy} \) where \( g_{sx} \) and \( g_{sy} \) are defined as the location in the west–east and the south–north directions, respectively, single coordinate units of which correspond...
Figure 1. Map of the study area, Hokkaido, being the northern-most island of Japan. The 189 studied populations have been grouped according to topographical characteristics (see Saitoh et al. (1998) for details).
exp\((-a_1x_{t-1} - a_2x_{t-2})\tau\) and \(R_{\text{winter}}\) proportional to exp\([(-a_1x_{t-1} - a_2x_{t-2})(1 - \tau)]\). A weakness of this re-parameterization is, however, that the winter and summer direct density dependencies \((a_1, a_2)\) are not directly comparable. (The second-order term is assumed to pick up the longer lags due, for example, to specialized predation.)

To avoid this deficiency, we assume some unknown spring density \((M_s, with \(u_s = \log(M_s))\): this paper’s third major improvement over Stenseth et al. (1998). In this new formulation, let \(R_{\text{summer}}\) depend on the density during the previous spring (rather than the previous autumn) and some delayed effect incorporated by the autumn density two years before (just as in the earlier model). With such a formulation of the summer dynamics, the autumn density will now be given as \(N_t = C_t M_t \exp\([-a_1u_t - a_2x_{t-2}]\tau\]\), where \(C_t\) is a scaling parameter. After some algebra, the new annual model (with seasonal components) can be given as a delay function of autumn densities:

\[
N_t = N_{t-1} R_{\text{summer}} R_{\text{winter}}^\tau \quad (3.2a)
\]

where

\[
R_{\text{summer}} = C_t \exp\([-a_1\log(C_t) + (1 - a_w + a_w(1 - \tau)x_{t-1} - a_w(1 - \tau)x_{t-2} - a_2x_{t-2})\tau\] \quad (3.2b)
\]

and

\[
R_{\text{winter}} = C_s \exp\([-a_1x_{t-1} - a_2x_{t-2})(1 - \tau)\]. \quad (3.2c)
\]

‘Seasonal forcing’ is interpreted within this model as the length of the season \((\tau)\) being a bifurcation parameter determining whether the dynamics is cyclic or non-cyclic. Below, we show that this is in fact the case (see figure 2). Based on equations (3.2b) and (3.2c), the annual density dependencies in equation (3.1) may be given by the seasonal density-dependent components (direct density dependence during summer \((a_1)\) and during winter \((a_2)\), and delayed density dependence during summer \((a_{1w})\) and during winter \((a_{2w})\)) and the season length \((\tau)\) is defined, after some algebra, to be

\[
a_1 = 1 - a_w + (a_1 - a_1 a_w + a_{1w})\tau - a_1 a_2 \tau^2, \quad (3.3)
\]

\[
a_2 = -a_2 + (a_1 a_w - a_2 + a_{2w})\tau - a_1 a_2 \tau^2. \quad (3.4)
\]

(The corresponding expressions (3.3) and (3.4) for the re-parameterization originally given by Stenseth et al. (1998) are \(a_1 = 1 - a_w + (a_1 - a_1)\tau\) and \(a_2 = -a_2 + (a_2 - a_2)a_1\tau\) respectively. The analysis described in Appendix B was performed using this original re-parameterization; the results are presented in electronic Appendix A, tables 4 and 5, available on The Royal Society’s Publications Web site.) We used equations (3.3) and (3.4) to estimate the parameters \(a_{1w}, a_{2w}, a_{1w1}\) and \(a_{2w2}\) by nonlinear regression through bootstrapping (see Appendix B).

(d) Deducing an index, \(\tau\), for the relative length of the summer season

The hypotheses regarding seasonal forcing discussed by Stenseth et al. (1998) relies on us having a reliable measure of the relative length of the breeding season \(\tau\). However, accurate and direct estimates for the relative length of the summer season are difficult to obtain, not least because it varies from year to year. Ideally, we would need some overall measure characterizing the typical season length for any given site.

One possible solution to this problem is further to develop the measure used by Stenseth et al. (1998); that is, a model assuming the relative length of the breeding season, \(\tau\), to be directly related to the warmth index, WI, given as \(\Sigma(Tem - 5)\), where the sum is taken over the months for which the average monthly temperature, ‘Tem’, is equal to or above 5 °C (see Kira 1949, 1971). Stenseth et al. (1998) demonstrated a close relationship between WI and the geographical scores \(g_{w0}\) and \(g_{w0}\) and therefore used a \(\tau\)-index defined on the basis of such geographical scores.

A more empirically (data-based) method of obtaining an assessment of the overall relative length of the seasons (the approach used in this paper) is to ask whether the geographical structure observed in the annual density-dependent structure (see §4a) can be modelled using the geographical scores to describe the length of the summer season, \(\tau\). This is this paper’s fourth major improvement over Stenseth et al. (1998).

The following relationship is assumed to represent a proxy measure for the relative length of the summer breeding season, \(\tau\) (motivated by the statistical results relating to the analyses of the geographical structure of the annual density-dependent structure, where \(g_{w0}\) and \(g_{w0}\) enter as significant predictors; see table 1):

\[
\tau = \exp(F)/[1 + \exp(F)],
\]

(3.5)

with

\[
F = (b_0 + b_1g_{w0} + b_2g_{w0} + b_3g_{w0}g_{w0}),
\]

(3.6)

where the parameters \(b_0, b_1, b_2\) and \(b_3\) are to be determined on the basis of data (see Appendix B). This logit-based function will, as required, vary between zero and unity. We expect that the estimated parameters of equation (3.6) yield a large \(\tau\) for the southwestern part of the island (where the summer breeding season is longest, being heavily influenced by warmer sea currents (e.g. Saitoh et al. 1998)). We further expect that \(\tau\) decreases going northwards and eastwards (towards regions that are increasingly influenced by the colder wind and sea currents (e.g. Saitoh et al. 1998)).

4. RESULTS

(a) The ecological annual model

Using state-space modelling, 189 pairs of estimates for direct annual density dependence \((a_1)\) and delayed annual density dependence \((a_2)\) have been obtained. (The obtained numerical results are presented in the electronic Appendix, table 3; see also figure 2a.) It is worth observing that there is a linear downward ‘trend’ from the upper-right corner towards the centre of the triangle (the blue line in figure 2a). It should also be noticed that if we only use the estimates from groups 1 and 2 (as originally used by Stenseth et al. (1996); populations, estimates and lines marked red in figures 1 and 2a), there is a counter-clockwise ‘movement’ in the statistical parameter space, just as observed by Stenseth et al. (1996); this indicates that the earlier demonstrated counter-clockwise ‘movement’ is
(b) The geographical structure in the density-dependent dynamics

Regressing the direct ($\alpha_1$) and delayed ($\alpha_2$) density dependencies on the geographical coordinates, it is seen that two of the three geographical location parameters (the position along the west–east axis, $g_{we}$, and the position along the south–north axis, $g_{an}$) had significant effect on $\alpha_1$, while only the position along the west–east axis ($g_{we}$) is a significant predictor of $\alpha_2$. An interaction between the effects of $g_{we}$ and $g_{an}$ is observed in the model for $\alpha_1$. Applying the Akaike’s Information Criterion (AIC) (see Burnham & Anderson 1998) instead of the backwards selection results in retention of both $g_{we}$ and the interaction between $g_{we}$ and $g_{an}$ in the best model for $\alpha_2$, but none of these models is profoundly different from the others.

Using the $\alpha_1$ and $\alpha_2$ as dependent variables and the geographical location as independent variables (according to the models summarized in table 1), we may predict the ‘movement’ in the ($\alpha_1, \alpha_2$) parameter space. This is depicted in figure 2b. As can be seen, the process of seasonal forcing emerges: as we move from the southwestern part of the island with long summers towards the northeastern part of the island with short summers, the dynamics changes directionally from non-cyclic to cyclic (multi-annual) dynamics.

(c) The index, $\tau$, for the relative length of the summer season

The optimization for finding the best estimates for the parameters ($b_{io}$, $b_1$, $b_2$ and $b_3$) of the model predicting the relative length of the seasons, $\tau$ (i.e. equations (3.5) and (3.6)), is given in figure 4. Notice that the altitude, $h$, does not enter into the best linear regression models as given in table 1. This result justifies that we use only the geographical coordinates $g_{we}$ and $g_{an}$ in the model for $\tau$. With optimal parameter values, equation (3.6) reads $\tau = 0.998 - 0.011 - g_{we} - 0.0059 - g_{an} + 4.5 \times 10^{-5} \times g_{we} g_{an}$. A graph of the resulting relative season length, $\tau$ across geographical space is presented in figure 5. The corresponding predicted trajectory in the ($\alpha_1, \alpha_2$) parameter space is depicted in figure 2c. Again, the seasonal forcing is apparent: decreasing the length of the summer season ($\tau$) changes the dynamics from multi-annual stable to multi-annual cyclic populations. Notice, however, that the lines in figure 2b are longer than the lines in figure 2c, although both are supposed to model the transition from the southwestern part of Hokkaido to the northeastern part of the island. This is likely to be due to some of the

---

Table 1. The geographical structure in the annual density dependence.

(The table shows the estimated parameters of the linear regression of (a) direct and (b) delayed density dependence on $g_{we}$, $g_{an}$ and $h$. (Best models obtained through backwards selection from the full model $\alpha_i = \rho_i + \rho_{i,we} g_{we} + \rho_{i,an} g_{an} + \rho_{i,h} h + \rho_{i,we} g_{we} + \rho_{i,an} g_{an}$.)) Confidence intervals (CIs) are based on estimates $\pm 1.96$ s.e.)

| parameters estimate s.e. lower 95% CI upper 95% CI t-value p-value |
|------------------|-------|------------------|------------------|-------|-------|
| (a) ($\alpha_1$) (residual error = 0.284; d.f. = 185; $r^2$ = 0.271; $F_{1,185} = 22.94; p = 1.14 \times 10^{-12}; n = 189$) |
| $\rho_{1,0}$ (intercept) | 0.779 | 0.101 | 0.580 | 0.977 | 7.698 | <0.0001 |
| $\rho_{1,1}$ ($g_{we}$) | $-0.005 74$ | 0.001 47 | $-0.008 61$ | $-0.002 86$ | $-3.906$ | 0.001 |
| $\rho_{1,2}$ ($g_{an}$) | $-0.004 04$ | 0.001 08 | $-0.006 16$ | $-0.001 91$ | $-3.726$ | 0.0003 |
| $\rho_{1,4}$ ($we$,$an$) | $3.18 \times 10^{-5}$ | $1.31 \times 10^{-5}$ | $6.15 \times 10^{-6}$ | $5.75 \times 10^{-5}$ | $2.431$ | 0.016 |

| (b) (a) ($\alpha_2$) (residual error = 0.265; d.f. = 187; $r^2$ = 0.0599; $F_{1,187} = 11.91; p = 0.000 691; n = 189$) |
| $\rho_{2,0}$ (intercept) | 0.000 194 | 0.0455 | $-0.088 99$ | 0.0893 | $0.004 27$ | 0.997 |
| $\rho_{2,1}$ ($g_{we}$) | $-0.001 63$ | 0.000 471 | $-0.002 55$ | $-0.007 02$ | $-3.451$ | 0.000 69 |

Only seen in the very northern part of the island and is overshadowed by the downward trend when all sites are used. In view of the much larger dataset used in the present paper, we are convinced that the linear ‘trend’ in the parameter space seems the more appropriate description of the dynamics on the island.

Table 2. Estimating the seasonal density dependence from the relationships between the annual density-dependent structure and the relative length of the summer, $\tau$.

(The table shows the estimated parameters for (a) direct and (b) delayed density dependence for winter ($a_{w1}$, $a_{w2}$) and summer ($a_{s1}$, $a_{s2}$) growth. Positive values indicated negative density dependence. The standard errors are based on 1000 bootstrap samples and confidence intervals (CIs) are based on estimates $\pm 1.96$ s.e. CIs based on 2.5 and 97.5 percentiles deviated less than 0.02 from the CIs reported here. In the electronic Appendix, table 4, we present the corresponding parameter estimates when it is assumed that spring densities may appropriately be mapped on to autumn densities.)

| parameters estimate s.e. lower 95% CI upper 95% CI t-value p-value |
|------------------|-------|------------------|------------------|-------|-------|
| (a) ($\alpha_1$) |
| $a_{w1}$ | 1.637 | 0.0365 | 1.565 | 1.709 | 44.795 | 0.0000 |
| $a_{s1}$ | $-0.402$ | 0.227 | $-0.846$ | 0.0417 | 1.776 | 0.0758 |

| (b) ($\alpha_2$) |
| $a_{w2}$ | 0.351 | 0.100 | 0.154 | 0.547 | 3.501 | 0.0005 |
| $a_{s2}$ | $-0.166$ | 0.135 | $-0.430$ | 0.0988 | 1.228 | 0.220 |

Figure 2. (a) The estimated direct ($\alpha_1$) and delayed ($\alpha_2$) annual density dependencies (see equation (3.1)) for all 189 populations. Two cubic smoothing splines (d.f. = 3) have been fitted: a blue line for all data and a red line for data from groups 1 and 2 (corresponding data-points are coloured red). (b) The movement within the ($\alpha_1$, $\alpha_2$) parameter space, along a straight line from the southwest ($g_{sw} = 0$, $g_{sn} = 24.7$) to the northeast ($g_{sw} = 200$, $g_{sn} = 179.1$) using the statistically derived model given in table 1. The $\alpha_1$ and $\alpha_2$ density dependencies are as predicted from the statistical analysis using the predictors $g_{sn}$ and $g_{sw}$ in models obtained by backwards selection (blue line) or using AIC (red line)). (c) The corresponding movement within the same parameter space using the $\tau$-model (see table 2). The contour lines under the parabola within the triangles indicate the period length of the cycle corresponding to the autoregressive parameters; the period increases as going from left to right in the figure.

Figure 3. Graphical representation of the annual model (equation (3.1)). The true population abundances are linked to the observations through an observation model (equations (A 1)–(A 3)). The arrows represent prior conditional dependence (stochastic relationship) between nodes (i.e. data observations or unknown parameters in the model). Observed nodes are represented by square boxes and unknown quantities by ellipses. Any node with an arrow emanating from it pointing to some particular node $v$ is referred to as 'parent' of $v$. There is one 'sheet' for each year $t$. Quantities without the index $t$ is common for all years.

The seasonal model: decomposing the annual density-dependent structure

The seasonal density parameters are shown in table 2. As can be seen, there is a significant direct density dependence during the winter ($-a_{w1} = -1.64$; CI: $-1.71$, $-1.57$). During summer, there seems to be a somewhat uncertain positive density dependence ($a_{s1} = 0.4$; CI: $0.04$, $0.85$); however, it is clearly weaker than that during the winter season. There is a weak, but statistically significant delayed density-dependent component during the winter ($a_{w2} = 0.35$; CI: $0.55$, $0.15$) but not during summer ($a_{s2} = 0.17$; CI: $0.10$, $0.43$). The simplifying assumption (made by Stenseth et al. (1996)) that spring densities are mapped onto autumn densities results in similar conclusions, except that summer growth is not found to be directly density-dependent, but strong and significantly positively delayed density-dependent, the latter of which is most probably an artefact of the simplifying assumption made by Stenseth et al. (1998) (see electronic Appendix A, tables 4 and 5).

5. DISCUSSION

In this study, we have demonstrated that the relative length of the seasons is a key factor in determining the
Population dynamics in voles  N. Chr. Stenseth and others 1859

Figure 4. The value of the optimization criterion (vertical axis) for different values of $b_2$ and $b_1$. For each point in $(b_2-b_1)$ parameter space, the values of $a_{11}$, $a_{23}$, $a_{w1}$ and $a_{w2}$ (equations (3.3) and (3.4)) have been found by nonlinear regression. The optimization criterion is the average of the two $r^2$ values.

density-dependent processes (which we have ignored).

length becomes, the more likely it is that multi-annual cycles will occur.

We are indebted to the Forestry Agency of the Japanese Government for providing the data analysed in this paper. The study was partly supported by a grant-in-aid from the Ministry of Education, Science and Culture of Japan (no. 14340240). Furthermore, we acknowledge the support that we, over the years, have received from the Japan Society for the Promotion of Science, Forestry and Forest Products Research Institute of Japan, the Norwegian Research Council (NFR/NT), the Centre for Advanced Studies of the Norwegian Academy of Science and Letters, as well as the University of Oslo. Erik Bølviken is thanked for a series of most valuable discussions over the issues discussed in this paper. Kung-Sik Chan, Torbjørn Ergon, Rune Johansen, Tero Klemola, Ole Chr. Lingjærde, Atle Mysterud, Nigel G. Yoccoz and several anonymous reviewers provided valuable comments upon earlier versions of this paper. In particular, we thank two of the anonymous Proceedings B-reviewers for forcing us to further develop our argument: one for forcing us (essentially) to link the population dynamics and the season length more empirically (our fourth improvement), and another for forcing us to improve the basic re-parameterization over and beyond the Stenseth et al. formulation relying on a major simplifying assumption (our third improvement).

APPENDIX A: THE STATISTICAL OBSERVATION MODEL

The expected number of voles caught during a trapping session is related to the abundance of voles at the site and the trapping effort. Let the number of voles caught at a given site in year $t$ to be given by $z_t$. The ecological annual process given by equation (3.1) is, as a first approximation, assumed to be linked to the observed number of voles caught through a Poisson model

$$P(z_t = x | T) = \exp(-\lambda_t) \lambda^x_t / x!,$$

(A 1)

where the Poisson mean (assumed to be proportional to the trapping effort and the population abundance) is defined as

$$\lambda_t = q T \exp(\mu + x_t).$$

(A 2)

The trapping effort $T$ is a known quantity (see § 2) and $x_t$ denotes the unknown log-abundance (centred around $\mu$) for any year $t$. The parameter $\mu$ represents the mean of the log-transformed (true) population abundances. From the nature of the data, we cannot estimate the average level $\mu$ of the (true) population, nor the ‘trappability’ of the species in the given environment, $q$. However, we can estimate the product of the average level and the trappability, defined as $\exp(\gamma) = q \exp(\mu)$. This yields the following parameterization

$$\lambda_t = T \exp(\gamma + x_t).$$

(A 3)

A graphical representation of the quantities in the annual model and their relationship is given in figure 3. (It is worth noticing that with this approach there is no need to add a constant in order to avoid taking logs of zeros (cf. Stenseth et al. 1996).)

A complete Bayesian model consists of the joint prior distribution for all unobservables $(a_{11}, a_{23}, q, \gamma, \lambda_t)$ and the log-abundance for each year $t$ ($x_{1t}, x_{2t}, \ldots, x_{nt}$) as well as the joint distribution of the observables (the abundance

geographical density-dependent structure, as well as a key factor in determining whether a population is cyclic or not (i.e. seasonal forcing). By doing so, we have demonstrated that the multi-annual density cycles seen in the grey-sided vole in Hokkaido may be regarded as an example of seasonally forcing. By doing so, we have demonstrated that, for the found sea-

density dependence deduced for the winter period may be seen as a result of depletion of the winter food supply. The delayed density dependence observed for the winter period may be seen as delayed density dependence during winter. The direct dependence deduced for the winter period is slightly uncertain. This may, however, be a result of predator swamping (e.g. least weasel will be able to build up its own populations, predators, such as the least weasel: the higher the vole density is during the winter two years earlier, the more the predators may not be able to respond sufficiently fast to have an impact on the vole population. Obviously, further empirical studies are needed in order to pursue this further.

Understanding what factors generate the deduced seasonal density-dependent structures remains a challenge, requiring in-depth experimental work. Care is certainly required when interpreting statistical results of this kind. Indeed, based on results reported by Kaitala & Ranta (2001) and Jonzén et al. (2002), the deduced statistical lag-model(s) may be due to both density-dependent processes (which we have assumed) as well as density-independent processes (which we have ignored). However, irrespective of which interpretation we choose to adopt, the dynamic effect of changing season length (i.e. seasonal forcing) remains: the shorter the summer

The interpretation of the positive direct density dependence deduced for the summer period is slightly uncertain. This may, however, be a result of predator swamping (e.g. high spring densities of voles, predators may not be able to respond sufficiently fast to have an impact on the vole population. Obviously, further empirical studies are needed in order to pursue this further.

Indeed, based on results reported by Kaitala & Ranta (2001) and Jonzén et al. (2002), the deduced statistical lag-model(s) may be due to both density-dependent processes (which we have assumed) as well as density-independent processes (which we have ignored). However, irrespective of which interpretation we choose to adopt, the dynamic effect of changing season length (i.e. seasonal forcing) remains: the shorter the summer
data \((x_1, x_2, \ldots, x_N)\) and the trapping effort \((T_1, T_2, \ldots, T_N)\). By conditioning on the data, the posterior distribution (i.e. the conditional probability of the unobservable quantities of interest, given the observed data) is calculated (by successive application of Bayes’ theorem (e.g. Gelman et al. 1995)). The posterior distribution may usually not be obtained analytically but can be computed using Markov Chain Monte Carlo methods, like, for example, Gibbs sampling (Gilks et al. 1996). Bayesian inference is easily utilizable through the software package BUGS (Bayesian inference using Gibbs sampling (Spiegelhalter et al. 1999)). A Bayesian analysis (through the use of BUGS) is flexible and also easier to carry out than the more classical approach of using maximum-likelihood estimation (Meyer & Millar 1999a,b; Tufto et al. 2000).

To fully specify our model, a prior distribution has to be defined for all parameters that are not directly conditioned on other quantity or observed data (i.e. nodes in the graph without any ‘parents’; \(a_1, a_2, \sigma\) and \(\gamma\). Only vague (i.e. essentially flat) prior distributions were used \((a_1 \sim N(0,100), a_2 \sim N(0,100), \gamma \sim N(0,100)\) and \(1/\sigma^2 \sim \text{gamma distribution (0.001, 0.001)}\), meaning that the prior assumes essentially nothing about the parameters relative to what is learned from the sample. We performed 90 000 iterations of the Gibbs sampler, using WinBUGS (the BUGS version for Windows; http://www.mrc-bsu.cam.ac.uk/bugs/) v. 1.2, after a ‘burn-in’ of 10 000 iterations. (Using a few arbitrary selected series, preliminary analyses (applying the extensive convergence statistics available in the coda software of Best et al. (1995)) suggested that the ‘burn-in’ period and the sample size were appropriate.) Convergence was assessed through the runs of multiple chains, and for each run comparing estimates from the first and second half of the chains. Moreover, autocorrelations within the chains seemed to be reasonably low (indicating that the mixing of the Gibbs sampler is not too slow; e.g. Raftery & Lewis 1992). Posterior means of \(a_1\) and \(a_2\) were taken as the estimates of annual direct and delayed density dependencies (see electronic Appendix A, table 3) and utilized in further analyses (using a frequentist approach).

APPENDIX B: DETERMINING THE PARAMETERS OF EQUATION (3.6)

We assume that \(\tau\), the length of the breeding season, is a logistic function of the geographical location:

\[
\tau = \frac{1}{1 + e^{-Z(z)}}
\]

where \(Z(z)\) is a logistic function of the geographical location \(z\).
\[
\tau = \frac{8.5}{12} \ln \left( \frac{\exp(f(\theta_{\text{we,2}}))}{1 + \exp(f(\theta_{\text{we,1}}))} \right)
\]

where \(f(\theta_{\text{we,1}}) = b_0 + b_1 \theta_{\text{we,1}} + b_2 \theta_{\text{we,1}}^2 + b_3 \theta_{\text{we,1}}^3 \).

To determine \(b_0, b_1, b_2\) and \(b_3\) of equation (B 1), we start by assuming that \(\tau_1\) is 8.5 months in the southwest (\(\theta_{\text{we,1}} = 4.3\)), \(\tau_2 = 4.5\) months in the northeast (\(\theta_{\text{we,2}} = 157.87\)), \(\theta_{\text{we,1}} = 146.54\) (e.g. Kaneko et al. 1998). Neither the locations of the geographical reference points nor the assumed season length at these points are critical assumptions; they are merely chosen to achieve an easier interpretation of the results in biological terms. These assumptions are expressed as

\[
b_0 + b_1 \theta_{\text{we,1}} + b_2 \theta_{\text{we,1}}^2 + b_3 \theta_{\text{we,1}}^3 = \ln \left( \frac{\tau_1}{1 - \tau_1} \right) = \logit(\tau_1) = 0.8873, \tag{B 2}\]

\[
b_0 + b_1 \theta_{\text{we,2}} + b_2 \theta_{\text{we,2}}^2 + b_3 \theta_{\text{we,2}}^3 = \ln \left( \frac{\tau_2}{1 - \tau_2} \right) = \logit(\tau_2) = -0.5108. \tag{B 3}\]

After some algebra, we can express \(b_1\) in terms of \(b_2\) and \(b_3\), and \(b_0\) in terms of \(b_1, b_2\) and \(b_3\):

\[
b_1 = -0.5108 - 0.8873 + b_2 (\theta_{\text{we,2}} - \theta_{\text{we,1}}) + b_3 (\theta_{\text{we,2}}^2 - \theta_{\text{we,1}}^2), \tag{B 4}\]

\[
b_0 = 0.8873 - b_1 \theta_{\text{we,1}} - b_2 \theta_{\text{we,1}}^2 - b_3 \theta_{\text{we,1}}^3. \tag{B 5}\]

We determined \(b_0, b_1, b_2\) and \(b_3\) by searching through a large number of \(b_2-b_3\) combinations. For each combination, we computed \(b_0\) and \(b_1\), then computed \(\tau\) for each location, after which we used nonlinear regression to determine the values of the parameters \(a_{i1}, a_{i2}, a_{w1}\) and \(a_{w2}\) providing the best fit of equations (3.3) and (3.4) to the data. Finally, we chose the \(b_2-b_3\) combination with the highest average \(r^2\)-value. We estimated the standard errors and confidence intervals (CIs) of \(a_{i1}, a_{i2}, a_{w1}\) and \(a_{w2}\) based on 1000 bootstrap samples of \(a_1, a_2\) and \(\tau\), where \(\tau\) was computed from the chosen optimal \(b_2-b_3\) combination.

The optimization with respect to \(b_2\) and \(b_3\), jointly with finding the parameters \(a_{i1}, a_{i2}, a_{w1}\) and \(a_{w2}\) by nonlinear regression, is depicted in figure 4, and the resulting \(\tau\)-function across the geographical space of Hokkaido is depicted in figure 5. The distributions of the bootstrapped estimates of \(a_{i1}, a_{i2}, a_{w1}\) and \(a_{w2}\) are shown in figure 6.

We have confirmed (results not shown) that the same geographical pattern as found in this paper arises if the original index of Stenseth et al. (1998), as well as modifications thereof, are used.

REFERENCES


Bjørnstad, O. N., Champley, S., Stenseth, N. C. & Saitoh, T.


Shenk, T. M., White, G. C. & Burnham, K. P. 1998 Sampling-variance effects on detecting density dependence from...


As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

Visit http://www.pubs.royalsoc.ac.uk to see an electronic appendix to this paper.