Is there direct and delayed density dependent variation in population structure in a temperate European cyclic vole population?

Pablo Inchausti, David Carslake, Carole Attié and Vincent Bretagnolle

P. Inchausti (inchausti@cebc.cnrs.fr), D. Carslake, C. Attié and V. Bretagnolle, Centre d'Etudes Biologiques de Chizé, FR–79360 Villiers en Bois, France. Present address for DC: Univ. of Warwick, Gibbet Hill Road, Coventry, CV4 7AL, UK.

Population structure, in terms of the body mass, condition, sex and reproductive status of individuals, has been found to vary in phase with population density in cyclic populations of microtine rodents. Because sustained population cycles involve delayed density dependent changes in the population growth rate, we would expect at least some life history traits also to depend on past densities. Detailed, long-term studies of changes in vole life history traits are however few, and are largely restricted to northern Europe. In view of the uncertainty as to whether the cyclic microtine populations of western Europe represent the same phenomenon as those of northern Europe, we studied temporal variation in the structure of a clearly cyclic population of the common vole *Microtus arvalis* Pallas, in the cereal plains of mid-western France. Our data set contains seasonal, individual-level data from long-term, large-scale trapping covering four entire population cycles. We found considerable cyclic variation in population structure in spring (April), but less so in summer (June). In spring of post-peak years, animals were of low body weight and body condition (particularly females), litter sizes were smaller and there was a reduction in the proportion of breeders. All of these could be proximal drivers of increased mortality rates, or decreased birth rates, contributing to the population declines. Few life history traits, however, showed direct density dependent variation, and none of the traits studied here showed delayed density dependence. We have shown declines in the fecundity and body condition of voles from a western European population that coincides with, and may be a proximal cause of, cyclic declines in population density. Closer attention to proximal causes, by which ecological processes drive cycles, could clarify the extent to which microtine cycles across Europe represent a single phenomenon.

Many populations of microtine rodents (voles and lemmings) undergo dramatic three- to five-year cycles in population density, which have fascinated population biologists for decades. Numerous hypotheses have been put forward over the years to explain the cycles (Krebs and Myers 1974, Krebs 1996, Boonstra et al. 1998, Stenseth 1999), and many remain under consideration. Particular recent attention has been paid to the specialist predator hypothesis (Hanski et al. 1991, 2001, Korpimäki and Norrdahl 1998; but see Oli 2003, Lambin et al. 2006, Hiutu et al. 2007). Whatever the ultimate cause(s) of small mammal cycles, they must involve changes in demographic rates (birth, death, immigration or emigration) at a proximal level. Because sustained population cycles involve delayed density dependent changes in the population growth rate, one would expect that a suite of life history traits also varies in a delayed density dependent fashion. Indeed, demographic changes in cyclic microtine populations have been associated with changes in population structure: the sex ratio, size and/or age structure, reproductive activity or individual quality (Hansson 1984, Erlinge et al. 2000, Norrdahl and Korpimäki 2002a, 2002b, Reed and Slade 2008).

Cyclic populations are characterized by both direct and delayed density dependence, the latter tending to destabilize population dynamics (Berryman and Turchin 2001, Lambin et al. 2006, Smith et al. 2006). Direct density dependence may induce population regulation through an immediate negative feedback from population density to the demographic rates that underlie population growth rate. In the case of short-lived organisms such as microtine rodents, population growth rate should be most sensitive to variation in reproductive rates and less to variation in juvenile and adult survival (Oli and Dobson 2003, Gaillard et al. 2005). If so, the signature of direct density dependent effects is expected to be found in reproductive rates, but empirical evidence for microtine rodents remains equivocal (Norrdahl and Korpimäki 2002a, Reed and Slade 2008). When dynamics are cyclic, delayed density dependent feedback has a prevailing role in destabilizing population dynamics (Berryman and Turchin 2001, Smith et al. 2006). While predicted changes in life history traits affecting the population growth rate in relation to direct density dependent changes are available (Gaillard and Yoccoz 2003, Oli and Dobson 2003), no equivalent theoretical expectations have been proposed with regard to

delayed density dependence. This is paradoxical since delayed density dependent variation in a suite of life history traits should, at a proximal level, underlie microtine cycles.

It is presently unclear whether changes in population structure are the immediate cause (driven by some ecological mechanism, and acting through changes in demographic rates) of the density cycles, or just an epiphenomenon of cyclic dynamics. One well-documented example of this is the 'Chitty effect', in which individuals of unusually high body size are more abundant during peaks of population density (Chitty 1952). While early papers interpreted this variation as evidence for intrinsic hypotheses of cycles (Chitty 1967), the Chitty effect is now seen more as a consequence of the cycles (Lidicker and Ostfeld 1991, Oli 1999). Large-bodied animals tend to be old individuals (Wolff 1993) that may have had higher survival as a result of lower reproductive effort (Oli 1999), a tradeoff that does not necessarily enhance fitness (Lidicker and Ostfeld 1991, Wolff 1993). Other studies of microtines have found poor body condition (Norrdahl and Korpimäki 2002a), reduced maturation rates (Norrdahl and Korpimäki 2002b, Ozgul et al. 2004) and litter size (Erlinge et al. 2000, Norrdahl and Korpimäki 2002b), high mortality rates (Ozgul et al. 2004), a high average age (Norrdahl and Korpimäki 2002b, Ozgul et al. 2004) and a male-biased sex ratio (Norrdahl and Korpimäki 2002b) during or immediately preceding population crashes. Given their direct or potential link with reproductive rates, these are all properties of potential demographic importance, but no satisfactory explanation for the multiannual cycles of microtine species yet proposed has accounted for their repeatable variation.

Most studies that have investigated temporal variation in population structure through vole cycles have been conducted on Fennoscandian populations (Hansson 1984, Halle and Lehmann 1987, Norrdahl and Korpimäki 2002a, 2002b, Ims et al. 2008). Many of the hypotheses proposed to explain vole cycles require conditions specific to high latitudes in Fennoscandia, yet microtine populations showing clear multiannual cycles also occur in the UK, France and Japan (reviewed by Lambin et al. 2006). In this paper, we analyse a long-term data set on the common vole *Microtus arvalis*, collected in intensive farmland habitat in mid-western France (latitude 46°N), and consisting of 11 years of seasonal, individual-level data covering four entire cycles (Lambin et al. 2006). Using long-term, large scale individual-level data, we first assess whether temporal variation in population structure and some life-history traits varies in relation with the density cycle. More specifically, we examine changes in body size and condition, breeding investment and sex ratio according to direct and delayed population density in the population cycle 'Second', because annual (e.g. wheat) and perennial (e.g. grassland) crops show contrasting levels of disturbance due to agricultural work, we hypothetise that voles living in these different habitats will show different life history traits or different levels of covariation between life history traits. We hypothesize that common voles in more stable habitats (semi-perennial crops such as grasslands) will have a clearer and much stronger covariation of population structure than those living in strongly disturbed habitats (annual crops such as cereals).

Material and methods

Vole trapping

Trapping was carried out in a long-term study site of around 400 km^2, situated in an area of intensive agriculture in mid-western France (46°2′N, 0°4′W). Land use in the study site consists primarily of a complex mosaic of annual crops (cereals 42% of total agricultural area in June, rapeseed 13%, sunflower and maize combined 27% and pea 3%) with a smaller proportion devoted to perennial grass meadows (8%), alfalfa (3%) and rye grass (3%). Over the course of the study, the proportion of the land area devoted to perennial crops fell from 18% to 15%. Each April and June from 1995 to 2005, between 72 and 96 agricultural fields were selected for trapping. In each trapped field, a line of 51 live traps, placed at 2 m intervals, was left for 24 h. Overall, we trapped 1972 fields with an effort of 100 572 trap-days over the 11 year study period. Selection of fields was stratified to maintain a constant representation of each major class of land use (perennial crops, autumn-sown annual crops and summer annual crops), and by eight spatial sectors (defined for logistical convenience), in order to achieve a thorough coverage of the study site (Fig. 1). The land use in each selected field was recorded in one of five classes (grass meadows, alfalfa, summer annuals, cereals or rapeseed; the variable 'crop' hereafter). Vole trapping was not done in autumn (as is typical in Fennoscandia) because the effect of harvesting and ploughing the fields during the summer constitutes a large perturbation for this population. We used unbaited traps, following the standardized protocol of the Inst. National de la Recherche Agronomique (Spitz et al. 1974, Lambin et al. 2006) and in accordance with French law for crop pests (Toussaint 1990, Quéré et al. 1991). A total of 3245 individuals (annual average 295.0, SE = 304.6, range = [34, 369] individuals) were captured during the 11 year study period involving four complete cycles. Population abundance in a field, crop, sector (Fig. 1), month and year was expressed as the ln (captures per 100 trap nights + 1), with mean values of 1.5 corresponding to a geometric mean density of approximately 104 common voles ha^{-1} over the whole study site (Lambin et al. 2006). Common voles in the study area have shown clear peaks in density every three years for the last 40 years (Lambin et al. 2006). Cycles in microtines are often divided into phases (peak, crash and intermediate); however, deciding which phase corresponds to which year is sometimes arbitrary, and therefore we opted to use density estimates rather than phase as explanatory variables, and thus tested for phase-related variation of population structure using direct and delayed density dependent values. Fields where more than 20 traps failed (found closed but empty due to severe disturbance by farming activities) were excluded from the analysis. Live-captured voles were weighed (Pesola spring balance, 0.5 g precision) and sexed before release. Those that died in the traps were kept for post-mortem examination. All dead animals were sexed and weighed (Ohaus corp. digital balance, 0.1 g precision). Adults were classed as reproductively active if post-mortem examination revealed them to be pregnant or lactating or if the testes were of a mature size. The number of embryos in
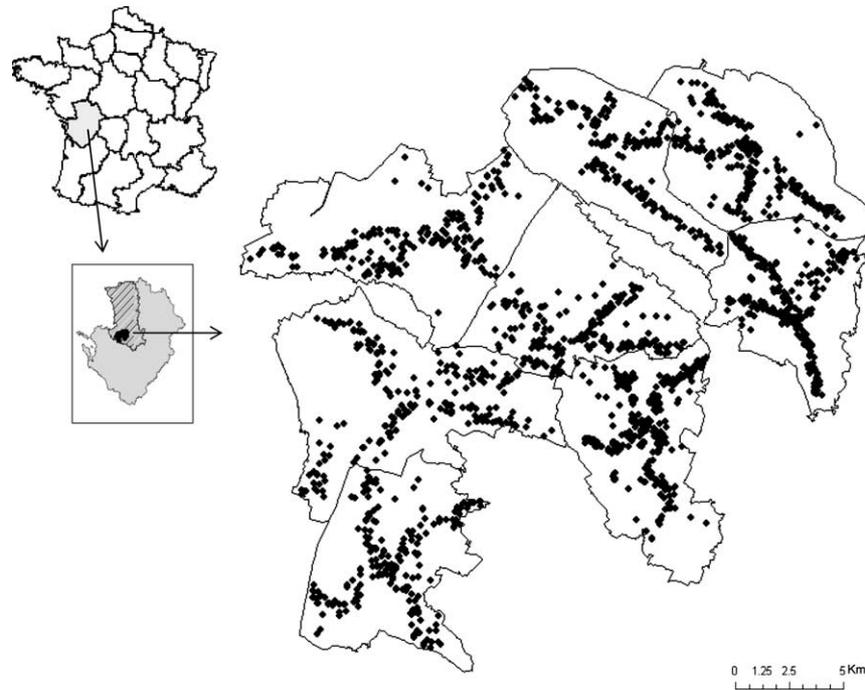
Figure 1. Location of the study site in mid-western France, and the locations where vole trapping took place in 1995–2005.

each pregnant female was counted and used as a measure of litter size. From 1999, the length of the femur, a linear measure of body size, was recorded (Tesa digital caliper, precision of 0.1 mm) for all dead animals and used with the body weight to calculate a body condition index.

Statistical analysis

We examined changes in population structure (measured by body weight, proportion of males, proportion of breeding individuals, litter size and body condition) in relation to cyclic changes in population density using nested linear and generalized linear mixed models on individual animal data. While these response variables were measured at the individual level, all individuals trapped in a field necessarily experienced the same concurrent population density. If not properly accounted for, this could lead to pseudo-replication (i.e. assuming that values of direct and delayed population densities corresponding to individual-level variables are statistically independent). In addition, the vagaries of crop rotation at the field level over time made it impossible to obtain the previous year's (i.e. delayed) population density for each field. Instead, we estimated the population density at year $t-1$ for each field sampled at year t, as the average population density of fields of the same crop that were sampled in the same sector (Fig. 1), month and year t–1. We accounted for these potential sources of pseudo-replication by using a nested hierarchical data structure; nesting the fields within each crop within each sector within each month and year. We used generalized linear mixed models, where fixed effects model the population structure as a function of explanatory variables, and random effects model the patterns in the residuals around the fixed effects due to the nested data structure (Pinheiro and Bates 2004). For each aspect of population

structure, we started with a given structure of fixed effects and proceeded to simplify it by backward elimination using the AIC criterion (removing a variable whenever its removal changed the model's AIC by less than $+2.0$) to obtain the most parsimonious structure of fixed effects (Crawley 2006). We removed random factors only when they were no longer necessary to prevent pseudo-replication for the structure of fixed effects at each step of the process of model simplification. Note that month (April, June) was included as both a fixed and a random effect in all models (Pinheiro and Bates 2004). Parameter estimates shown in Table 1 were obtained using REML (Crawley 2006).

Body condition scores were calculated for each animal as the residuals from a linear model (identity link, Gaussian errors) having ln(body weight) as the response variable and ln(femur length) and a grouping (males, pregnant and non-pregnant females) factor as interacting explanatory variables. The second explanatory variable was necessary because the relationship between weight and femur length would clearly be affected by pregnancy in females. Animals heavier than average for their linear body size were thus assumed to be in better energetic condition (Jakob et al. 1996, see discussion in Green 2001, Schulte-Hostedde et al. 2005).

Body condition and ln(body weight) were analyzed using identity link functions and Gaussian error distributions. The fixed effects of the starting (most complex) model included direct and delayed population density each in interaction with sex and month but not with each other (Table 1). For litter size, sex ratio and the proportion of breeding individuals, the fixed effects of the starting models comprised direct and delayed population density, each in a three-way interaction with month and log-transformed body weight. We used a logarithmic link and Poisson errors for litter size and a logit link function and binomial errors for the other response variables. Some analyses (body

1203

Table 1. Hierarchical, generalized linear mixed models of variation in population structure of common voles in western France. Proportions of males and of breeders were analyzed with binomial errors and a logit link function, litter size with Poisson errors and a logarithmic link function and body weight and individual condition (see Table 2 and main text for definition and estimation) with Gaussian errors and an identity link function. Results are shown only for the final, most parsimonious model obtained by backward model selection using AIC to simplify the structure of the fixed effects (see text for details). Body weight was always Ln-transformed when used as either explanatory or response variable. N(t) is ln(N(t)+1) transformed population abundance at year t. Fixed effects are expressed in terms of the coefficients of the explanatory variables and their interactions (indicating the reference group) with their standard errors in parentheses and their statistical significance assessed by t-test (Crawley 2006). Random effects are expressed as the variance of each variable in the nested structure of variation considered. Sample sizes used in each model are given for each aspect of population structure. The starting model used in the analyses is shown for each variable.

Starting model	Body weight		Proportion of breeders		Proportion of males		Litter size		Individual condition	
	$N(t) \times Month \times Sex + N(t-1) \times Month \times Sex$		$N(t) \times Month \times Body\ weight + N(t-1) \times Month \times Body\ weight$		$N(t) \times Month \times Body\ weight + N(t-1) \times Month \times Body\ weight$		$N(t) \times Month \times Body\ weight + N(t-1) \times Month \times Body\ weight$		$N(t) \times Month \times Sex + N(t-1) \times Month \times Sex$	
Fixed effects	Intercept	2.827 (0.082) T = 34.690	Intercept	10.794 (4.223) Z = 2.556	Intercept	−0.443 (0.607) Z = −0.730	Intercept	2.992 (1.090) T = 2.740	Intercept	0.118 (0.048) T = 2.429
	Month (June)	−0.002 (0.015) T = −0.100	Month (June)	−4.337 (0.869) Z = −4.994	Month (June)	0.030 (0.058) Z = 0.510	Month (June)	−0.612 (0.218) T = −2.800	Month (June)	−0.029 (0.008) T = −3.103
	Sex (males)	0.566 (0.081) T = 6.960	Body weight	−2.871 (1.543) Z = −1.861	Body weight	0.351 (0.172) Z = 2.050	Body weight	−0.296 (0.349) T = −0.850	Sex (males)	0.024 (0.001) T = 2.459
	N(t)	0.052 (0.016) T = 3.340	Month(June) × Body weight	1.545 (0.323) Z = 4.783	N(t)	−0.230 0.054 Z = −4.240	Month (June) × Body weight	0.166 (0.070) T = 2.380		
	Dead (yes)	−0.103 (0.015) T = −6.701								
	Sex(males) × N(t)	−0.096 (0.017) T = −5.780								
	Sex(males) × Month (June)	−0.059 (0.014) T = −4.230								
Random effects	Year/Month/ Sector/ Crop/Field	0.012		0.462		0.730		<0.001		0.003
	Year/Month/ Sector/Crop	0.003		0.166		0.441		<0.001		0.001
	Year/Month/ Sector	0.002		0.248		0.140		<0.001		0.002
	Year/Month	0.001		0.123		0.019		<0.001		0.001
	Year	0.002		1.260		0.010		0.035		0.002
	Residual	0.128		−		−		−		0.025
Sample size	3020		1567		3020		517		1123	

weight, sex ratio) were conducted on all captured voles; while the others (body condition, litter size, proportion of breeders, etc) could only be done on the subset that died in the traps and was subject to post-mortem examination. We further checked whether body weight and sex ratio differed between live and dead animals. We therefore repeated the analyses for body weight and sex ratio after including a binary (dead/alive) independent variable in the final models.

Finally, we assessed the covariation of the five components of population structure. First, we calculated averages (for ln(body weight), body condition and litter size) or proportions (of males and of breeding individuals) for each component within each combination of year, month and crop type. We then calculated Spearman correlation coefficients for each pair of components, among these 108 combinations. Patterns of covariation were further investigated by dividing the data by month, sex or crop type (contrasting grass meadows and alfalfa versus all annual crops) and recalculating the correlation coefficients. Statistical analyses were carried out using the libraries lme4, nlme and MASS in R 2.5 (R Development Core Team 2006).

Results

Body weight and body condition

Time series of population abundance from both April and June (Fig. 2a) clearly revealed the three-year cycle, with peak years in 1996 and every third year thereafter. In April, body weight of both sexes varied with the density cycle (Fig. 2b), with animals about 3 g lighter (a 14% reduction from the average April body weight of 21.5 g) in post-peak years than in other phases. Female body weight significantly increased with higher concurrent (but not delayed) population densities, while males showed a decrease in body mass at high concurrent density (significant interaction $N(t) \times sex$ in Table 1, Fig. 4a). Males were on average about 2 g heavier than females in the spring, a difference which was consistent over time (Fig. 2b). In summer, they were still heavier in most years (Fig. 2b) but less so (Table 1; significant interaction $sex \times month$). This was due largely to males being lighter than females in the summers with the highest population density (Fig. 2b), although this effect was not significant (no sex:month:Nt interaction in Table 1). For both sexes, in April and June, animals that died in traps were on average 10% lighter than those that survived (Table 1).

All classes of animals (i.e. males, pregnant and non-pregnant females) showed a strong log-linear relationship between body weight and femur length (Fig. 3), although there were statistically significant differences in the slopes depending on sex and pregnancy (interaction femur length × class, p <0.001). The slopes of allometric regressions for females were significantly smaller than 3.0, suggesting that larger animals were proportionally less bulky than smaller animals. On average, body condition was lower in June than in April (Table 1), and it increased

slightly (though not significantly) for higher population densities.

Sex ratio

The captured population was male biased overall (considering all captures, 54.1% male; binomial test, p <0.001) and there was evidence that the magnitude of this bias varied during the cycle with males being scarcer at high population densities (Fig. 2d, Table 1). Sex ratios were most male-biased in June after high population densities (reaching up 64% males) and in April of pre-peak years (62% males), and became less male-biased through the rest of the cycle. Unsurprisingly, heavier animals were more likely to be male (Table 1, Fig. 4c). The male bias appeared to be strongest among heavier animals in spring and lighter animals in summer (Fig. 4c), although this effect was not significant (no body weight:month interaction in Table 1). Overall, the sex ratio was significantly more male-biased in June (Table 1, Fig. 4c).

Proportion of breeders and litter size

The proportion of breeders decreased significantly with body weight and was higher in June than in April (Table 1, Fig. 2c, 4d). While the proportion of breeders increased linearly with body weight up to 20 g, it had thereafter either an irregular (April) or a monotonic increase (June; Fig. 4d), which explains the significant interaction body weight: month (Table 1). Delayed population density did not significantly affect the proportion of breeders (Table 1). Extended periods of high reproductive activity result in the production of (initially non-reproductive) young, counteracting the high levels of reproductive activity in older animals. Some studies have suggested that animals may become sexually mature at an earlier age during population increases (Ehrlinge et al. 2000, Oli and Dobson 2001). Nevertheless, the interaction body weight:population abundance was not retained in the final model explaining the proportion of breeders.

We found that litter size in June was significantly smaller than in April (mean difference between corresponding April and June mean values = 0.57 embryos, paired sample t-test, p = 0.001), though the magnitude of these seasonal declines was smaller for animals with higher body weight (Table 1, Fig. 4e). The mean litter size in April was similar in years of peak and pre-peak population abundance (5.97 and 5.96; respectively), being smaller when population abundance was low (5.19; Fig. 1e); a similar, and more obvious pattern was observed in June data.

Covariation of traits in population structure

Body weight was significantly and positively correlated with body condition both in spring and summer (Table 2). This is surprising, since body condition is obtained as the linear residuals of the relationship between log-transformed body weight and body size, and the likely explanation is that larger
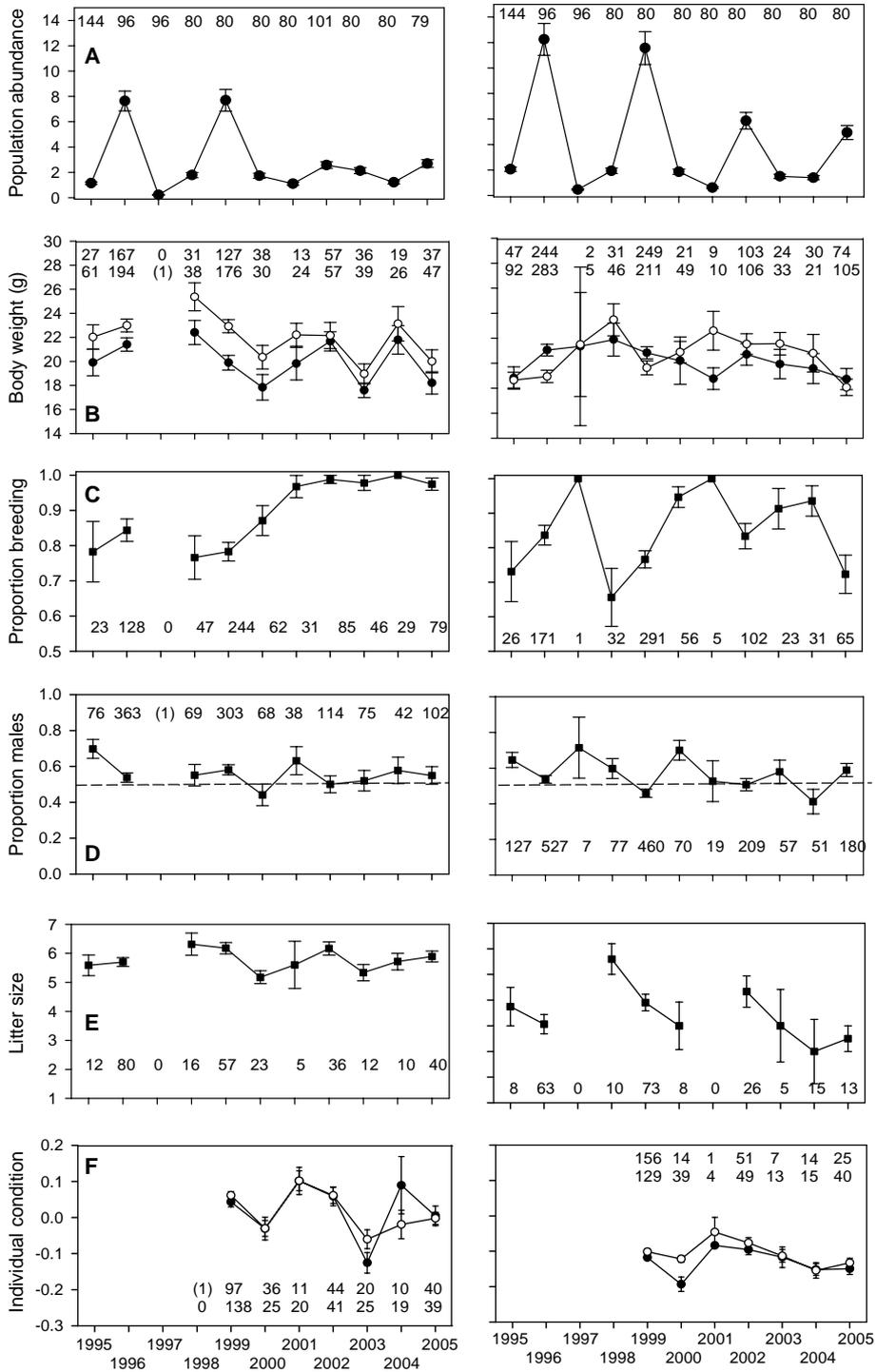
Figure 2. April (left) and June (right) time series of (a) population abundance (expressed as mean abundance per 100 trap nights per line), (b) mean body weight, (c) proportion of breeding individuals, (d) proportion of males, (e) mean litter size, and (f) mean individual condition (residuals of log(weight) on log(femur length). Error bars correspond to the standard errors. Sample sizes used to calculate the mean and standard errors are indicated in each graph (values in parenthesis indicate that sample sizes for a sex or month were too low to calculate a variable), except for panels A where the number of lines trapped is shown. Females are indicated by filled circles and sample sizes in the bottom rows, and males by unfilled circles and samples sizes in the top rows (b) and (f).

animals tend to have larger residuals, i.e. proportionately larger body reserves than smaller animals. Body weight and/ or body condition were further correlated with litter size, proportion of males, and proportion of breeders in some subsets of the data (Table 2), highlighting the pivotal role of

body weight as a key variable organizing the variation of population structure, and possibly of other vole life history variables. Similar patterns were found when the data were subdivided by sex (data not shown). When separating data by season, we found that in April (but not in June),
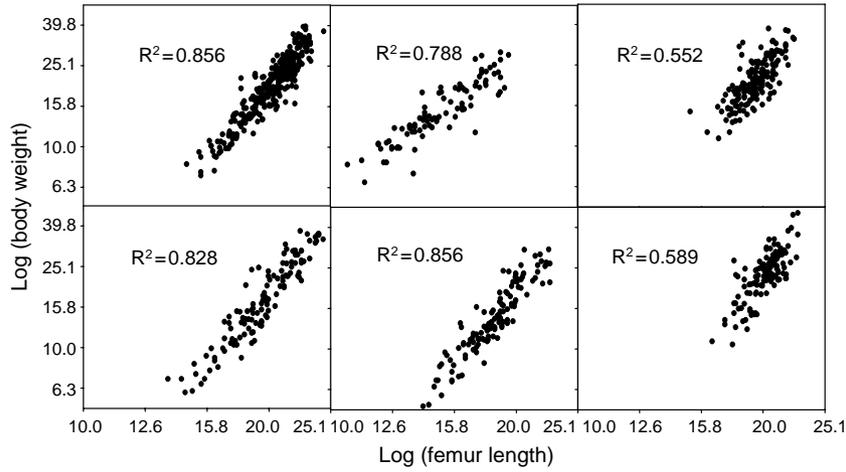
Figure 3. The relationship between body weight and femur length (a linear measure of body size) according to the month (April: top; June: bottom) and status (males, non-pregnant females and pregnant females from left to right). Residuals from log-linear models were used as a measure of body condition.
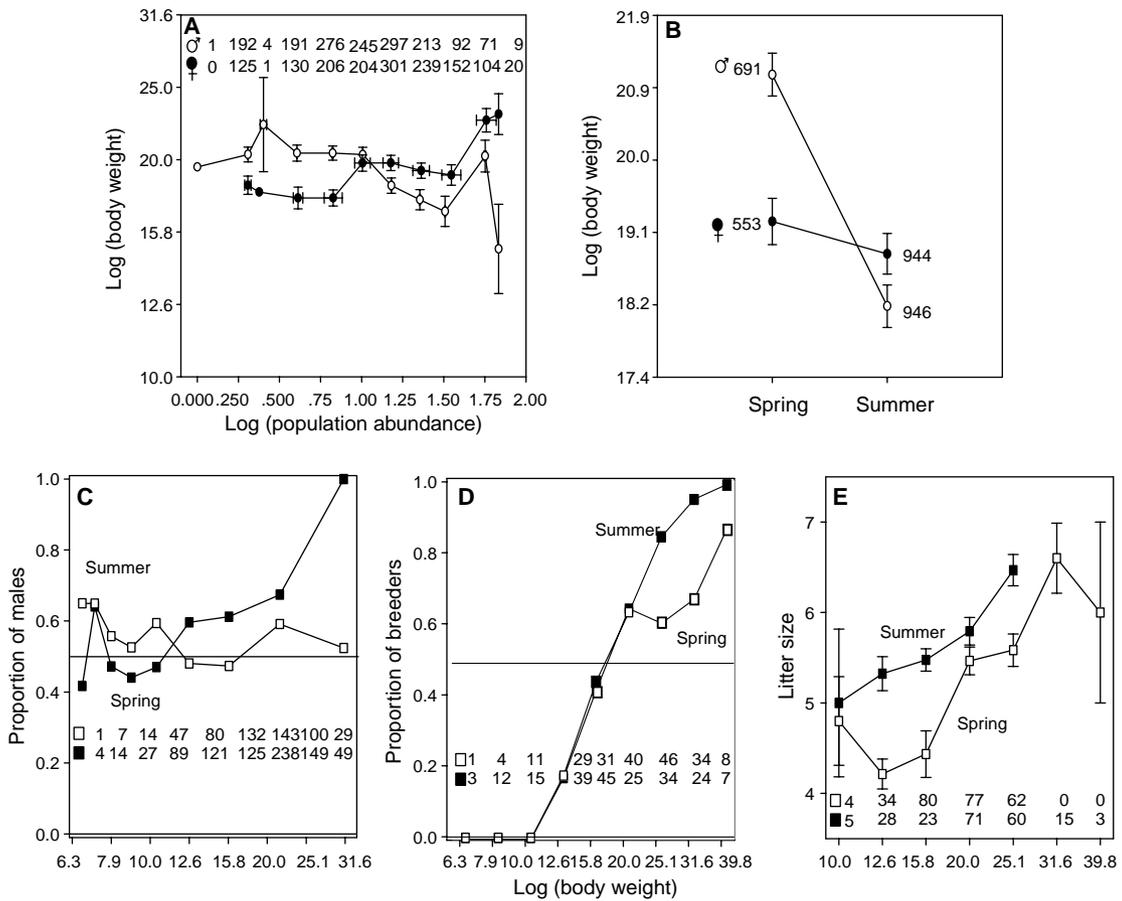

Figure 4. Statistically significant interactions involved in the covariation of population structure indicated in Table 1. Error bars correspond to the standard errors and sample sizes used to calculate each mean and standard error are indicated. (A) and (B) show the variation of body weight with concurrent population abundance and month, respectively (males and females are indicated by empty and filled circles). (C), (D) and (E) show changes in the proportion of males, the proportion of breeding individuals and in litter size in relation to body weight for April (filled squares) and June (empty squares). Body weight was log-transformed for all statistical analyses, but is shown here on a linear scale to aid interpretation.

Table 2. Correlated variation of population structure based on either the average (body weight, individual condition, litter size) or the proportion (of males and of breeders) of individuals at the field level in April (above the diagonal) and June (below the diagonal) during the entire study period for all crops, prairies and all annual crops combined. Statistically significant Spearman correlations are shown in bold.

	Body weight	Proportion of males	Proportion of breeders	Litter size	Individual condition
All crops					
Body weight	–	0.154	−0.165	0.246	**0.542**
Proportion of males	0.129	–	0.036	0.028	−0.051
Proportion of breeders	−0.007	0.189	–	−0.091	**−0.334**
Litter size	**0.376**	−0.113	**−0.320**	–	0.071
Individual condition	**0.453**	−0.209	−0.134	0.011	–
Prairies					
Body weight	–	**0.718**	**−0.600**	0.486	**0.893**
Proportion of males	0.028	–	−0.219	0.255	0.250
Proportion of breeders	0.207	−0.405	–	**−0.768**	−0.374
Litter size	**0.667**	−0.033	−0.133	–	0.108
Individual condition	**0.829**	**−0.580**	**0.657**	**0.700**	–
Annual crops					
Body weight	–	0.091	−0.081	0.215	**0.485**
Proportion of males	0.143	–	0.107	0.058	−0.090
Proportion of breeders	−0.081	**0.306**	–	−0.045	**−0.319**
Litter size	0.024	−0.114	**−0.378**	–	0.030
Individual condition	**0.463**	−0.129	−0.256	−0.160	–

individual condition was significantly and negatively correlated with the proportion of breeders. In contrast, larger litter sizes were positively associated with large body weight and a smaller proportion of breeders in June (Table 2).

When the data were subdivided between grass meadows/alfalfa and annual crops (wheat, rapeseed), we found that the overall patterns of the two sub-data sets resembled each other (Table 2). We detected no significant differences in the time series of density estimates (average ln-densities = 0.787 (SE = 0.017) and 0.792 (SE = 0.013) for annuals and perennials; $p < 0.05$), but the covariation in population structure in grass meadows/alfalfa differed from, in being stronger than, those of annual crops. In grass meadows/alfalfa in June, populations having better average individual condition were more male-dominated (average paired difference in the proportion of males = 0.05, SE = 0.02, n = 11), tended to breed more, and had larger litters in producing on average 0.23 (SE = 0.22, n = 10) embryos more. None of these correlations were significant for June in annual crops or overall, and the significant correlation between condition and the proportion of breeders found in annual crops and overall in April, by contrast, was negative. In April, the grass meadows/alfalfa with the highest average body weight was significantly more male-biased and had fewer breeders. The proportion of breeders was also negatively correlated with litter size (Table 2).

Discussion

Vole population structure according to cycles in population density

This population of common voles from mid-western France showed consistent patterns in population structure during the density cycle (four complete cycles available). We analyzed several life history traits, variation in which might be expected to underlie microtine cycles, but found no sign of delayed density dependence. Indeed, direct density dependence only entered the models in a few cases (body weight, sex ratio). Population abundance (be it concurrent or delayed) was unrelated to reproductive parameters, suggesting that vole reproductive investment and performance (as measured by the proportion of breeders and by litter size, respectively) were neither limited by concurrent resource availability nor by other interactions (predators, parasites or within-population social processes) that could generate a 'memory' in the population (Ergon et al. 2001).

The cyclic variation in population density was clearer in June than in April (Fig. 2a). June vole populations from different phases appeared to differ in density but less so in composition, while April populations differed in composition, but less so in density. Why might this be? It has been suggested (Stenseth et al. 1998, Hansen et al. 1999, Stenseth 1999, Smith et al. 2006) that density dependent processes during long winters play an important role in the maintenance of northern vole cycles. The difference in natural conditions between summer and winter must be smaller at our study site than in Fennoscandia (for instance, there is no winter snow cover in our study site). However, we argue first that summer is likely to be a more difficult season for voles than winter in our study site, and second that the land use in this area of intensive agriculture acts to exaggerate the amplitude of seasonality experienced by voles. In mid-summer (typically early July), most annual crops are harvested and the fields are ploughed. This is also a period of drought. For a folivorous vole species, this effectively brings about a harsh, early start to a period of hardship, even though climatic conditions during the later summer months ought to be the most favorable for population growth. We believe that the intensive land use in our study area may generate a strong seasonality in the patterns of density dependence that have been shown to be crucial for the microtine cycles in northern Europe (Smith et al. 2006). Between April and late June the sown crops develop, bringing conditions favorable for rapid population growth. In contrast to the April populations, which consist mainly of overwintered adults (hence with a larger average body size), we therefore expect the population in June to

contain large numbers of young of the year (Hansson 1984, Halle and Lehmann 1987). Since this young cohort has not been exposed to harsh post-harvest and winter conditions, the quality of individuals is less likely to be related to current population density.

Between April and June of post-peak years, sex ratios changed from being close to 50% to being strongly male biased. This male bias remained until the following April, after which sex ratios were close to 50%, or only slightly male biased. These observed differences in the sex ratio might be due to changes in the relative home range size of males and females depending on population density, since animals with larger home ranges are more likely to be trapped (Hansson 1984). Few data are available for *M. arvalis*, but in most species of *Microtus* males have bigger home ranges (Gliwicz 1997, Borowski 2003), and a greater tendency to disperse than females (Boyce and Boyce 1988), which could result in an apparent overall male bias. Alternatively, secondary sex ratios can truly deviate from the expected evenness as a result of sex-dependent mortality rates, or a bias in the primary sex ratio (for data collected over a large spatial extent, we can discount the local effects of immigration). The sex ratio at any one time is a function of sex-dependent birth or mortality rates integrated over the species' lifespan, so the sex ratio in June may therefore be determined as much by conditions in April as by those in June. For such a dramatic change in sex ratio to take place between April and June when population density is high and fecundity rates are low (Table 1), female-biased mortality rates seem the most likely explanation. This, however, contrasts with most other studies of sex ratio in cyclic microtines. Chitty (1960) stated that mortality rates were male-biased during *M. agrestis* population declines. Halle and Lehmann (1987) found a male sex ratio bias in the same species in April of a crash year that was no longer present in June. Norrdahl and Korpimäki (2002b) found that a cyclic *M. agrestis* population was more male-biased during population crashes. Other studies have found that sex ratio did not vary consistently with population density (Hansson 1984 on *Myodes* (formerly *Clethrionomys*) *glareolus*, Norrdahl and Korpimäki 2002b *M. glareolus* and *Microtus levis* (formerly *rossiaemeridionalis*). This variation within and between species may be partly because crash years, when our study population appears to undergo a dramatic shift in sex ratio and which have been recognised as being particularly critical in vole cycles (Boonstra et al. 1998), are times when the sample size is necessarily small, making a powerful analysis of sex ratios difficult.

Investment in reproduction, so costly for female microtines (Lambin and Yoccoz 2001, Koivula et al. 2003), was low during the April of population crashes (Fig. 2e; Hansson 1984, Norrdahl and Korpimäki 2002b). There is evidence from *M. agrestis* (Koskela et al. 2004) that mothers bias their investment (though not their primary sex ratio) towards male offspring under favorable conditions. This could result in higher survival of young males when population density is low. Such a bias in survival of young animals might explain the continuation of the male bias into April of pre-peak years, but it runs contrary to the establishment of the biased sex ratio in June of post-peak years. Strongly male-biased sex ratios may reduce population growth rates due to a shortage of females (Aars and Ims 2002), since a male-biased sex ratio

at high population densities might delay the recovery of the population from low density, contributing to the cycle. However, the persistence of the male biased sex ratio at all cyclic densities would suggest it ought to be considered as a consequence, rather than a cause, of the ecological processes causing multiannual cycles in our study site.

Vole breeding investment, body condition and the population cycle

Mean body weight in both sexes was on average reduced by about 10% in April during population crashes. In magnitude this is a typical Chitty effect (Boonstra and Krebs 1979, Norrdahl and Korpimäki 2002a). Interestingly, we found that body weight characteristically peaked one year before population density and that body weights in pre-peak years were equal to, or higher than those in the peak ones. This is similar to results found in other studies (Lidicker and Ostfeld 1991, Norrdahl and Korpimäki 2002a) although the Chitty effect is often described as a difference between peak years and all others (Boonstra and Krebs 1979, Oli 1999). It is unlikely that the low mean body weight during population crashes was due to a high proportion of juvenile animals in the population, since declining microtine populations usually consist primarily of old animals with low reproductive activity (Ozgul et al. 2004). Small litter sizes during population crashes (Fig. 2e) suggest that our study population is no exception. This reduction in reproductive activity probably reduced the total weight of embryos carried by adult females in post-peak years. However, we estimate this to account for a difference of only 0.3 g in mean female body weight between peak and post-peak years, compared to the observed reduction of 2.7 g. Further, a similar result was found in males, whose weight is obviously not affected by pregnancy. The results for body condition (Table 1) mirror the results for body weight, suggesting that voles differed relatively little in linear size in relation to population density, and that differences in body weight are due primarily to voles being in poor condition at high population densities, thus presumably leading to reduced fitness (Ergon et al. 2001). Norrdahl and Korpimäki (2002a) found a similar reduction in body condition during population crashes in three other species of voles. Being a reflection of the amount of energy stored by an individual, body condition is both the result of the interactions between individuals and their environment (as implied by the relation between body weight and population density) and a constraint on their reaction to changes in resource abundance and predators (as indicated by the effect of body weight on several breeding parameters). The considerable differences in body condition (individuals being heavier or lighter than expected according to their body size) during the density cycle may therefore be an important proximal cause underlying the decline in vole population density after peaks of population density. The suppression of female reproductive maturation at high population density is well documented in a number of microtine populations (Ostfeld and Canham 1995, Prevot-Julliard et al. 1999, Erlinge et al. 2000). Our study also showed large seasonal differences in the proportion of breeding individuals but rather than

being directly affected by concurrent population density, it was related to changes in body size during the density cycle. The productivity index (the mean litter size multiplied by the proportion of females reproductively active; Shaffer and Tamarin 1973) in April is 3.5 offspring per female during population crashes, compared to 4.6 in peak years and 4.8 in years of intermediate population density. Norrdahl and Korpimäki (2002b), working with *M. agrestis* and *M. levis*, also found a reduction in litter size after years of peak population density, but in contrast to our results, this effect was strongest in the summer and absent in spring. By virtue of their short generation time, fast maturation and high reproductive rates, microtines can be placed at the 'fast' extreme of the 'slow–fast' gradient of life histories (Gaillard et al. 1989, Oli and Dobson 2003). When explaining the changes in population growth occurring through a microtine cycle, changes in adult fecundity and age at first reproduction should be more important than changes in juvenile survival (Oli and Dobson 1999, 2001). Unfortunately, the fast turnover of vole populations means that a reasonably precise estimation of these important parameters would require year-round individual-based studies at fine temporal resolution that are beyond the reach of the methods here used.

The observed covariation among components of population structure is probably due to the compounded effect of the seasonal variation in habitat use by voles in relation to resource abundance and of perturbations related to intense farming in our study area. The negative covariation between body condition and the proportion of breeders in spring (April) could result from the combined effect of 1) grass meadows being a high quality overwintering habitat, thus containing voles in spring that are of good body condition, but of a high enough density to suppress reproduction, and 2) a high cost of reproduction in spring. The fast growth of crops between April and June is likely to relieve resource limitation for folivorous voles and hence explain the vanishing of this negative correlation in summer (June). In contrast, the negative covariation between the proportion of breeders and litter size in June may illustrate the tradeoff implicit in the productivity index as voles are unlikely to be able to simultaneously maximize both the proportion of breeders and the production of large litters. In early spring, food resources for folivorous voles in the intensively managed agricultural fields of our study area are mostly concentrated in winter cereal and alfalfa/grass meadows, and at least 60% of the trapped field voles were found in these two crops. The weaker covariation of population structure of voles living in annual crops therefore supports our prediction that the regime of perturbations inherent to intensive farming disrupts the life cycle and patterns of habitat use of common voles compared to those of perennial habitats.

Conclusions

This study has shown declines in the fecundity and body condition of voles from a western European population that coincides with, and may be a proximal cause of, cyclic declines in population density. While this pattern is similar to that found in Fennoscandian voles (Hansson 1984,

Norrdahl and Korpimäki 2002a, 2002b), cycles in the latter populations are thought to be driven by a direct mortality effect of predation, a process that is unlikely to lie behind the cycles in our population (Salamolard et al. 2000, Lambin et al. 2006). The absence of direct and delayed density dependant variation in population structure in our long term data sets is surprising as they should underlie the cyclic variation in population abundance. We are unaware of other datasets of comparable length in temperate and northern Europe that have been used to assess the density dependent variation of life history traits in cyclic voles. Further research is needed to understand life history variation in cyclic voles and to ascertain whether cycles across Europe represent a single phenomenon.

References

Aars, J. and Ims, R. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. – Ecology 83: 3349–3456.

Berryman A. and Turchin, P. 2001. Identifying the density dependent structure underlying ecological time series. – Oikos 92: 265–270.

Boonstra, R. and Krebs, C. J. 1979. Viability of large- and small-sized adults in fluctuating vole populations. – Ecology 60: 567–573.

Boonstra, R. et al. 1998. Population cycles in small mammals: the problem of explaining the low phase. – Ecology 79: 1479–1488.

Borowski, Z. 2003. Habitat selection and home range size of field voles *Microtus agrestis* in Slowinski National Park, Poland. – Acta Theriol. 48: 325–333.

Boyce, C. C. K. and Boyce, J. L. 1988. Population biology of *Microtus arvalis*. II. Natal and breeding dispersal of females. – J. Anim. Ecol. 57: 723–736.

Chitty, D. 1952. Mortality among voles *Microtus agrestis* at Lake Vyrnwy, Montgomeryshire in 1936–9. – Philos. Trans. R. Soc. Lond. B 263: 505–552.

Chitty, D. 1960. Population processes in the vole and their relevance to general theory. – Can. J. Zool. 38: 99–113.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. – Proc. Ecol. Soc. Aust. 2: 51–78.

Crawley, M. J. 2006. The R book. – Wiley.

Ergon, T. et al. 2001. Life-history traits of voles in a fluctuating population respond to the immediate environment. – Nature 411: 1043–1045.

Erlinge, S. et al. 2000. Reproductive behaviour of female Siberian lemmings during the increase and peak phase of the lemming cycle. – Oecologia 123: 200–207.

Gaillard, J.-M. and Yoccoz, N. G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? – Ecology 84: 3294–3306.

Gaillard, J.-M. et al. 1989. An analysis of demographic tactics in birds and mammals. – Oikos 56: 59–76.

Gaillard, J.-M. et al. 2005 Generation time: a reliable metric to measure life history variation among mammalian populations. – Am. Nat. 166: 119–123.

Gliwicz, J. 1997. Space use in the root vole: basic patterns and variability. – Ecography 20: 383–389.

Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? – Ecology 82: 1473–1483.

Halle, S. and Lehmann, U. 1987. Population dynamics and individual features during the phase of decline in the field vole. – Acta Theriol. 32: 21–29.

Hansen, T. F. et al. 1999. Multiannual vole cycles and population regulation during long winters: An analysis of seasonal density dependence. – Am. Nat. 154: 129–139.

Hanski, I. et al. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – J. Anim. Ecol. 60: 353–367.

Hanski, I. et al. 2001. Small rodent dynamics and predation. – Ecology 82: 1505–1520.

Hansson, L. 1984. Composition of cyclic and non-cyclic vole populations: on the causes of variation in individual quality among Clethrionomys glareolus in Sweden. – Oecologia 63: 199–206.

Huitu O. et al 2007. Phase dependence in winter physiological condition of cyclic voles. – Oikos 116: 565–577.

Ims. R. et al. 2008. Collapsing population cycles. – Trends Ecol. Evol. 23: 79–86.

Jakob, E. M. et al. 1996. Estimating fitness: a comparison of body condition indices. – Oikos 77: 61–67.

Koivula, M. et al. 2003. Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. – Ecology 84: 398–405.

Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small rodent cycles. – Ecology 79: 2448–2455.

Koskela, E. et al. 2004. Sex-biased maternal investment in voles: importance of environmental conditions. – Proc. R. Soc. Lond. B 271: 1385–1391.

Krebs, C. J. 1996. Population cycles revisited. – J. Mammal. 77: 8–24.

Krebs, C. J. and Myers, J. H. 1974. Population cycles in small mammals. – Adv. Ecol. Res. 8: 267–399.

Lambin, X. and Yoccoz, N. G. 2001. Adaptive precocial reproduction in voles: reproductive costs and multivoltine life-history strategies in seasonal environments. – J. Anim. Ecol. 70: 191–200.

Lambin, X. et al. 2006. Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern? – J. Anim. Ecol. 75: 340–349.

Lidicker, W. Z. and Ostfeld, R. S. 1991. Extra-large body size in California voles: causes and fitness consequences. – Oikos 61: 108–121.

Norrdahl, K. and Korpimäki, E. 2002a. Changes in individual quality during a 3-year population cycle of voles. – Oecologia 130: 239–249.

Norrdahl, K. and Korpimäki, E. 2002b. Changes in population structure and reproduction during a 3-yr population cycle of voles. – Oikos 96: 331–345.

Oli, M. K. 1999. The Chitty effect: a consequence of dynamic energy allocation in a fluctuating environment. – Theor. Popul. Biol. 56: 293–300.

Oli, M. K. 2003. Population cycles of small rodents are caused by specialist predators: or are they? – Trends Ecol. Evol. 18: 105–107.

Oli, M. K. and Dobson, F. S. 1999. Population cycles in small mammals: the role of age at sexual maturity. – Oikos 86: 557–565.

Oli, M. K. and Dobson, F. S. 2001. Population cycles in small mammals: the alpha-hypothesis. – J. Mammal. 82: 573–581.

Oli, M. K. and Dobson, F. S. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. – Am. Nat. 161: 422–440.

Ostfeld, R. S. and Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. – Ecology 76: 521–532.

Ozgul, A. et al. 2004. Demography of fluctuating populations: temporal and phase-related changes in vital rates of Microtus ochrogaster. – J. Anim. Ecol. 73: 201–215.

Pinheiro J. and Bates, D. 2004. Mixed-effects models in S and Splus. – Springer.

Prevot-Julliard, A. C. et al. 1999. Delayed maturation in female bank voles: optimal decision or social constraint? – J. Anim. Ecol. 68: 684–697.

Quéré, J. et al. 1991. Le campagnol des champs. – Bull. Tech. d'Inf. Ministère l'Agric. Forêt, France, No. 3 (May–June).

Reed A. and Slade, N. 2008. Density-dependent recruitment in grassland small mammals. – J. Anim. Ecol. 77: 57–65.

Salamolard, M. et al. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. – Ecology 81: 2428–2441.

Schaffer, W. M. and Tamarin, R. H. 1973. Changing reproductive rates and population cycles in lemmings and voles. – Evolution 27: 111–124.

Schulte-Hostedde, A. I. et al. 2005. Restitution of mass–size residuals: validating body condition indices. – Ecology 86: 155–163.

Smith, M. et al. 2006. Delayed density dependent season length alone can lead to rodent population cycles. – Am. Nat. 167: 695–704.

Spitz, F. et al. 1974. Standardisation des piègages en ligne pour quelques espèces de rongeurs. – Terre Vie Rev. Ecol. 28: 564–578.

Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – Oikos 87: 427–461.

Stenseth, N. C. et al. 1998. Seasonal forcing on the dynamics of Clethrionomys rufocanus: modeling geographic gradients in population dynamics. – Res. Popul. Ecol. 40: 85–95.

Toussaint M. 1990. Le campagnol des champs (Microtus arvalis P.). – Défense Vég. 260: 22–31.

Wolff, J. O. 1993. Does the "Chitty effect" occur in Peromyscus? – J. Mammal. 74: 846–851.