Changes over Time in the Spatiotemporal Dynamics of Cyclic Populations of Field Voles (*Microtus agrestis* L.)

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**Abstract:** We demonstrate changes over time in the spatial and temporal dynamics of an herbivorous small rodent by analyzing time series of population densities obtained at 21 locations on clear cuts within a coniferous forest in Britain from 1984 to 2004. Changes had taken place in the amplitude, periodicity, and synchrony of cycles and density-dependent feedback on population growth rates. Evidence for the presence of a unidirectional traveling wave in rodent abundance was strong near the beginning of the study but had disappeared near the end. This study provides empirical support for the hypothesis that the temporal (such as delayed density dependence structure) and spatial (such as traveling waves) dynamics of cyclic populations are closely linked. The changes in dynamics were marked by season specific, and changes in overwintering dynamics were most pronounced. Climatic changes, resulting in a less seasonal environment with shorter winters near the end of the study, are likely to have caused the changes in vole dynamics. Similar changes in rodent dynamics and the climate as reported from Fennoscandia indicate the involvement of large-scale climatic variables.

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The mechanisms underlying the dynamics of animal populations that exhibit multiannual cycles in abundance have not been unambiguously demonstrated for any study system. However, a consensus view is emerging that both direct and delayed density-dependent feedbacks—which are thought to arise from trophic interactions between, for example, prey and predators—and density-independent factors, such as the seasonality in the climate, are required for generating population cycles (Leirs et al. 1997; Lima et al. 2002; Stenseth et al. 2002, 2003; Turchin 2003). In addition to the difficulties involved in determining the importance of density-dependent and climatic factors, it has long been recognized that complex spatiotemporal patterns that cannot be explained by patterns in the environment may result from local movements of trophic interactants (Hassell et al. 1994; White et al. 1996; Ranta and Kaitala 1997; Bascompte and Sole 1998; Bjørnstad et al. 2002; Murray 2003).

Previous analysis of long-term (1984–1998) estimates of abundances of field vole (*Microtus agrestis* L.) populations, collected at 21 locations over 60 km² within a British plantation forest, revealed the presence of a pattern resembling a traveling wave in estimated vole abundances (Lambin et al. 1998). Here, we considered longer time series (1984–2004) that reveal obvious changes over time in the dynamics of the vole populations, most notably the appearance near the end of the study period (2000–2004) of a hitherto absent seasonal pattern overlaid on the multiannual cycle. We investigated whether these observed changes in dynamics coincided with changes over time in the evidence for the occurrence of the traveling wave, amplitude, and period of oscillations and season-specific density-dependent feedback on population growth rates. We compared the obtained season-specific temporal gradients in the spatiotemporal dynamics of field voles with evidence of changes over time in the climate in Kielder Forest. This allowed us to evaluate the roles that seasonality, the cli-
mate, and complex spatiotemporal patterns play in the
dynamics of field voles in Kielder Forest.

Methods

The Data

Seasonal estimates (spring [March], summer [July], and
autumn [September–October]) of the population density
(in voles ha⁻¹) of field voles were undertaken from sum-
mer 1984 to spring 2004 (not summer 1999 and 2000) in
21 grass-dominated clear-cut areas over 60 km² within a
coniferous plantation forest (Kielder Forest) in North-
umberland, England. Replacement sites as close as possible
to the original sites were chosen before tree growth made
sampling sites unsuitable for voles. For a full description
of the method of data collection and the abundance es-
imation procedure, see Lambin et al. (1998, 2000).

Changes in the Climate

We used a remotely sensed index for vegetation greenness,
the normalized difference vegetation index (NDVI), from
the National Oceanic and Atmospheric Administration’s
Advanced High Resolution Radiometer Land Pathfinder.
The data consisted of three 10-daily NDVI values per month
per pixel of 1° × 1° spatial resolution and were available at
the National Aeronautics and Space Administration’s
Distributed Active Archive Center (see http://daac.gsfc.nasa
.gov/interdisc/readmes/pal_NDVI.shtml). The NDVI has
been shown to be correlated with total green biomass
and leaf area index and may be used as a standardized
index to compare vegetation greenness between satellite
images (Sellers et al. 1994). We used the NDVI values in
March 1983–2001 to investigate changes in the vegetation
greenness in the early spring at two sites, located approx-
imately 10 miles east of Kielder Forest. The maximum of
three 10-daily NDVI values in March was used to reduce
noise in the monthly values (the main source of mea-
surement noise is the presence of cloud cover, which
decreases NDVI values; see Sellers et al. 1994). The two sites
consist of grasslands without trees (grazed by sheep) with
a vegetation that is similar to that found in the clear-cut
areas in Kielder Forest. Site 2 contained one pixel only,
which was located at a latitude of 55.139454°N and a
longitude of −2.143190°W. Site 1 contained two pixels, lo-
cated at (55.299207°N, −2.225187°W) and (55.299270°N,
−2.111485°W), and the mean of the two NDVI values
only was used in each month. We assumed that the ob-
tained NDVI values at the two sites were positively cor-
related with the vegetation greenness in the clear-cut sites
in Kielder Forest.

Changes in Spatial Patterns

To describe changes over time in the spatial patterns in
population synchrony, we used as a framework the model
of a unidirectional wave in abundance, traveling with con-
stant speed, which was used by Lambin et al. (1998) in
the previous analysis of the shorter time series. In the
presence of a unidirectional traveling wave, the degree
of between-site synchrony of the populations at sites i and j
with geographical location (xᵢ, yᵢ) is a function of time, the
speed at which the wave is traveling, and the spatial posi-
tion of this site after projection onto a straight line in
the direction in which the wave is traveling (Lambin et
al. 1998; Bjørnstad et al. 1999). We measured the decline
of between-site synchrony with between-site distance by
calculating the Mantel correlation of the matrix of be-
tween-site population synchronies ρᵢ (correlations of pairs
of time series of first-differenced log abundances; see
Bjørnstad et al. 1999) with the matrix of between-site Eu-
clidean distances, Rₑᵤₑ, or between-site distances after pro-
jection, Rᵢproj. We calculated Rᵢproj for different angles from
north and took as an estimate of the direction of the wave
the angle from north with the strongest correlation of
between-site synchrony with between-site distance after
projection of site-locations.

Changes over time in the evidence of the traveling wave
were investigated by computing the directionality in spatial
asynchrony in consecutive time windows of lengths of 12
seasons each. In the presence of a unidirectional travel-
ning wave, we expect between-site synchrony to be nega-
tively correlated with between-site projected distance in the
estimated direction of the wave. In contrast, we expect
weaker correlations of synchrony with between-site Eu-
clidean distance or between-site distance in the direc-
tion perpendicular to the cardinal direction of the wave.
We used this contrast to investigate whether the observed
spatial patterns in asynchrony can be explained by random
orderings of time series across locations (further details of
the randomization test are given in app. A in the online

Changes in Density Dependence

Let xᵢ,t and yᵢ,t denote the log abundances of the esti-
mated spring and autumn densities of the vole populations
at site i and year t (in voles ha⁻¹). The seasonal models for
net population growth rates over the winter, Wᵢ,t
(= xᵢ,t − yᵢ,t−1), and summer, Sᵢ,t (= yᵢ,t − xᵢ,t−1), are given as
populations were strongly cyclic, with no apparent overlaid seasonal pattern in growth rates (fig. 1A). However, near the end of the study (2000–2004), the dynamics appeared less strongly cyclic, and a clear (repeatable) intra-annual seasonal pattern in population growth rates could be observed, with increases in density from spring to summer and subsequent decreases from summer to autumn and autumn to spring. We calculated the s index (\(\text{SD of log}_{10}\) density estimates) in consecutive time windows of the time series of spring and autumn population densities of lengths of 6 years to study changes over time in the crude variability in population densities. The variability in spring densities decreased over the study period from approximately 0.45 near the beginning to 0.25 near the end of the study period, whereas the variability in autumn densities remained relatively constant (fig. 1B). Time series of NDVI values and number of days with snow cover over the winter (from December 1 to March 31) in Kielder Forest are given in figure 1C and 1D, respectively.

\[
S_{\tau r} = a_{1r}x_{\tau r} + a_{2r}y_{\tau r-1} + a_{3r}x_{\tau r-1} + a_{4r}y_{\tau r-2} + \delta_{s} + \varepsilon
\]

(1a)

\[
W_{\tau r} = b_{1r}y_{\tau r-1} + b_{2r}x_{\tau r-1} + b_{3r}y_{\tau r-2} + b_{4r}x_{\tau r-2} + \varepsilon
\]

(1b)

where \(\delta_{s}\) and \(\varepsilon\) are normally distributed error terms with mean 0 and variance \(\sigma_{\delta_{s}}^{2}\) and \(\sigma_{\varepsilon}^{2}\).

The sets of parameters \(a_{1...4}\) and \(b_{1...4}\) define the seasonal density-dependent feedback structure of population growth over the summer and winter, respectively. The annual net population growth may be derived by rewriting equations (1a) and (1b) in terms of population densities in the winter only (Stenseth et al. 2003):

\[
R_{\tau r} = \Omega_{1r}y_{\tau r-1} + \Omega_{2r}y_{\tau r-2},
\]

(2)

where the parameters \(\Omega_{1r} (a_{1r} + b_{1r} + a_{2r} + b_{2r} + a_{3r} + b_{3r})\) and \(\Omega_{2r} (a_{1r} + b_{1r} + a_{2r} + b_{2r} + a_{3r} + b_{3r} - b_{2r}a_{3r})\) represent direct and delayed density dependence, respectively. The behavior of this model (eq. [2]) has been described by Royama (1992), and it varies from point stability to regularly cyclic and chaotic dynamics, depending on the values of the parameters \(\Omega_{1r}\) and \(\Omega_{2r}\).

When fitting the autoregressive models with time-varying parameters, we have to take into account that the explanatory variables (the vole densities at various lags) are interrelated because of the autocorrelation in the time series of vole abundances. A suitable method to deal with time series of explanatory variables in regression models is to restrict parameters at neighboring time points to change smoothly over time by penalizing their first differences (Elston and Proe 1995; Eilers and Marx 1996; further details on this method are given in app. B and fig. B1 in the online edition of the American Naturalist).

The autoregressive models (eqq. [1]) were fitted within a Bayesian framework using the WinBUGS package (Spiegelhalter et al. 1999). Our prior beliefs for all autoregressive parameters were that they were uniformly distributed on \([-100, 100]\) and that the inverse of all variance parameters were gamma distributed with shape and scale values of 0.001. The WinBUGS code is available in appendix C in the online edition of the American Naturalist.

Results

Near the beginning of the study, the dynamics of the vole populations were strongly cyclic, with no apparent overlaid seasonal pattern in growth rates (fig. 1A). However, near the end of the study (2000–2004), the dynamics appeared less strongly cyclic, and a clear (repeatable) intra-annual seasonal pattern in population growth rates could be observed.
Figure 1: A, Mean (SE given by vertical lines) of the estimated seasonal log densities (in voles ha$^{-1}$) of the vole populations on all locations in Kielder Forest from 1984 to 2004. Triangles, summer; squares, autumn; circles, spring. B, Changes over time in the crude variability in population densities in these seasons given by the $s$ index (= SD of log$_{10}$ density estimates) in consecutive time windows of the time series of spring (circles) and autumn (triangles) population densities of lengths of 6 years. C, Normalized difference vegetation index values in the month of March in two sites approximately 10 miles east of Kielder Forest (and at a similar altitude). The sites consist of grasslands (grazed by sheep) and have a vegetation similar to that in clear-cut areas in Kielder Forest that provide habitat for field voles (triangles and dashed line, site 1; circles and solid line, site 2). D, Number of days with ground snow cover in Kielder Forest from November 1 to March 31 during the winter from 1984–1985 to 2000–2001.

against yearly number of days with snow and NDVI values (fig. 4). In addition to the seasonal models, we also fitted the autoregressive models with time-varying parameters to annual spring-to-spring and autumn-to-autumn time series separately. The results of this analysis are given in figure B3 in the online edition of the American Naturalist. The strength of direct density dependence decreased for both spring-to-spring and autumn-to-autumn fluctuations. However, the strength of delayed density dependence decreased markedly for spring-to-spring but appeared constant over time for autumn-to-autumn fluctuations.

Discussion

We demonstrated coincident changes in the temporal and spatial dynamics of cyclic vole populations using a data set of time series of estimates of population densities obtained on clear cuts within a plantation forest. Marked and season-specific changes over time had taken place in the synchrony, amplitude, and periodicity of population cycles. Density-dependent feedback on the growth rates of vole populations over the winter changed from acting predominantly with a delay near the beginning of the study to acting exclusively without a delay near the end of the study. The seasonal estimates of density dependence appeared linearly related to indices of snow cover and spring plant phenology. In addition, changes over time had taken place in the spatial covariance in density fluctuations and evidence of the presence of a unidirectional traveling wave in abundance.

The detection of spatiotemporal patterns in the dynamics of cyclic populations using sets of time series is often complicated by changes over time in dynamics such as the dominant period, mean, or variance of oscillations (Grenfell et al. 2001). Even though the dynamics of many cyclic populations have been shown to change over time (Chitty and Chitty 1962; Hansson and Henttonen 1985; Steen et al. 1990; Hanski and Henttonen 1996), few studies adjust
Figure 2: Changes over time in the evidence of the presence a unidirectional traveling wave in abundance. The solid line indicates the correlation of between-site synchrony with between-site distance in the estimated direction of the wave ($R_{\text{proj}}$). The dashed line indicates the correlation of between-site synchrony with between-site Euclidean distances ($R_{\text{eucl}}$). The dotted line indicates the correlation of between-site synchrony with between-site distance perpendicular to the estimated direction of the wave ($R_{\text{proj}}(\theta + 90^\circ)$). The horizontal line at the bottom of the graph indicates the starting points of the time windows in which evidence for the existence of a unidirectional traveling wave was strong.

Figure 3: Changes over time in the estimated strengths of direct and delayed density dependence in the time series of annual autumn densities. Estimates of the parameters were obtained using the means of the posterior distributions of the autoregressive models for the seasonal density-dependent structure for winter and summer growth rates (eqq. [1]) and writing the seasonal models in terms of autumn densities only (eq. [2]). The estimated values of the parameters changed from $1 + \Omega_{1,\text{cyc}} = -0.05$ to $1 + \Omega_{1,\text{cyc}} = 0.44$ and from $\Omega_{2,\text{cyc}} = -0.80$ to $\Omega_{2,\text{cyc}} = 0.36$. Stationary and cyclic dynamics are predicted for combinations of the parameters ($(1 + \Omega_{2,\text{cyc}})$, $\Omega_{1,\text{cyc}}$) that fall below the semicircle, with the predicted dominant period of the cycle indicated by the contour lines. Above the semicircle and below the triangle, the predicted dynamics are point stability. For a full exposition of the dynamics of this model, see Royama (1992).
Figure 4: Scatter plots of seasonal density dependencies against the number of days with snow cover, and the mean of the NDVI of areas 1 and 2. A, B, Density dependencies of net population changes over the winter, given by the means of the posterior distributions of the parameters $b_{1...4}$ (eq. [1b]), are plotted against days with snow. C, D, Density dependencies of net population changes over the summer, given by the means of the posterior distributions of the parameters $a_{1...4}$ (eq. [1a]), are plotted against NDVI values. For clarity, the graphs have been split into four panels, and in each panel the estimated time-varying values of two model parameters are given (circles and triangles are used to distinguish the two different sets of parameters).

Cycle phase dependent over the winter season: winter survival, body mass, and propensity of winter breeding are higher during the increase phase of the cycle (Ergon et al. 2001a, 2001b). The results of this study also strongly suggest that delayed density-dependent population regulation during the winter is a key factor involved in the generation of vole population cycles because of the following: first, the observed changes in dynamics are most clearly indicated by the disappearance of delayed density-dependent feedback on population growth rates over the winter (figs. 3, 4, B2); second, changes in overwintering dynamics are more likely to influence spring abundances than autumn abundances, and the changes in vole dynamics were much more pronounced in annual spring-to-spring than in autumn-to-autumn time series (figs. 1, B3). We therefore hypothesize that the shortening of the winter season has reduced the period over which delayed density-dependent processes can act over the period September-October to March (see also Stenseth et al. 2002).

The processes responsible for delayed density dependence over the winter (or any other season) are not unambiguously known for rodents from Kielder Forest or any other location. A commonly invoked hypothesis is that delayed density dependence on vole population growth rates is caused by a numerical response of the abundance of specialist predators (least weasels in Kielder Forest) on the abundance of voles. However, empirical evidence collected in Kielder Forest does not support the assumption of the specialist predation hypothesis that weasel numerical response should be delayed on vole density, and weasel
predation only accounts for a small fraction of variability in vole survival in Kielder Forest (Graham and Lambin 2002). Recently, Cavanagh et al. (2004) showed that the prevalence of antibodies to cowpox virus and signs of advanced *Mycobacterium microti* infection (vole tuberculosis) in field voles in Kielder Forest were related to vole population growth rates with a delay of 3–6 months. There is growing empirical evidence of the occurrence of traveling waves in host-pathogen systems, such as measles (Grenfell et al. 2001) and dengue fever (Cummings et al. 2004), and transient waves have been shown to occur in the abundance of mammalian hosts after invasion by diseases (Murray 2003, pp. 661–720). We therefore hypothesize that the interactions between voles and diseases caused delayed density dependence, and (transient) traveling waves in abundance, in field voles in this area.

Long-term changes in the amplitude and regularity of rodent oscillations, as reported from Fennoscandia, are in many ways similar to the changes in field vole dynamics in Kielder Forest. Namely, an increased seasonality in population fluctuations and an increased frequency and severity of winter declines associated with a decrease in delayed density dependence of population density changes over the winter (Hörnfeldt 2004). Despite the fact that vole densities in Kielder Forest are higher than in Fennoscandia, the obvious similarity in dynamics of these geographically disjoint cyclic populations adds weight to the suggestions that similar ecological processes generate delayed density dependence in both areas. As in Kielder Forest, a decrease in the amount of snow cover and length of the winter season has been reported from Fennoscandia (Hörnfeldt 2004). Because of the similarities in changes in dynamics and changes in winter climate, we cannot ignore the hypothesis that changes in the climate over large spatial scales have been involved in the changes in rodent dynamics in Kielder and Fennoscandia.

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**Literature Cited**


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