A new geographical gradient in vole population dynamics

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A new geographical gradient in the dynamics of small rodents is demonstrated by analysing 29 time series of density indices of the common vole (*Microtus arvalis*) from Poland, the Czech Republic and the Slovak Republic. This gradient extends from more stable northerly populations in coastal Poland to more variable and cyclic populations in the southernmost parts of the Slovak Republic, and is hence a reversal of the Fennoscandian gradient. All studied variables (such as mean density, cycle amplitude, density variability and the coefficients in a second-order autoregressive model) exhibit consistent latitudinal variation. Possible underlying factors are discussed. In particular, we suggest that seasonality may be a key element in explaining the observed new gradient.

Keywords: common vole; density dependence; microtines; population cycles; seasonality

1. INTRODUCTION

The population sizes of several vertebrate species fluctuate multi-annually (Finerty 1980; Kendall *et al.* 1998; Stenseth 1999). The dynamic patterns of these fluctuations vary over extensive geographical areas (Bjørnstad *et al.* 1995; Stenseth *et al.* 1999; Erb *et al.* 2000; Johnson *et al.* 2000). For arvicoline rodents (voles and lemmings), two geographical gradients exemplifying the regional transition from purely seasonal fluctuations to multi-annual periodic fluctuations have thus far been established, one in Fennoscandia (Henttonen *et al.* 1985; Hanski *et al.* 1993; Bjørnstad *et al.* 1995) and the other in Hokkaido, Japan (Bjørnstad *et al.* 1996; Stenseth *et al.* 1996a,b; Saitoh *et al.* 1998). In both cases, cycle amplitude and periodicity increase with latitude.

Many data on vole dynamics exist from central Europe, a region that has been characterized by massive vole outbreaks since (at least) the beginning of the last century (Elton 1942; Frank 1957; Mackin-Rogalska & Nabaglo 1990; Romankow-Zmudowska & Grala 1994); however, these data have not yet been fully analysed. Here, we add new evidence to a European geographical pattern of small-mammal fluctuations by presenting the first thorough analysis of microtine population dynamics in central Europe. By analysing the data from Poland, the Czech Republic and the Slovak Republic, we have revealed a new gradient in the common-vole dynamics. Contrary to the gradients in Fennoscandia and Hokkaido, population cyclicity in central Europe increases with decreasing latitude from the Baltic sea coastline of Poland to the river Danube in the Slovak Republic.

2. MATERIAL AND METHODS

(a) *Species, study area and data*

The common vole, *Microtus arvalis* (Pallas, 1778), is the most abundant vole species in central Europe, inhabiting open agricultural and natural habitats such as alfalfa or grassy fields.

Females are capable of breeding at the age of two weeks (Tkadlec & Zejda 1995) and build complex underground burrows inhabited by several related individuals, commonly referred to as a colony (Frank 1957). These conspicuous features, coupled with high fecundity, easily generate high-density conditions characterized by more than 1000 individuals per hectare in peak years (see Jedrzejewski & Jedrzejewska 1996).

Here, we analyse time series of density indices for a total of 29 districts in three central European countries: Poland (eight time series), the Czech Republic (12 time series) and the Slovak Republic (nine time series) (figure 1). The data from all three countries were collected by state plant-protection agencies using the same density index, namely the number of re-opened burrow entrances per hectare. This index has been shown to be a reliable measure of population abundance (Liro 1974). For each district (province), several agricultural habitats (*ca.* ten) were surveyed in the autumn, after harvest time, by counting re-opened holes (EPPO 1975). On each field of at least 1 ha, all burrow entrances in four random quadrats measuring 10 m × 10 m were closed, and re-opened entrances were counted the following day. Indices were averaged across the district in order to obtain an overall yearly index. The time series data for Poland (published as charts in Romankow-Zmudowska & Grala 1994) were obtained from the Natural Environment Research Council Centre for Population Biology, Imperial College, London (1999; <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>). The Polish time series data cover 16 years (1977–1992). The time series data for the Czech Republic and the Slovak Republic cover 15 years (1968–1982). The data from Poland and the former Czechoslovakia were collected independently and could, therefore, be influenced by country-specific differences in the organization and monitoring of the common-vole densities. This additional noise would be likely to show up as a drop in the degree of spatial synchrony between neighbouring Polish and Czech districts. However, we found no evidence for such an effect. The synchrony between the districts Opole (Poland, number 8 in figure 1) and Opava (Czech Republic, number 9 in figure 1), as measured by cross-correlation coefficients for six overlapping ln-densities (1977–1982), is 0.91, which is well above the region-wide mean synchrony of 0.73 calculated for nine nearby Czech districts (numbers 9 and 13–20 in figure 1). Thus,

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Figure 1. (a) Map of Europe showing the location of the central European region relative to Fennoscandia. Arrows depict the transitions from seasonal to multi-annual (and increased) fluctuations in both Fennoscandia and central Europe. (b) Detailed map of the geographical transect and the positions of the 29 districts from which the time series used in this study were obtained. The studied locations roughly demarcated a latitudinal transect extending northwards from the river Danube in the southernmost part of the Slovak Republic (48° N) to the Baltic Sea coast in Poland (54° N) and ranged longitudinally from 14° N to 22° N. Geographical coordinates for the centre of each district were read to the nearest 10' from maps. Triangles refer to Poland populations, circles to Czech populations and squares to Slovak populations. Solid symbols denote populations that were best described by a second-order autoregressive model with periodic multi-annual fluctuations. The numbers refer to districts as follows: 1, Koszalin; 2, Pila; 3, Poznan; 4, Konin; 5, Leszno; 6, Jelenia Gora; 7, Wroclaw; 8, Opole; 9, Opava; 10, Kolin; 11, Kutna Hora; 12, Pribram; 13, Svitavy; 14, Prostejov; 15, Prerov; 16, Zdar nad Sazavou; 17, Vyskov; 18, Brno; 19, Znojmo; 20, Breclav; 21, Topolcany; 22, Galanta; 23, Dunajska Streda; 24, Komarno; 25, Nove Zamky; 26, Levice; 27, Bardejov; 28, Trebisov; 29, Michalovce. The inserts show the dynamics of ln-densities for six districts along the transect.

time series appear to be consistent across countries in terms of the way they capture population processes.

(b) Statistical analysis

As in other studies (e.g. Hanski *et al.* 1991; Bjørnstad *et al.* 1995; Saitoh *et al.* 1998; Johnson *et al.* 2000), each time series was ln-transformed and characterized by mean abundance, cycle amplitude and s index. The cycle amplitude was estimated as the average difference between the highest and lowest ln-abundances within a window of three to five years, which is the typical length of an arvicoline population cycle (see Saitoh *et al.* 1998). The s index (the standard deviation of $\log_{10}$ -abundances) was used to measure variability in population size (Stenseth & Framstad 1980).

The geographical pattern in the autocovariance structure of the time series was analysed using autoregressive modelling (Royama 1992; Bjørnstad *et al.* 1995; Stenseth *et al.* 1996a; Stenseth 1999). All ln-transformed time series were detrended through a smoothing spline using a smoothness parameter [$\lambda \in (100\text{--}300)$] implemented in JMP (SAS Institute Inc. 1995). Assuming that population growth rate changes linearly with ln-abundance (i.e. according to the Gompertz assumption; cf. Stenseth *et al.* 1996b), autoregressive modelling on a log scale

was used to examine density-dependent structure (Bjørnstad *et al.* 1995):

$$X_t = b_0 + (1 + b_1)X_{t-1} + b_2X_{t-2} + \varepsilon_t, \quad (1)$$

where X_t is the natural logarithm of the density index and the coefficients b_1 and b_2 measure the strengths of the annual direct density dependence and the delayed density dependence, respectively, in a population with growth rate $R_t = X_{t+1} - X_t$ (see, for example, Stenseth 1999). The term ε_t is a normally distributed and time-independent noise term. Selection of the order of the model (the number of lags to be included) was based on AIC_c (corrected Akaike information criterion) values computed as $2 \times \log\text{-likelihood} + 2p + 2(p+1)(p+2)/(n-p-2)$, where p is the number of lags (the number of previous densities used to predict X_t) and n is the length of the time series (Hurvich & Tsai 1989). AIC_c is a recommended measure of the appropriateness of the model (given the data) and penalizes both the inclusion of additional estimable parameters in the model and small sample size (Anderson *et al.* 2000). The best model is that with the smallest AIC_c , assuming that a difference of less than one in AIC_c values is not significant (cf. Bjørnstad *et al.* 1995). Statistical models were fitted using PROC AUTOREG

Figure 2. Relationships between latitude and (a) mean density index, (b) cyclic amplitude and (c) s index. Triangles refer to Polish populations, circles to Czech populations and squares to Slovak populations. Solid symbols denote populations that were best described by a second-order autoregressive model. (d) The temporal (and synchronized) dynamics of the seven Czech and Slovak populations found to be best described by a second-order autoregressive model.

with the maximum-likelihood option (SAS Institute Inc. 1993). Only the ln-data from Leszno (Poland) indicated a slight deviation from a normal distribution, as tested by the Shapiro–Wilk's test ($W = 0.86$, $p = 0.02$).

As we made no *a priori* assumptions as to the geographical direction that any gradient might have, we used latitudinal and longitudinal coordinates as independent descriptors in searching for a clinal variation in density dependence. Their effects were examined by fitting linear regression using weighted least squares to give the best linear unbiased estimate (SAS Institute Inc. 1995). The weights were the reciprocals of the error variances of the estimated autoregressive coefficients.

3. RESULTS

The mean density ranged from 68 (Konin, Poland) to 2141 (Dunajska Streda, Slovak Republic) burrow entrances per hectare, with an overall mean of 909 burrow entrances per hectare. The highest yearly abundance index (9000) occurred for the district of Komarno (Slovak Republic) near the river Danube. A clear latitudinal variation in the mean density index was observed, increasing from northern coastal Poland southwards to the Danube area of the Slovak Republic ($R^2 = 0.64$, $F_{1,27} = 48.4$, $p < 0.001$; figure 2a); there was, however, no clear-cut longitudinal variation ($R^2 = 0.03$, $F_{1,27} = 0.75$, $p = 0.40$).

The cycle amplitude varied from 0.42 (Koszalin, Poland) to 4.31 (Prostejov, Czech Republic) corresponding to 41 and 4812 burrow entrances per hectare, respectively, on the untransformed density scale. The overall mean for all time series was 2.19. As with the mean abundance index, the cycle amplitude increased with decreasing latitude towards the southern Slovakian populations along the river Danube ($R^2 = 0.39$, $F_{1,27} = 17.6$, $p < 0.001$; figure 2b). Again, there was no longitudinal variation in cycle amplitude ($R^2 = 0.00$, $F_{1,27} = 0.001$, $p = 0.97$).

The s index varied from 0.09 (Jelenia Gora, Poland) to 0.66 (Galanta, Slovak Republic), with a mean of 0.46. In 11 districts the s index was higher than 0.5 (the threshold value suggested for separating cyclic and non-cyclic populations; Henttonen *et al.* 1985). No Polish population had an s index above 0.5. Geographical variation in s indexes followed the same latitudinal pattern as that observed for the other indicators, increasing southwards ($R^2 = 0.38$, $F_{1,27} = 16.5$, $p < 0.001$; figure 2c).

Using AIC_c , a second-order autoregressive model (AR(2) model) was found to provide the best fit for nine time series, of which two were in Poland (Poznan and Opole), five in the Czech Republic (Brno, Opava, Prostejov, Vyskov and Znojmo) and two in the Slovak Republic (Komarno and Levice). Abundances of these

Figure 3. (a) Scatter plot of $1 + b_1$ against latitude. The line depicts the best predictor of the coefficient $1 + b_1 = 148.79$ (s.e.m. = 44.28, $p = 0.002$) $- 6.018 \times \text{latitude}$ (s.e.m. = 1.75, $p = 0.002$) $+ 0.061 \times \text{latitude}^2$ (s.e.m. = 0.017, $p = 0.002$). AIC_S for models with and without latitude as an independent variable were 12.58 and 20.69, respectively. (b) Scatter plot of b_2 against latitude: $b_2 = -3.38$ (s.e.m. = 1.48, $p = 0.03$) $+ 0.058 \times \text{latitude}$ (s.e.m. = 0.0298, $p = 0.06$). AIC_S for models with and without latitude were 3.27 and 4.63, respectively. (c) A second-order autoregressive parameter space within which $1 + b_1$ is plotted against b_2 . Superimposed is the arrow depicting the latitudinal increase in cyclicity from the Baltic (54.5° N) to the river Danube (47.5° N). Triangles refer to Poland populations, circles to Czech populations and squares to Slovak populations. Solid symbols denote populations that were best described by a second-order autoregressive model. The periodicity and stability of the dynamics depend on the values of b_1 and b_2 . The cyclic populations, in which density, X_t , is a periodic function of time, are those located below the semicircle, with the cycle length increasing from left to right and the tendency for convergence decreasing downward (Royama 1992). (d) Relationship between population growth rate ($X_{t+1} - X_t$) and $\ln$ -density (X_t). The linear regression slope (mean $\pm$ s.e.m. = -0.73 ± 0.048) was significantly different from zero ($t = 15.19$, $p < 0.001$).

populations exhibit a clear cyclic behaviour (figure 2d). An AR(1) model was the most appropriate for Koszalin (Poland) and an AR(3) model was most appropriate for Prostějov (Czech Republic). The remaining 18 time series were most appropriately described by a simple model containing only the constant term determining the average density. Depicting the dynamics using the coefficients of an AR(2) model reveals a transition from a stable region, comprising the Polish populations, to a region of damped oscillations with periods of three to four years further south (cf. Royama 1992; Bjørnstad *et al.* 1995; Stenseth 1999) comprising the Czech and Slovak populations (figure 3c). This gradient runs in a north–south direction. However, its shape in parameter space appears somewhat more complex, suggesting that yet another transition may exist, going south eastwards from the Czech Republic to the Slovak Republic. The curvilinear latitudinal pattern of direct density dependence

reflects this complexity when a second order polynomial, explaining 52% of the observed variation, is fitted (figure 3a). Delayed density dependence appears to increase southwards in a linear manner (figure 3b). The Polish populations are highly scattered, indicating a fairly large variability in dynamics across the studied transect. Population growth rates were linearly dependent on the $\ln$ -transformed densities (figure 3d).

Altogether, this analysis demonstrates clear cyclicity in the Czech and Slovak Republics. Furthermore, among the cyclic populations there is a clear north–south gradient in the nature of the cyclicity.

4. DISCUSSION

There has been much recent interest in studying geographical variation in vertebrate population dynamics (for a review, see Kendall *et al.* 1998 or Stenseth 1999).

Figure 4. The length of the breeding season in central European populations of the common vole as a function of latitude. The two points for latitudes above 50° N refer to German populations, the three points for latitudes below 50° N refer to Czech and Slovak populations (based on Tkadlec 2000).

Here, we add two important results. First, the high correspondence of second-order autoregressive models to the fluctuations of central European common-vole populations unquestionably suggests cyclic dynamics. Second, the dynamic pattern varies geographically, with stable (purely seasonally fluctuating) populations in the north and unstable (multi-annually fluctuating) populations in the south. The first conclusion is not new, but we provide strongly suggestive evidence of such southern cyclic populations. The second conclusion is, to our knowledge, new.

Extensive outbreaks of the common vole in central Europe have long been known to ecologists (Elton 1942; Stein 1952). However, statistical analyses of time series have only occasionally been attempted (Straka & Gerasimov 1971; Mackin-Rogalska & Nabaglo 1990). This lack of analysis may have led to the misleading generalization that populations at northern latitudes are the only ones that can be considered as 'truly' cyclic (Hansson & Henttonen 1985, 1988; Henttonen *et al.* 1985; Hanski *et al.* 1991, 1993; Norrdahl 1995). Our empirical evidence, along with that from other parts of Europe (Delattre *et al.* 1992; Lambin *et al.* 2000; Salamolard *et al.* 2000), clearly demonstrates that cyclic population dynamics are also present at much lower latitudes in Europe. Assuming that the dynamics of other vole species in central Europe follow a similar pattern, which is, indeed, quite likely (cf. Pucek *et al.* 1993; Tkadlec & Zejda 1998a), then our analysis clearly contradicts the view that the Fennoscandian gradient extends southwards into central Europe (Hansson & Henttonen 1985, 1988; Hanski 1987). A similar point has recently been made by Lambin *et al.* (2000).

The discovery of yet another gradient in vole population dynamics provides additional opportunities for testing theories regarding the causation of cycles. It would, for instance, be of interest to examine whether the proportion of specialists in central European predator communities increases southwards from the Baltic to the interior, as predicted by the so-called predation hypothesis suggested by Hanski *et al.* (1991, 1993).

Interestingly, vole gradients seem to fit a geographical pattern of seasonality (usually defined as yearly amplitude in temperature), a factor that might destabilize populations through interactions with life history and density dependence, as pointed out by both theoreticians and empiricists (Stenseth *et al.* 1998; Grenfell & Finkenstadt 1998; Tkadlec & Zejda 1998b). Increasing seasonality is typically coupled with shortened breeding seasons in arvicoline rodents (Stenseth 1985; Tkadlec 2000). There is empirical evidence that some German populations of the common vole, although located at higher latitudes, have longer breeding seasons and experience less seasonality (smaller yearly temperature amplitudes) than the Czech populations at lower latitudes (figure 4). This suggests that seasonality in the studied transect may, in fact, increase southwards away from the coast, probably due to the moderating effect of the sea. Shortened breeding seasons may have two dynamic effects. First, as a result of temporal limitations, the variation in life-history traits increases through the introduction of cohort variation (i.e. differences in life histories between spring-born and autumn-born animals). Increased demographic variation inevitably allows greater variation in population growth rates and population size (Tkadlec & Zejda 1998b). Second, longer winters may be critical to short-lived voles due to limited resources. Hence, changes in population growth rates over long winters could cause stronger delayed density dependence than those over short winters or over summer breeding periods, as has been demonstrated for voles (Stenseth *et al.* 1998; Hansen *et al.* 1999). These two features, increased variation in life-history traits and winter delayed density dependence, may cause populations to be less stable in more seasonal environments. The gradient in Poland, the Czech Republic and the Slovak Republic was hardly influenced by altitudinal variation away from the coast as the most cyclic populations were found in lowland districts not exceeding 200 m above sea level.

Any reasoning in favour of seasonality will, at present, necessarily be based upon purely theoretical arguments and circumstantial evidence. This emphasizes a need for further analyses of vole dynamics over extensive geographical scales.

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