Vole population cycles in northern and southern Europe: Is there a need for different explanations for single pattern?

XAVIER LAMBIN, VINCENT BRETAGNOLLE* and NIGEL G. YOCCOZ†

*Aberdeen Population Ecology Unit (APERU), School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, Scotland, UK; *Centre d'Etude Biologiques de Chizé, CNRS UPR 1934, BP 14, 79360 Villiers-en-Bois, France; †Ecology Unit, Institute of Biology, University of Tromsø, N-9037 Tromsø, Norway*

Summary

1. Students of population cycles in small rodents in Fennoscandia have accumulated support for the predation hypothesis, which states that the gradient in cycle length and amplitude running from southern to northern Fennoscandia reflects the relative influence of specialist and generalist predators on vole dynamics, itself modulated by the presence of snow cover. The hypothesized role of snow cover is to isolate linked specialist predators, primarily the least weasel, *Mustela n. nivalis* L. and their prey, primarily field voles *Microtus agrestis* L., from the stabilizing influence of generalist predators.

2. The predation hypothesis does not readily account for the high amplitude and regular 3-year cycles of common voles documented in agricultural areas of western, central and eastern Europe. Such cycles are rarely mentioned in the literature pertaining to Fennoscandian cycles.

3. We consider new data on population cycles and demographic patterns of common voles *Microtus arvalis* Pallas in south-west France. We show that the patterns are wholly consistent with five of six patterns that characterize rodent cycles in Fennoscandia and that are satisfactorily explained by the predation hypothesis. They include the: (a) existence of cycle; (b) the occurrence of long-term changes in relative abundance and type of dynamics; (c) geographical synchrony over large areas; (d) interspecific synchrony; and (e) voles are large in the increase and peak phase and small in decline and low phase, namely. There is a striking similarity between the patterns shown by common vole populations in south-west France and those from Fennoscandian cyclic rodent populations, although the former are not consistent with a geographical extension of the latitudinal gradient south of Fennoscandia.

4. It is possible that the dominant interaction leading to multiannual rodent oscillations is different in different regions. We argue, however, that advocates of the predation hypothesis should embrace the challenge of developing a widely applicable explanation to population cycles, including justifying any limits to its applicability on ecological and not geographical grounds.

Key-words: *Clethrionomys*, cycles, lemmings, *Microtus*, population dynamics, predation, parsimony, voles.

Introduction

Ecologists formulate empirically supported explanations of natural processes that can be used to generate

Correspondence: X. Lambin School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK. Tel.: +44(0)1224 273259; E-mail: x.lambin@abdn.ac.uk

predictions. Such predictions must not only be applicable to the organism and region on which knowledge has been acquired, but also to other organisms or regions that are similar. Limits to the scope of any well-supported explanation must be based on a set of auxiliary hypotheses or assumptions on the manner in which processes operate (e.g. Forster & Sober 1994). Unless they correspond to ecological differences

interpretable in terms of these hypotheses, geographical or taxonomic considerations *per se* are not appropriate limits to the applicability of an explanation.

Students of population cycles in small rodents have developed a mechanistic understanding of these striking natural processes through a combination of time-series-based, experimental and theoretical studies. Whereas early investigators set their sight on finding a common explanation for population cycles that were thought to be geographically widespread (Krebs 1996), following the seminal work of Andersson & Erlinge 1977) and Hansson & Henttonen (1985) attention has been focused almost exclusively on rodent dynamics in Fennoscandia where sufficiently long rodent abundance time series allowed statistical analyses of cyclic dynamics. Instrumental in this shift was the documentation of a gradient in cycle length and amplitude running from southern to northern Fennoscandia (Hansson & Henttonen 1985). According to the predation hypothesis, this gradient in dynamics reflects the relative influence of destabilizing specialist and stabilizing generalist predators on vole dynamics, itself modulated by the presence of snow cover (Hanski, Hansson & Henttonen 1991). The hypothesized role of snow cover is to 'isolate linked specialist predators and their prey from the stabilizing influence of generalist predators'. The key species said to be involved in a strong predator–prey interaction are the least weasel, *Mustela n. nivalis*, field voles *Microtus agrestis*. and the ecologically related grey-sided voles *Clethrionomys rufocanus*, Sundevall, with other members of the diverse northern rodent communities being entrained by the interaction between the above species (Hanski & Henttonen 2002).

Over the last two decades, much evidence in support of this interpretation has accumulated from studies performed in Fennoscandia (recent review in Hanski & Henttonen 2002). Further support for the key role of seasonality and processes operating during the winter season, when voles normally do not reproduce, has been provided by detailed analysis of time series of abundance of grey-sided voles from Hokkaido, northern

Japan. A robust conclusion is that winters are prerequisite for cycles and long winters are associated with long cycles (e.g. Stenseth *et al.* 2003). Even though no detailed evidence on predators is available, hypotheses on factors regulating cyclic vole populations in Hokkaido have been mostly based on the predation hypothesis developed for populations with similar dynamics in Fennoscandia (Stenseth, Saitoh & Yoccoz 1998, but see Saitoh *et al.* 2003).

While the search for a common explanation may have been fruitful, perhaps the biggest remaining challenge to the predation hypothesis as a general explanation for rodent population cycles is to account for the widespread regular cycles of the common vole populations, well to the south of Fennoscandia. High amplitude and regular 3-year cycles have long been documented in agricultural areas of western, central and eastern Europe ever since the outset of investigation in rodent dynamics (Elton 1942; Frank 1957; Van Wijngaarden 1957; Ryszkowski, Goszcynski & Truszkowski 1973; Mackin-Rogalska & Nabaglo 1990; Butet & Spitz 2001; Tkadlec & Stenseth 2001). In spite of common vole cycles being documented in international scientific journals as well as in the plant protection literature, most recent reviews on rodent population cycles ignore the geographically widespread cycles of common voles: indeed, we could only find two mentions of common vole cycles (one of which without any reference to a paper) in the eight most recent reviews of cyclic dynamics of small rodents (Table 1). Typically, the puzzle of rodent population cycles is reframed as that of the '*Northern* population cycle' (e.g. Norrdahl 1995; Stenseth 1999; Hanski *et al.* 2001; Turchin & Hanski 2001; Hanski & Henttonen 2002). In spite of differences between northern vole species and lemming ecologies, and dynamics being larger than differences in the ecologies of the former and of common voles, the view of most Fennoscandian workers appears to be that common vole cycle may represent a different phenomenon. Whether patterns seen in *M. arvalis* pertain to explanations on *M. agrestis* and *Clethrionomys*

Table 1. Overview of the extend to which recent review paper on Fennoscandian vole cycle mention or cite paper on cycles of other microtine rodents including *Microtus arvalis* in other geographical locations

	Mention of cycles of				
	European common vole	Japanese grey-sided vole	Swiss water voles	Scandinavian lemmings	British field voles
Turchin & Hanski (1997)	N	N	N	Y	Y
Stenseth (1999)	Y	Y	Y	Y	Y
Turchin & Hanski (2001)	Y*	Y	Y	Y	Y
Turchin (2003)	Y	Y	Y	Y	Y
Hanski *et al.* (2001)	N	Y	N	Y	N
Hanski & Henttonen (2002)	N	Y	N	Y	Y
Norrdahl (1995)	N	N	N	N	N
Klemola *et al.* (2003)	N	N	N	N	N
Korpimäki *et al.* (2004)	N+	N	N+	Y	N+

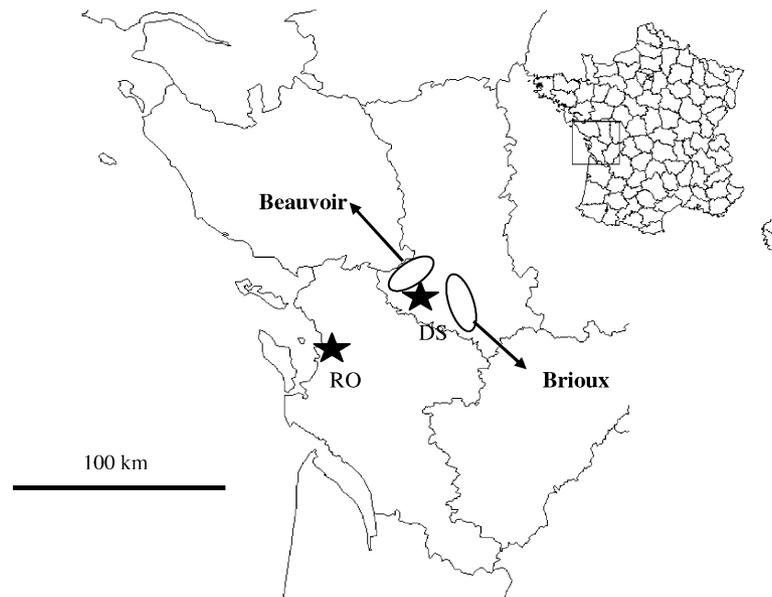*Species mentioned but no reference cited; +, Temperate Europe cycle mentioned but no species cited.

Fig. 1. Map of south-west France showing the location of data collection for the four time series of small mammal abundance.

vole species depends in part on the degree of similarity in overall dynamics, and specifically, on whether ecologically significant differences make a common driving process more or less likely.

In this paper, we consider new data on population cycles and demographic patterns of common voles in south-west France. We show that the patterns are wholly consistent with all but one (latitudinal gradient) of the six main patterns that characterize rodent cycles in Fennoscandia and are satisfactorily explained by the predation hypothesis according to Hanski & Henttonen (2002). Having shown that common vole cycles cannot be treated as anomalous outliers, we argue that advocates of the predation hypothesis should embrace the challenge of developing a widely applicable explanation to population cycles, including justifying any limits to its applicability on ecological and not geographical grounds.

Methods

STUDY AREAS

Data were collected in two distinct study areas in central western France (Fig. 1): the Marais de Rochefort (hereafter RO; 45·57°N, 0·55°W) between 1986 and 2004, and the south of Deux-Sèvres (hereafter DS; 46·11°N, 0·28°W) between 1994 and 2004 (see Arroyo, Garcia & Bretagnolle 2003; Millon & Bretagnolle 2005 for details). These study sites, respectively, cover 182 and 340 km². The DS study area consists of intensive agricultural landscape, and is dominated by a cropping system including intensive cereals, colza and spring-sowed crops (maize, sunflower and pea). Built-up and forested areas are marginal, and nearly 95% of the surface is covered with agriculture. Between 1970 and 2000, grassland (both permanent and temporary) decreased from *c.* 60% of surface to less than 10%

(Delattre *et al.* 1992; V. Bretagnolle unpubl. data). Old hedgerows and small meadow are still present but are confined to the vicinity of villages and farms. The RO study area is part of a large wetland increasingly converted from wet meadows to cereal fields, and annual crops have increased from less than 2% in 1975 to 49% in 1994 (Butet & Spitz 2001).

VOLE SAMPLING

The abundance of the common vole was assessed at two trapping sessions each year since the study started in 1986 (Butet & Leroux 1993; Salamolard *et al.* 2000). The first session occurred in spring (end of April) while the second took place in summer (end of June). A trap line consists in sampling a 100-m transect with 51 live traps without bait spaced every 2 m for 24 h. For each session a total of 24–36 lines in RO (*n* = 836 lines from 1986 to 2004) and 80–96 lines in DS (*n* = 1693 lines from 1994 to 2004) were deposited (for a total of 128 879 trap-nights). Data are presented here in number of voles caught per 100 trap-nights, averaged per study site, year and session. Using this index, over the complete study areas, values range from 0 to 26, which roughly corresponds to variation in average vole density ranging from 1 to 200 voles ha^{-1} (Salamolard *et al.* 2000). However, locally (at the patch level), densities can reach *c.* 1000 individuals ha^{-1} (VB pers obs).

Vole sampling was designed according to habitat types (i.e. crops). In RO, three main habitats (cereal, pasture and fallow: see Salamolard *et al.* 2000) were used, while in DS, land use was determined yearly and mapped on to a GIS at the patch level, according to seven different categories (cereal, maize/sunflower, rye-grass, alfalfa, pasture, pea and colza). As the relative proportions of crop types in the sampling design differed between years, we first averaged trapping indices

per crop type (for each site, session and year). Conversely to DS for which there was no detectable trend in the relative proportion of crop types over the study period (therefore, the DS trapping index was simply the mean of crop trapping indices), RO showed a temporal trend, and we thus corrected vole indices according to land use so as to obtain an index reflecting landscape scale abundance. Weighting took into account changes in land management over the study period: percentage of annual crops (hence its weighing coefficient) varied in RO from < 2% in 1975, to 12% in 1987, 41% in 1990, 49% in 1994, and 52% in 2000. Vole index values for RO in this paper are the same as those used in Salamolard *et al*. (2000) for years 1986–97, but they differ from those published in Butet & Leroux (2001) (though based on the same original data), as the latter are expressed as vole density per hectare, and are uncorrected by land use.

Additionally, two long-term series of small mammal abundance were also available from the *Service de Protection des Végétaux* (these series have been published in part in Toussaint (1990), Butet & Leroux (2001) and Delattre *et al*. (1992). The first time series was established at Beauvoir (Fig. 1), from 1968 to 1992, and overlaps with the DS study site. The second time series was obtained near Brioux (see Fig. 1), and data are available from 1969 to 2002. In contrast to DS and RO time series, these trapping data were obtained mainly in winter (December to February; and only in winter since the eighties), but obtained using exactly the same trapping method as for DS and RO. They are expressed as vole density per hectare following conversion indices developed by Spitz (1977), and do not take into account landscape changes. Analyses in this paper are based on population growth rates, $\text{Ln}(N_t) - \text{Ln}(N_{t-1})$. Only winter abundances (January whenever available, otherwise December or February) are used for Beauvoir and Brioux.

Patterns of vole cycles in south-west France

Hanski & Henttonen (2002) discussed six patterns relevant to the dynamics of common voles in relation to the predation hypothesis. These were: (1) population cycles exist; (2) long-term changes in relative abundance and type of dynamics; (3) latitudinal gradient – 'There is a definite geographical pattern in both the amplitude and period of the cycle, which both increase with latitude in Fennoscandia'; (4) geographical synchrony – 'Populations typically show a high level of geographical synchrony over large areas'; (5) interspecific synchrony – 'Inter-specific synchrony is particularly apparent in northern populations'; (6) Chitty effect – 'Voles are large in the increase and peak phases and small in decline and low phases'.

PATTERN 1: POPULATION CYCLES EXIST

Common voles in south-west France experienced high amplitude fluctuations from 1968 to present, with S-index

Std ($\text{Log}_{10}(N)$) = 0·51–0·61. Oscillations were extremely regular with 11 peaks in growth rates precisely at 3-year intervals over 36 years. Using autoregressive model on population growth rate and AICc to select order, second-order models AR(2) were selected for most common vole time series, and were very close to the best model when not (Table 2). When plotted in the second-order autoregressive parameter space within which $1 + b1$ is plotted against $b2$ (Table 2), common vole time series naturally fall within the region with 3-year cycles, in the vicinity of populations from south-west Finland and northern England (Stenseth 1999). There is therefore strong evidence for population cycles as defined by time-series analysis in this part of western Europe.

Given the highly heterogeneous environment where common vole cycles take place, estimates of peak and trough abundance are scale-sensitive. Values quoted here are based on a calibration relationship between index-trapping and capture–recapture data (Spitz *et al*. 1974). Landscape-scale (i.e. > 100 km^2) peak population densities averaged up to 215 ha^{-1} in the RO area (1987), and about 100 ha^{-1} in DS (1996). Vole populations declined to low but detectable landscape-scale abundance in the range of 0·8–7·9 voles ha^{-1} (Butet & Leroux 1993; Salamolard *et al*. 2000). The amplitude of fluctuation range of common vole densities is similar to that displayed by *Microtus* and *Clethrionomys* voles in habitat complexes in the tundra of Norwegian Lapland (Oksanen & Oksanen 1992; Korpimäki *et al*. 2004) but greater than that occurring at the landscape scale in patchwork of spruce plantation and clear-felled areas in Britain (Lambin, Petty & MacKinnon 2000). The within-culture amplitude is of course much greater with maximum and minimum estimated local densities ranging from 1200 to 2000 voles ha^{-1} and apparent absence in DS (see also Spitz 1977), although there is much uncertainty around peak density estimates. Local maximum densities of common voles are certainly much greater than those reported for any other cyclic rodent, except perhaps *Arvicola terrestris* L. that can reach locally > 200 ind ha^{-1} (Giraudoux *et al*. 1995). For instance maximum field vole density in clear felled area in northern Britain was 800 voles ha^{-1}, whereas peak densities in Fennoscandia boreal habitats rarely exceed 40 voles ha^{-1} (Prevot-Julliard *et al*. 1999), and 10 lemmings ha^{-1} in Greenland (Gilg 2002), although reliable quantitative estimates of extreme values are scarce.

The behaviour of logistic predator–prey models is known to depend critically on values of carrying capacity. Existing parameterized weasel–vole models assume vole carrying capacities from 100 to 150 voles ha^{-1} (Turchin & Hanski 1997) or that vole maturation rates are 50% of maximum at 10 voles ha^{-1} (Klemola, Pettersen & Stenseth 2003). Notwithstanding known problems with estimating K, values of K for *M. arvalis* found in south-west France are plausibly one order of magnitude higher and major changes in other model parameters would be required if weasels were to regulate their

Table 2. (a) Order and difference in AICc value of autoregressive models (AR) on population growth rate of small mammals at Rochefort and Deux-Sèvres. (b) estimates of first and second order autoregressive parameters

(a)

		ΔAICc			
	Order	AR(0) AR(1)	AR(0) AR(2)	AR(1) AR(2)	AR(3) AR(2)
Microtus arvalis					
Rochefort 1986/91–2004					
April, *n* = 13	0 or 2		−0·15	0·46	3·27
June, *n* = 18	2		12·90	9·42	3·35
Brioux 1970–2002					
Winter, *n* = 22	2 or 3		18·21	16·65	−0·51
Beauvoir 1968–90					
Winter, *n* = 22	2		3·25	4·64	3·02
Deux-Sèvres 1994–2004					
April, *n* = 10	2		1·36	1·45	3·05
June, *n* = 10	2		2·55	4·00	5·26
Crocidura russula					
Deux-Sèvres 1994–2004					
April, *n* = 10	0	−2·84	−3·35		
June, *n* = 10	0	−3·15	−6·33		
Apodemus sylvaticus					
Deux-Sèvres 1994–2004					
April, *n* = 10	0	−0·43	−4·59		
June, *n* = 10	0	−0·32	−4·04		

*Note that sample size is reduced due to a missing value in April 1990 for RO.

(b)

	Rochefort		Deux-Sèvres	
	AR(1)	AR(2)	AR(1)	AR(2)
April	−0·600	−0·511	−0·860	−0·661
June	−0·909	−0·704	−0·703	−0·751

common vole prey in such models. Given the similarities in vole life history, it would be difficult to justify such changes.

The delayed density-dependent pattern in population growth was sufficiently strong to mask any seasonal pattern linked to vegetation growth and vole reproduction. High-density common vole populations declined during the breeding season (between the April and July samples) and populations that previously experienced low density grew in between July and April Overall, details of seasonality of dynamics closely match those observed in all other cyclic vole populations in Fennoscandia (Hörnfeldt 1994; Strann, Yoccoz & Ims 2002), Britain (Lambin *et al.* 2000) and Hokkaido (Stenseth *et al.* 2003), and is another well-established pattern common to all cyclic vole populations.

PATTERN 2: LONG-TERM CHANGES IN RELATIVE ABUNDANCE AND TYPE OF DYNAMICS

Vole dynamics in parts of Fennoscandia has changed markedly from the end of the 1980s with a decline in the strength of delayed density dependence in winter. Dynamics has become increasingly dominated by seasonal patterns and the amplitude of multiannual fluctuations has decreased (Yoccoz *et al.* 2001; Hörnfeldt 2004). There is no evidence of any change over time in population growth rate of common voles in central western France (Fig. 2), but suggestions of a gradual decline in absolute abundance in peak years at least in DS (Fig. 3), Beauvoir time series (Butet & Leroux 2001) and RO (see figure in Millon & Bretagnolle 2005). Given that highest densities (regularly up to 400 voles ha^{-1}) are reported from temporary (mainly alfalfa) grasslands as well as abandoned pastures (Butet & Leroux 2001), and that the area devoted to these land uses has declined dramatically at all study sites, changes in abundance may not reflect real changes in dynamics of the kind observed since the mid-1980s in Fennoscandia (Hörnfeldt 2004) and Britain (Bierman *et al.*, in press). Note, however, that outbreaks of common voles causing damage to agriculture (Spitz 1977) are no longer reported from northern and eastern France (Fichet-Calvet *et al.* 2003) and the last vole outbreak damaging to crops in south-west France was in 1996 (VB pers. obs.).
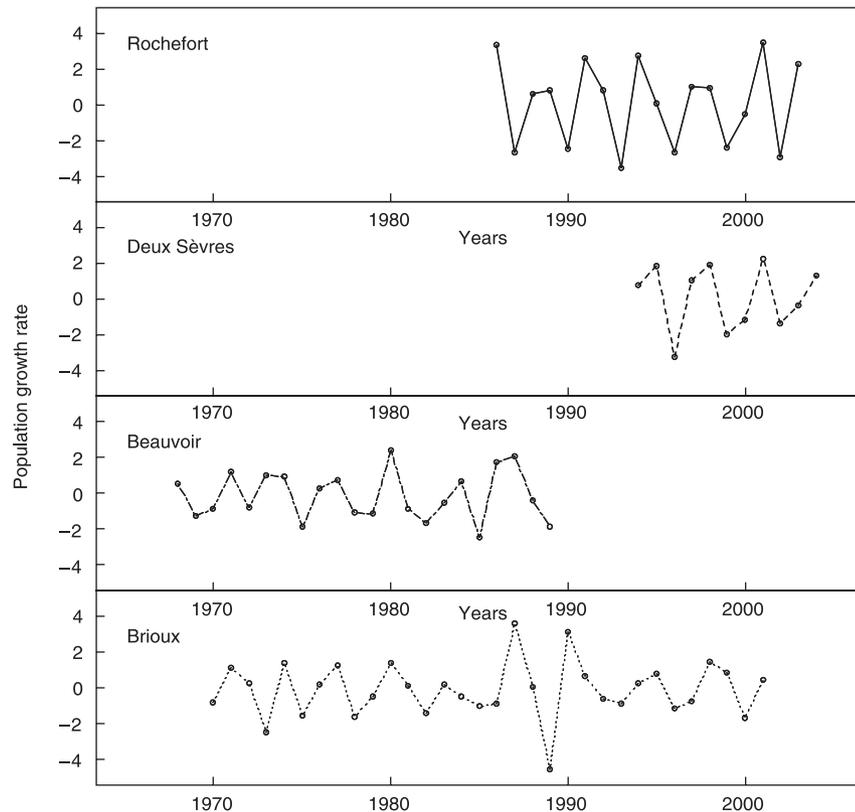
Fig. 2. Time series of common vole population growth rates $Ln(N_t) - Ln(N_{t-1})$ at four sites south-west France.
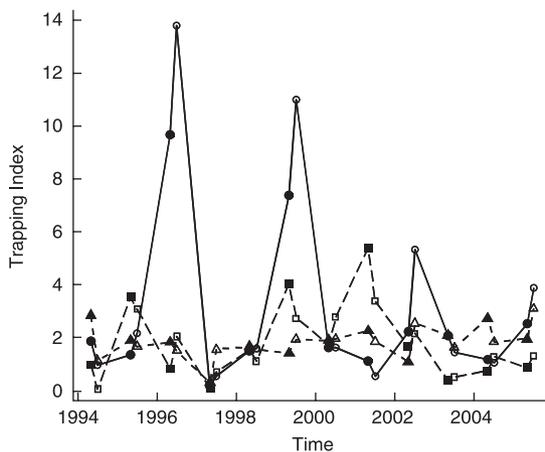

Fig. 3. Landscape-scale abundance of different small mammal species at DS from 1994 to present. Common vole abundance is depicted with circles and continuous line. Garden shrews by dashed line and squares and wood mice by dashed lines and triangles. Full symbols are April indices and open symbols June indices.
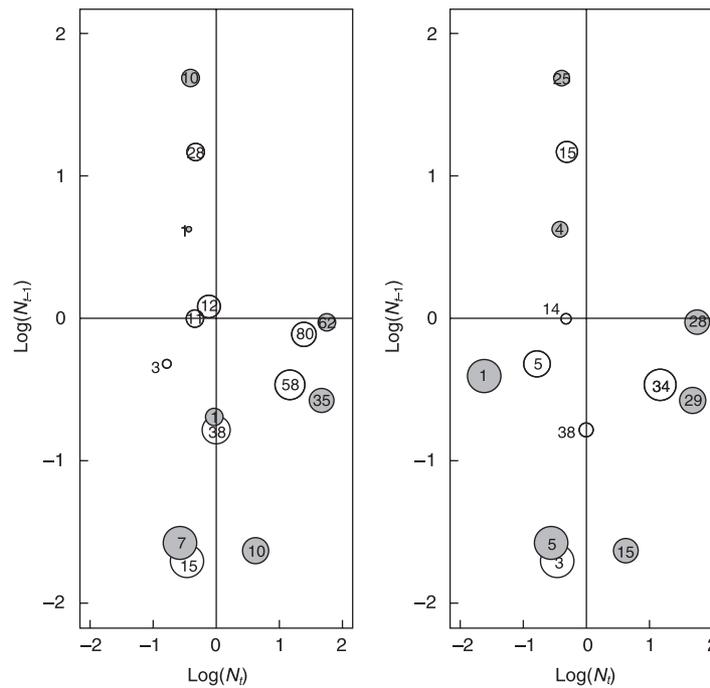
PATTERN 3: LATITUDINAL GRADIENTS

The present data collected at latitude 46°N reinforces earlier observations that the latitudinal gradient (Pattern 3) documented in Fennoscandia does not apply to mainland Europe (Tkadlec & Stenseth 2001) and Britain (Lambin *et al.* 2000), nor does it apply to coastal Fennoscandia (Strann *et al.* 2002). In the present case, regular vole cycles occur in spite of nearly absent snow cover (no snow cover lasting more than 3 days since at least 1987 in either DS or RO). Thus the contention that cyclic small mammal populations are invariably found in environments with strong seasonal or between year variation, e.g. snow or drought (e.g. Korpimäki *et al.* 2004) is not supported by evidence from common voles from south-west France.

PATTERN 4: GEOGRAPHICAL SYNCHRONY

Common vole populations 60 km apart in RO and DS were closely synchronized (Fig. 2; see also Millon & Bretagnolle 2005). Within each area, synchrony prevailed over the scales of 350 km^2 (DS) and 200 km^2 (RO) as well as locally, between different crop types. A more precise characterization of the scale of synchrony in *M. arvalis* fluctuations requires data collected over a larger spatial extent. Indirect evidence (not based on trap sampling but on raptor specialist invasions, e.g. short-eared owl *Asio flammeus* Pontoppidan) suggests that synchrony in the common vole occurs at the level of the entire country, as outbreaks in 1993, 1996 (Michelat 1997; de Cornulier *et al.* 1998) and 1999 at least (the 2002 outbreak was weak) occurred both in south-west France and eastern France (500 km apart). Contrary to Korpimäki *et al.*'s (2004) assertion that cycles in temperate Europe south of 60°N are 'low-amplitude … small-scale phenomena' we document

© 2006 The Authors.
Journal compilation
© 2006 British
Ecological Society,
*Journal of Animal
Ecology*, **75**,
340–349

Fig. 4. Variation in relative male body mass (left) and litter size (right) of common voles in April (white) and June (grey) relation to past and present density. The size of the circles reflects the magnitude of deviation from the minimum annual mean body size (15 g) and litter size (3·5 pups). Litter size was determined by counting embryos from pregnant females that died in traps (sample size indicated within the circles). Body mass is that of animals in reproductive condition.

here high amplitude (*c.* 200 fold) and broad scale (> 1000 km^2) cyclic patterns.

PATTERN 5: INTER-SPECIFIC SYNCHRONY

In addition to common voles, the abundance of wood mice *Apodemus sylvaticus* L. and two shrew species (*Crocidura suaevolens*, Pallas and *C. russula*, Hermann) was monitored in the last 11 years from DS (Fig. 2). The dynamics of wood mice or garden shrews, two alternative prey species for predators of common voles was of first order (Table 2) and showed no evidence of cyclicity. Despite this, there was evidence of significant interspecific synchrony in growth rates commensurate to those reported from Fennoscandia (Huitu, Norrdahl & Korpimaki 2004) (*Crocidura* vs. *M. arvalis*, $r_p = 0.51$, $P = 0.02$, *Apodemus* vs. *M. arvalis*, $r_p = 0.445$, $P = 0.049$). This reflected the occurrence of population declines synchronous with those of common voles. Thus, as in Fennoscandia (e.g. Korpimäki *et al.* 2002) there is evidence of coupling of the dynamics of several small-mammal species.

PATTERN 6: THE CHITTY EFFECT

Like voles in other cyclic populations, common voles in DS show phase-related changes in body size and litter size and timing of reproduction that are primarily related to past density, with relatively little direct density dependence. Voles were heaviest and produced the largest litters in the increase and peak phase of cycles and were lightest and produced small litters in the

decline and low phases (Fig. 4). The effects of maternal mass and year of sampling on litter size were additive (GLM of Litter size in April: Mass: $F_{1,228} = 40.74$, $P < 0.001$, Year: $F_{7,228} = 2.86$, $P < 0.01$, Year∗Mass: $F_{7,228} = 0.61$, $P > 0.5$). There was also evidence of earlier reproduction in increase years reflected by the presence of pregnant 10-g females in the spring samples of those years, as well as an increased prevalence of nonreproductive subadults in peak densities. Taken together, variation in these demographic parameters no doubt contributes to cycle phase related variation in population growth rate and is also a universal characteristic of microtine population fluctuations.

Common vole cycles and the predation hypothesis

THE PREDATION COMMUNITY IN SOUTH-WEST FRANCE

The common vole is the main prey of Montagu's harrier *Circus pygargus* in western France and accounts for 60–90% of the diet in biomass according to years at the chick rearing stage (Butet & Leroux 1993; Salamolard *et al.* 2000; Arroyo *et al.* 2003). This species is, at least in this region, a specialist predator of the common vole (Salamolard *et al.* 2000), and its density over the study areas can vary by a 10-fold factor according to prevailing vole density in spring. There is no delay in the numerical response of this nomadic predator. Other specialist predators include the long-eared owl *Asio otus* L. (other owl species, such as barn owls *Tyto alba* and little owls *Athene noctua* are restricted to villages),

and in peak vole years, short-eared owls can breed in rather large numbers (see de Cornulier *et al.* 1998; Arroyo & Bretagnolle 1999).

Mammal specialist predators are very scarce, at least mustelids (domestic and feral cats are much more frequent than wild carnivores). Although no density estimates are available (for any mammal predator), *Mustela nivalis vulgaris*, has been only caught twice in trapping sessions in DS over 11 years, and is not seen on more than three to five occasions per spring/summer despite the daily presence in the field of five to eight persons. *Mustela erminea*, L. is even scarcer, and neither marten *Martes* sp. forage away from villages and trees. Other vole-eating (but generalist) predators in the community include black kite *Milvus migrans*, kestrel *Falco tinnunculus*, L. and buzzard *Buteo buteo* among raptors, and fox *Vulpes vulpes*, L. for mammals (though mainly limited to forest areas). Based on the limited evidence at hand, it appears most unlikely that any numerical response of a specialist mammal predator drives the voles cycle in south-west France. This is fully consistent with Delattre's (1984; Delattre, Damange & Roger 1986) conclusion that *M. nivalis* can reach high densities only in areas dominated by permanent grassland (i.e. > 50% of cover), which only covers at best 7–10% of the total area today in DS and less than 30% in RO.

COMMON PATTERNS, DIFFERENT EXPLANATIONS?

Historically, a common explanation was sought for all vole population cycles that were then defined according to the so-called 'biological definition' which stressed phase-related changes in vole life history and gave no explicit consideration to their regularity (Krebs 1996). Following the realization that many of the North American *Microtus* populations do not show regular fluctuations, there was a shift in focus to Fennoscandia where regular cycles were best documented in long time series. Subsequently, some authors took the erroneous view that 'genuine' cycles occur only in Fennoscandia, and included the presence of summer crashes and large-scale synchrony in the definition of such 'genuine' cycles. They also adopted the terminology of the 'northern' or 'Boreal cycles' (Norrdahl 1995; Oksanen *et al.* 2001) and the belief that such cycles are unique and deserving of their own explanation, e.g. vole cycles in Britain are 'entirely different from the northern vole cycles' and '… confounding this cycle with the entirely different Northern vole cycle appears unhelpful for understanding vole dynamics in either zone' (Korpimäki *et al.* 2003, but see Hanski *et al.* 2001).

Turchin (2003) computed autocorrelation functions of time series of common voles from Continental Europe including the time series from Beauvoir we consider above (his table 12·2). Contrary to our conclusion that common vole dynamics are in fact very similar to those occurring in Fennoscandia, he concluded that this and other time series from this species

were first-order processes, whereas cycles in Fennoscandia and Hokkaido are of second order. First-order vole cycles are described by Turchin 2003) as being characterized by winter crashes followed by 1–2 years of exponential increase until population density exceeds its winter food supply, yielding 2-year cycles or 3 years if it takes 2 years of exponential growth to reach the peak. If Turchin's (2003) conclusion stood, it would vindicate the view that different patterns prevail in cyclical vole populations in Fennoscandia and temperate Europe and that there is little scope for a general, nongeographically based explanation for such processes. As it turns out, had Turchin used partial rate correlation function based on growth rate instead of partial autocorrelation function based on abundance as he advocates elsewhere (Berryman & Turchin 2001), he would have concurred with us and concluded that French common vole cycles are not dissimilar from other vole cycles.

There have been limited attempts to discuss the relevance of the predation hypothesis derived from Fennoscandian research to other geographical area, namely Hokkaido Japan (e.g. Henttonen, Hansson & Saitoh 1992; Hansson & Henttonen 1998; Hanski & Henttonen 2002). They mostly stressed differences in amplitude in relation to the diversity of generalist predator guilds rather than similarities in patterns or in the process that might cause cycles in the first instance. It is indeed the component of the predation hypothesis invoking variation in the impact of generalist predators in modulating the degree of coupling between specialist and their prey that is most strongly refuted by the reality of widespread common vole cycles in areas with abundant and diverse generalist predators and limited or absent snow cover. When trying to reconcile the grey-sided vole cycles in Hokkaido with the predation hypothesis, Henttonen (Henttonen, Hansson & Saitoh 1992; Hansson & Henttonen, 1998) stressed that the maximum amplitude of cycles and prevalence of summer declines in Hokkaido is less than in northern-most Fennoscandia. We have shown above that common vole cycles are of very high amplitude and summer declines are the norm in decline phases. In this respect, common vole cycles are similar to cycles occurring in northern Fennoscandia despite dramatically different ecological conditions. Whether relatively uniformity and/or lower biodiversity of agricultural areas, or the subterranean habits of common voles, translate into an ecological equivalence between high latitude and agricultural plains is an interesting but unexplored issue. On the other hand, in the absence of detailed investigation, there is no direct or indirect evidence from cyclic common vole populations that contradicts or supports the specialist predation component (i.e. the destabilizing influence of weasels) of the predation hypothesis.

Conclusions

There is a striking similarity between the patterns shown by common vole populations in south-west France

and those from Fennoscandian cyclic rodent populations that have been the subject of an enormous volume of research. On that basis, and despite the substantial differences between the ecosystems involved, it would be surprising if different ecological processes caused the instability of vole populations in both areas, though different processes might account for variation in cycle amplitude. Given that at least some of the data presented above (and additional data from central and western and eastern Europe) have been published from some time, it is most puzzling that the challenge presented by the dynamics of common vole is hardly, if ever, mentioned in the context of investigation on the dynamics of small rodents (Table 1).

While it is now uncontroversial that many vole populations show no evidence of cyclical dynamics, we contend that the search for generality may have been unduly replaced by a willingness to accept that different patterns and processes operate in different populations. Abandoning the search for common principles that would apply to cyclical vole populations with the closely similar dynamics not only reduces parsimony of ecological explanation, but also could also easily preclude confronting hypotheses against data other than those used to erect these hypotheses. Whereas it is indeed conceivable that the dominant interaction leading to multiannual rodent oscillations is different in different regions, common explanations should be sought for common patterns unless clear ecological differences are demonstrated. The scope of a process-based hypothesis such as the predation hypothesis must be defined not by geographical considerations, but by specific variation in one or several of the processes invoked. We are not aware of any clearly stated auxiliary hypotheses or assumptions on the manner in which specialist predation operate that would restrict its applicability and, as a matter of fact, preclude it from being tested, outside Fennoscandia.

Acknowledgements

References

Andersson, M. & Erlinge, S. (1977) Influence of predation on rodent populations. *Oikos*, **29**, 591–597.

Arroyo, B.E. & Bretagnolle, V. (1999) Breeding biology of the Short-eared Owl (*Asio flammeus*) in agricultural habitats of south western France. *Journal of Raptor Research*, **33**, 287–294.

Arroyo, B.E., Garcia, J.T. & Bretagnolle, V. (2003) Land use, agricultural practices and conservation of the Montagu's Harrier (*Circus pygargus*). *Birds of Prey in a Changing Environment* (eds D.B.A. Thompson, S.M. Redpath, A.H. Fielding, M. Marquiss & C.A. Galbraith). Scottish Natural Heritage, Edinburgh.

Berryman, A. & Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos*, **92**, 265–270.

Bierman, S., Fairbairn, J., Petty, S., Elston, D., Tidhar, D. & Lambin, X. (2006) Changes over time in the spatiotemporal dynamics of cyclic populations of field voles (*Microtus agrestis* L.). *American Naturalist*, in press.

Butet, A. & Leroux, A. (1993) Effect of prey on a predators breeding success. A 7-year study on common vole (*Microtus arvalis*) and Montagu's harrier (*Circus pygargus*) in a West France marsh. *Acta Oecologica*, **14**, 857–865.

Butet, A. & Leroux, A.B.A. (2001) Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biological Conservation*, **100**, 289–295.

Butet, A. & Spitz, F. (2001) Cyclic fluctuations of microtine populations: half a century of research. *Revue d'Ecologie-la Terre et la Vie*, **56**, 353–372.

de Cornulier, T., Bernard, R., Pinaud, D., Arroyo, B. & Bretagnolle, V. (1998) Nidification du Hibou des marais *Asio flammeus* en plaine céréalière intensive. *Alauda*, **66**, 229–234.

Delattre, P. (1984) Influence de la pression de prédation exercée par une population de belettes (*Mustela nivalis* L.) sur un peuplement de microtidés. *Acta Oecologica, Oecologia Generalia*, **5**, 285–300.

Delattre, P., Damange, J.-P. & Roger, M. (1986) Analyse comparative des fluctuations de populations de rongeurs. Rôle de la prédation et de la structure des paysages. *Colloque CNRS, Biologie des Populations* (ed. CNRS), pp. 537–545. CNRS, Paris.

Delattre, P., Giraudoux, P., Baudry, J., Musard, P., Toussaint, M., Truchetet, D., Stahl, P., Poule, M.L., Artois, M., Damange, J.P. & Quere, J.P. (1992) Land-use patterns and types of common vole (*Microtus arvalis*) population-kinetics. *Agriculture Ecosystems and Environment*, **39**, 153–169.

Elton, C. (1942) *Voles, Mices and Lemmings Problems in Population Dynamics*. Clarendon Press, Oxford.

Fichet-Calvet, E., Giraudoux, P., Quéré, J., Ashford, R. & Delattre, P. (2003) Is the prevalence of the *Taenia taeniaeformis* in *Microtus arvalis* dependent on population density? *Journal of Parasitology*, **89**, 1147–1152.

Forster, M. & Sober, E. (1994) How to tell when simpler, more unified, or less ad-hoc theories will provide more accurate predictions. *British Journal for the Philosophy of Science*, **45**, 1–35.

Frank, F. (1957) The causality of microtine cycles in Germany. *Journal of Wildlife Management*, **21**, 113–121.

Gilg, O. (2002) The summer decline of the collared lemming, *Dicrostonyx groenlandicus*, in high arctic Greenland. *Oikos*, **99**, 499–510.

Giraudoux, P., Pradier, B., Delattre, P., Deblay, S., Salvi, D. & Defaut, R. (1995) Estimation of water vole abundance by using surface indices. *Acta Theriologica*, **40**, 77–96.

Hanski, I. & Henttonen, H. (2002) Population cycles of small rodents in Fennoscandia. *Population Cycles: the Case for Trophic Interactions* (ed. A.A. Berryman), pp. 44–68. Oxford University Press, Oxford.

Hanski, I., Hansson, L. & Henttonen, H. (1991) Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, **60**, 353–367.

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001) Small-rodent dynamics and predation. *Ecology*, **82**, 1505–1520.

Hansson, L. & Henttonen, H. (1985) Gradients in density variations of small rodents – the importance of latitude and snow cover. *Oecologia*, **67**, 394–402.

Hansson, L. & Henttonen, H. (1998) Rodent fluctuations in relation to seasonality in Fennoscandia and Hokkaido. *Researches on Population Ecology*, **40**, 127–129.

Henttonen, H., Hansson, L. & Saitoh, T. (1992) Rodent dynamics and community structure *Clethrionomys rufocanus* in Northern Fennoscandia and Hokkaido. *Annales Zoologici Fennici*, **29**, 1–6.

Hörnfeldt, B. (1994) Delayed density dependence as a determinant of vole cycles. *Ecology*, **75**, 791–806.

Hörnfeldt, B. (2004) Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. *Oikos*, **107**, 376–392.

Huitu, O., Norrdahl, K. & Korpimaki, E. (2004) Competition, predation and interspecific synchrony in cyclic small mammal communities. *Ecography*, **27**, 197–206.

Klemola, T., Pettersen, T. & Stenseth, N.C. (2003) Trophic interactions in population cycles of voles and lemmings: a model-based synthesis. *Advances in Ecological Research*, **33**, 75–160.

Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002) Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society of London Series B-Biology Sciences*, **269**, 991–997.

Korpimäki, E., Klemola, T., Norrdahl, K., Oksanen, L., Oksanen, T., Banks, P.B., Batzli, G.O. & Henttonen, H. (2003) Vole cycles and predation – a reply to Oli. *Trends in Ecology and Evolution*, **18**, 492.

Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004) The puzzles of population cycles and outbreaks of small mammals solved? *Bioscience*, **54**, 1071–1079.

Krebs, C.J. (1996) Population cycles revisited. *Journal of Mammalogy*, **77**, 8–24.

Lambin, X., Petty, S.J. & MacKinnon, J.L. (2000) Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, **69**, 106–118.

Mackin-Rogalska, R. & Nabaglo, L. (1990) Geographical variation in cyclic periodicity and synchrony in the common vole, *Microtus arvalis*. *Oikos*, **59**, 343–348.

Michelat, D. (1997) La nidification du Hibou des marais *Asio flammeus* en France en 1993. *Ornithos*, **4**, 35–40.

Millon, A. & Bretagnolle, V. (2005) Non-linear and population-specific offspring sex ratios in relation to high variation in prey abundance. *Oikos*, **108**, 535–543.

Norrdahl, K. (1995) Population-cycles in northern small mammals. *Biology Reviews of the Cambridge Philosophical Society*, **70**, 621–637.

Oksanen, L. & Oksanen, T. (1992) Long-term microtine dynamics in North Fennoscandian Tundra – the vole cycle and the lemming chaos. *Ecography*, **15**, 226–236.

Oksanen, T., Oksanen, L., Schneider, M. & Aunapuu, M. (2001) Regulation, cycles and stability in northern carnivore-herbivore systems: back to first principles. *Oikos*, **94**, 101–117.

Prevot-Julliard, A.C., Henttonen, H., Yoccoz, N.G. & Stenseth, N.C. (1999) Delayed maturation in female bank voles: optimal decision or social constraint? *Journal of Animal Ecology*, **68**, 684–697.

Ryszkowski, L., Goszcynski, J. & Truszkowski, J. (1973) Trophic relationships of the common vole in cultivated fields. *Acta Theriologica*, **18**, 125–165.

Saitoh, T., Stenseth, N.C., Viljugrein, H. & Kittilsen, M.O. (2003) Mechanisms of density dependence in fluctuating vole populations: deducing annual density dependence from seasonal processes. *Population Ecology*, **45**, 165–173.

Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V. (2000) Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology*, **81**, 2428–2441.

Spitz, F. (1977) Le Campagnol des champs (*Microtus arvalis* [Pallas]) en Europe. *Bulletin of the OEP*, **7**, 165–175.

Spitz, F., Le Louarn, H., Poulet, A. & Dassonville, B. (1974) Standardisation des piégeages en ligne pour quelques espèces de rongeurs. *Terre et Vie (Revue Ecologie)*, **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., Saitoh, T. & Yoccoz, N.G. (1998) Frontiers in population ecology of microtine rodents: a pluralistic approach to the study of population ecology. *Researches on Population Ecology*, **40**, 5–20.

Stenseth, N.C., Viljugrein, H., Saitoh, T., Hansen, T.F., Kittilsen, M.O., Bolviken, E. & Glockner, F. (2003) Seasonality, density dependence, and population cycles in Hokkaido voles. *Proceedings of the National Academy of Sciences of the USA*, **100**, 11478–11483.

Strann, K.B., Yoccoz, N.G. & Ims, R.A. (2002) Is the heart of Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. *Ecography*, **25**, 81–87.

Tkadlec, E. & Stenseth, N.C. (2001) A new geographical gradient in vole population dynamics. *Proceedings of the Royal Society of London Series B-Biology Sciences*, **268**, 1547–1552.

Toussaint, M. (1990) Le campagnol des champs, *Microtus arvalis*. *La Défense Des Végétaux*, **260**, 22–31.

Turchin, P. (2003) *Complex Population Dynamics: a Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, NJ.

Turchin, P. & Hanski, I. (1997) An empirically based model for latitudinal gradient in vole population dynamics. *American Naturalist*, **149**, 842–874.

Turchin, P. & Hanski, I. (2001) Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecology Letters*, **4**, 267–276.

Van Wijngaarden, A. (1957) The rise and disappearance of continental vole plagues zones in the Netherlands. *Verslagen Van Landbouwkundige Onderzoekingen*, **63**, 1–21.

Yoccoz, N.G., Stenseth, N.C., Henttonen, H. & Prevot-Julliard, A.C. (2001) Effects of food addition on the seasonal density-dependent structure of bank vole *Clethrionomys glareolus* populations. *Journal of Animal Ecology*, **70**, 713–720.