POPULATION ECOLOGY

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Landscape effects on temporal and spatial properties of vole population fluctuations

Abstract Populations of northern small rodents have previously been observed to fluctuate in spatial synchrony over distances ranging from tens to hundreds of kilometers between sites. It has been suggested that this phenomenon is caused by common environmental perturbations, mobile predators or dispersal movements. However, very little focus has been given to how the physical properties of the geographic area over which synchrony occurs, such as landscape composition and climate, affect spatial population dynamics. This study reports on the spatial and temporal properties of vole population fluctuations in two areas of western Finland: one composed of large interconnected areas of agricultural farmland interspersed by forests and the other highly dominated by forest areas, containing more isolated patches of agricultural land. Furthermore, the more agricultural area exhibits somewhat milder winters with less snow than the forested area. We found the amplitude of vole cycles to be essentially the same in the two areas, suggesting that the relative amount of predation on small rodents by generalist versus specialist predators is similar in both areas. No seasonal differences in the timing of synchronization were observable for *Microtus* voles, whereas bank vole populations in field habitats appeared to become synchronized primarily during winter. *Microtus* populations in field habitats exhibited smaller spatial variation and a higher degree of synchrony in the more continuous agricultural landscape than in the forest-dominated landscape. We suggest that this inter-areal difference is due to differences in the degree of inter-patch connectivity, with predators and dispersal acting as the primary synchronizing agents. Bank vole populations in field habitats were more synchronized within the forest-dominated landscape, most likely reflecting the suitability of the inter-patch matrix and the possibility of dispersal. Our study clearly indicates that landscape composition needs to be taken into account when describing the spatial properties of small rodent population dynamics.

Keywords Bank vole · *Microtus* · Population dynamics · Synchrony · Vole cycle

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Introduction

Populations of small mammal species in northern regions commonly exhibit pronounced multi-annual cyclic fluctuations in density (Elton 1924; Kalela 1962; Krebs and Myers 1974; Hansson and Henttonen 1985; Stenseth and Saitoh 1998). In the boreal zone of Fennoscandia, these cycles typically have a period of 3–5 years and are manifested most pronouncedly in populations of the vole genera *Microtus* and *Clethrionomys* (Hansson and Henttonen 1985, 1988; Korpimäki et al. 1991; Hanski et al. 2001). Characteristic for these cycles is that they often occur in temporal synchrony across various species and taxa, such as shrews, mice, and voles (Hansson 1984; Henttonen 1985; Korpimäki 1986). Furthermore, cyclic small mammal populations commonly fluctuate in spatial synchrony over distances of tens or even hundreds of kilometers (Myrberget 1973; Mackin-Rogalska and Nabaglo 1990; Steen et al. 1996; Ranta and Kaitala 1997; Ims and Andreassen 2000).

The cyclic behavior of Fennoscandian vole populations is currently most commonly thought to be brought about by the combined effects of mortality by specialist predators (Korpimäki and Norrdahl 1998; Hanski et al. 2001; Korpimäki et al. 2002) and winter food limitation (Klemola et al. 2000; Hansson 2002; Huitu et al. 2003). Predation has also been proposed to be the mechanism causing the observed interspecific temporal synchrony in small mammal cycles (Angelstam et al. 1984; Norrdahl and Korpimäki 2000). Factors inducing spatial synchrony in vole population fluctuations, on the other hand, have remained more elusive. This phenomenon has been

suggested to potentially arise by three mechanisms: correlated environmental perturbations, dispersal, or predation (reviewed by, e.g., Bjørnstad et al. 1999a; Koenig 1999).

Fluctuating populations with similar structures of density dependence are expected to become synchronized under the influence of spatially correlated environmental disturbances, such as weather or climatic fluctuations. This type of effect, later coined the Moran effect (Royama 1992), was first described by Moran (1953) as an explanation for spatial synchrony in the Canadian lynx (*Lynx canadensis*) cycle. The Moran effect has since been invoked as a synchronizing mechanism in a number of population studies, both theoretical and empirical (e.g., Hanski and Woiwod 1993; Ranta et al. 1997, 1999; Grenfell et al. 1998; Myers 1998; Cattadori et al. 2000; Benton et al. 2001; Post and Forchhammer 2002). Dispersal has been shown to be able to induce spatial synchrony in population fluctuations through the movement of individuals between populations, albeit at a much more restricted scale than the Moran effect (Blasius et al. 1999; Schwartz et al. 2002). At a scale intermediate to the Moran effect and dispersal, predation by mobile, most often avian, predators has also been suggested to be capable of synchronizing animal population fluctuations (Ydenberg 1987; Korpimäki and Norrdahl 1989; Ims and Steen 1990; Heikkilä et al. 1994; Norrdahl and Korpimäki 1996; Bjørnstad et al. 1999a; Ims and Andreassen 2000). The aforementioned three mechanisms are not mutually exclusive and may act in concert, at different scales, in causing geographically distinct populations to fluctuate in synchrony (Lande et al. 1999; Paradis et al. 1999; Kendall et al. 2000; Ripa 2000).

Although research on the spatial aspect of population dynamics has been extensive, still very little is known about the effects of the actual physical properties of the spatial domain in question on the outcome of population dynamics, especially spatial synchrony. Hansson and Henttonen (1985) analyzed Fennoscandian small mammal trapping series and found a latitudinal gradient in density variations, such that increasing snow cover from south to north was associated with increasingly pronounced small mammal cycles. The observed differences were explained by the relative abundances of generalist and specialist predators of voles, such that southern localities would be able to support more generalists, which in turn are capable of stabilizing vole population dynamics (Andersson and Erlinge 1977; Erlinge et al. 1983; Hansson 1987; Hanski et al. 1991; Korpimäki et al. 2002).

Subsequent studies have indicated that also an increase in the proportion of agricultural land in the landscape predicts a decrease in the amplitude of population cycles (Martinsson et al. 1993; Hansson 1999, 2002). This decrease has likewise been linked to increasing predation pressure by generalist predators, such as corvids and red foxes (*Vulpes vulpes*), which are suggested to thrive in agricultural surroundings due to an abundance of alternative prey types (Angelstam et al. 1984; Andrén et al. 1985; Martinsson et al. 1993). Hansson (2002) compared the dynamics of small rodents in two different landscape types, both types situated in two regions with differing climatic conditions, and concluded that regional effects override smaller-scale landscape effects in shaping population fluctuations. Along the lines of Hansson and Henttonen (1985), however, the results of Hansson (2002) were also best explained by regional differences in snow cover, which in turn influences the relative rates of specialist and generalist predation.

Landscape structure has also been shown to influence spatial dynamics of small mammal populations. Adler (1994) studied populations of a frugivorous rodent in Panama and concluded that tropical forest fragmentation and habitat isolation increased the level of asynchrony among population fluctuations. Another clear indication of the significance of landscape structure is provided by Sherratt et al. (2002), who reported on the direction of travelling waves in vole population fluctuations being guided by landscape features. Hansson (1999) further postulated that vole population dynamics are influenced to a great extent by human-induced alterations in boreal landscapes, namely, forestry practices, such that the most profitable habitats for small rodents are spatially and temporally all but constant.

The causal mechanism inducing spatial synchrony among a group of populations is commonly interpreted from a measure of how rapidly the degree of synchrony declines with increasing distance between populations (e.g., Hanski and Woiwod 1993; Ranta et al. 1995a; Steen et al. 1996; Cattadori et al. 1999). More often than not, this approach has not taken into account the structure of the space over which the populations are observed. The effects of dispersal, for example, in inducing spatial synchrony are expected to be magnified in homogeneous landscapes comprised of uniform suitable habitat, as compared to landscapes comprised of isolated patches of suitable habitat embedded in a hostile matrix. A number of studies exist indicating that the interchange of individuals between habitat patches decreases with a decrease in their connectivity (e.g., Lawrence 1988; Holyoak and Lawler 1996; Ims and Yoccoz 1997; Andreassen and Ims 1998), but this has not been firmly linked to effects on spatial synchrony. However, Holyoak (2000) demonstrated experimentally with ciliates that a negative association does exist between inter-patch distance and spatial synchrony among populations of both prey and their predators.

This study reports on the characteristics of temporal and spatial dynamics of cyclic vole populations in two areas of western Finland, which differ both in landscape structure and, to some degree, also in climate. Our aim is to address the following questions:

1. Are there inter-areal differences in the temporal properties of the vole cycles?
2. Are there landscape-related inter-areal differences in the spatial dynamics of vole populations?
3. Are there interspecific and habitat-specific differences in spatial population dynamics between *Microtus* voles

(pooled field voles, *M. agrestis*, and sibling voles, *M. rossiaemeridionalis*) and bank voles (*Clethrionomys glareolus*)?

Materials and methods

Study areas and vole trapping

The study area is centered at 63°N, 23°E in western Finland and encompasses ca. 150×120 km (Fig. 1). The area was divided into two (hereafter western and eastern area) on the basis of landscape composition and climatic conditions (FMI 1994; Solantie et al. 1996; Solantie 2000) (Fig. 1). The western area is composed of large interconnected areas of agricultural farmland interspersed by forests and exhibits relatively mild winters and little snow. The eastern area, on the other hand, is highly dominated by forests imbedded with more isolated patches of agricultural farmland and exhibits somewhat colder winters, with a thicker and longer-lasting snow cover (Tables 1 and 2). With respect to predator communities, the species composition and number of breeding owls have both been shown to differ between the landscapes, such that more vole-specialized owls inhabit the western area than the eastern area (Korpimäki 1987).

The small mammal trapping data were collected in six municipalities per area by members of the Ornithological Society of Suomenselkä. Trapping was conducted in one field habitat site and one forest habitat site per municipality, except in Kauhava in the western area, where trapping was carried out in two field habitat
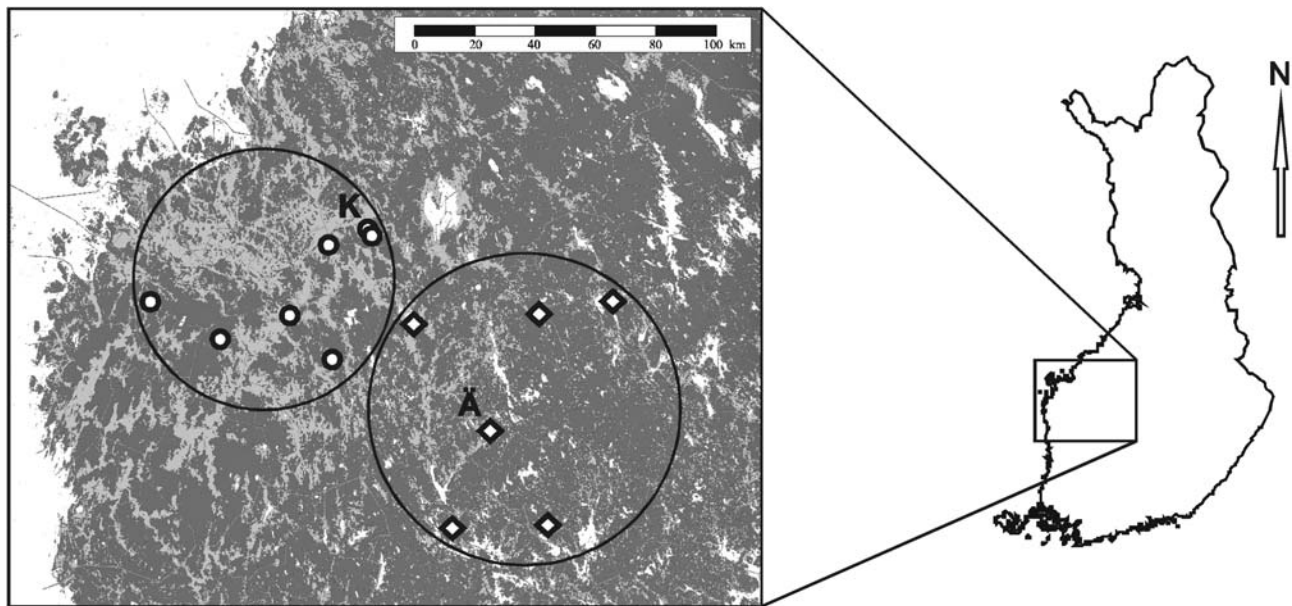

Fig. 1 Location of the western and eastern study areas in western Finland, as defined by the *large circles*. *Dark gray* coloration indicates forest, and *light gray* indicates agricultural field areas and white water bodies. *Small circles* indicate trapping sites of the western area, and *diamonds* indicate sites of the eastern area. *K* and *Ä* denote the meteorological data collection sites of Kauhava and Ähtäri, respectively (see Table 2)

Table 1 Characteristics of landscape composition and trapping effort in the small rodent trapping municipalities and their general region of location

Region	Municipality	Area (km^2)	Fields (%)	Forests (%)	Field-forest ratio	No. trapping occasions[a]
West	Ilmajoki	609	29.7	62.8	0.47	40
	Jurva	448	14.0	77.2	0.18	30
	Kauhava	485	25.8	64.7	0.40	44/42[b]
	Lapua	751	26.6	65.0	0.41	44
	Nurmo	361	14.9	76.4	0.20	31
	Seinäjoki	134	17.9	60.1	0.30	43
Western circle		5810	40.2	58.8	0.68	
East	Karstula	962	5.5	81.4	0.07	25
	Keuruu	1431	3.4	79.3	0.04	36
	Kuortane	485	14.8	72.6	0.20	33
	Soini	573	5.6	83.7	0.07	28
	Virrat	1299	5.4	77.6	0.07	15
	Ähtäri	908	4.7	77.4	0.06	33
Eastern circle		8330	11.8	83.9	0.14	

[a] Biannual trappings between 1979 and 2000, maximum 44 occasions
[b] Two field trapping sites in the municipality of Kauhava; see Materials and methods

Fig. 2 Spatial synchrony in the long-term population fluctuations of vole populations in field and forest habitats in the two studied regions of western Finland. Each curve represents a trapping series from one trapping site. All data are ln $(x+1)$-transformed and standardized to mean = 10 and SD=1
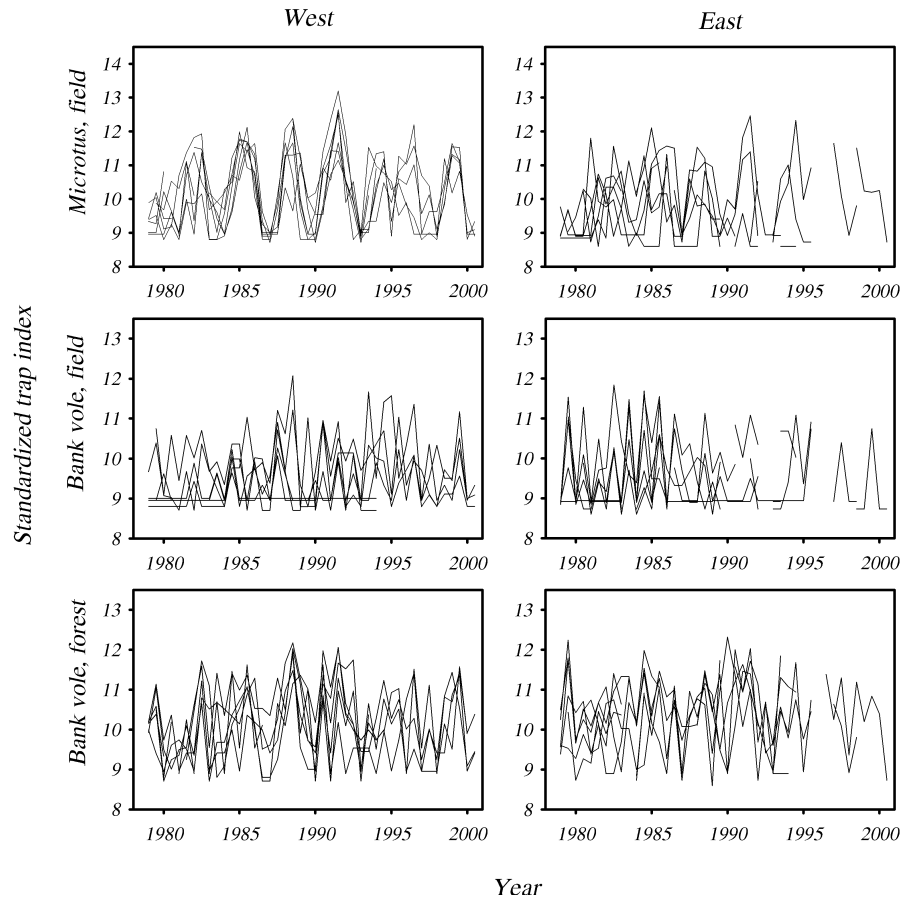

Table 2 Characteristics of climate in the western and eastern region of the study area. Data were collected in meteorological observation stations in two municipalities, each located representatively of climatic conditions within their respective region (Kauhava in the western region and Ähtäri in the eastern region; see Fig. 1)

Month	Temp (°C)[a] 1961–1990		Snow (cm)[b] 1961–1990		Snow (days)[c] 1977–1988	
	West	East	West	East	West	East
Jan	−9.2	−9.8	21	35	29.8	31.0
Feb	−8.9	−9.4	32	49	28.3	28.2
Mar	−4.4	−4.9	29	51	30.8	31.0
Apr	1.7	1.1	7	28	15.1	25.8
May	8.7	8.2	0	0	0.2	2.0
Jun	13.8	13.4	0	0	0	0
Jul	15.5	15.1	0	0	0	0
Aug	13.5	13.1	0	0	0	0
Sep	8.5	8.1	0	0	0.2	0.1
Oct	3.7	3.3	0	0	2.3	2.9
Nov	−1.9	−2.3	4	5	14.0	18.0
Dec	−6.8	−7.3	11	20	28.8	30.5

[a] Mean monthly temperature
[b] Mean snow depth on the 15th day
[c] Mean number of days with snow cover

sites and one forest habitat site. Field and forest sites within the municipalities were separated by 2–10 km. Trappings were conducted biannually (May and late September–early October) between the years 1979 and 2000, with the length of the trapping series per site ranging from 15 trapping occasions to a maximum of 44 trapping occasions (Table 1). At each site, 20–100 mouse snap traps (Finnish commercial metal traps) were placed in 2–10 rows, with a distance of 10 m between traps. Traps were set for 3–4 nights and checked, and reset if necessary, once a day. Bread was used as bait. All trapping series used in the calculations are derived from trapping indices expressed as individuals trapped per 100 trap

nights. All trapping series exhibit cyclic dynamics, with a period of 3–4 years (Fig. 2). Furthermore, long-term trapping data from the western area shows that *Microtus* voles and bank voles fluctuate in close temporal synchrony (cross-correlation coefficient with no time lag = 0.69; E. Korpimäki, K. Norrdahl, O. Huitu, T. Klemola, unpublished).

Analyses

We characterized the composition of the landscape in the western and eastern areas from the smallest possible non-overlapping circles that encompass all trapping sites (Fig. 1). This was done by calculating by division the total ratio of agricultural land to forest (hereafter field-forest ratio) within the encircled areas (Table 1). We also calculated the municipality-wise field-forest ratio from municipalities where trappings were conducted, to demonstrate the relative evenness in the distribution of agricultural land and forests within the two regions (Table 1). The municipality Kuortane (westernmost site in eastern circle) is grouped into the eastern area, despite exhibiting a field-forest ratio more similar to municipalities in the western area (Table 1). The climatic conditions and general topography of Kuortane, however, are more similar to the eastern than to the western sites (E. Korpimäki, K. Norrdahl, personal observation). Furthermore, the degree of connectivity between Kuortane and the other eastern sites is comparable to the overall degree of connectivity between the eastern sites (Fig. 1). In addition, trial analyses with Kuortane included into the western area indicated that vole dynamics in Kuortane are more similar to the eastern sites than to the western sites. This strongly supports the inclusion of Kuortane into the eastern area. Field and forest area data for the municipalities were obtained from Tomppo et al. (1998) and http://fennica.net.

We compiled separate, municipality-wise trapping series for *Microtus* voles and bank voles, for both agricultural habitat trappings and forest trappings, thus yielding four sets of trapping series per municipality (six for Kauhava; see above). Both spring and autumn trapping indices were used in the series. Since field voles and sibling voles were rarely caught in the forests, all series for *Microtus* in the forest trappings were excluded from the analyses. For the remaining series, all analyses were performed separately for each species in both trapping habitats. To identify whether the amplitude of vole cycles differs between the two areas, we computed a coefficient of variation $[CV = (SD/\bar{X}) \times 100]$ for each trapping series (see Hansson and Henttonen 1985). These were then compared between areas with a standard analysis of variance, using the maximum likelihood method [procedure MIXED, SAS (Littell et al. 1996)].

For analyses of seasonal and landscape effects on spatial variation in population dynamics, all trapping series were ln $(x+1)$-transformed and standardized to mean = 10 and SD=1, to reduce correlation between the mean and the variance of the series and to remove trapping site-specific differences possibly caused by differences in trapping protocols (Ranta et al. 1995b; Koenig 1999). We adopted a twofold approach to the identification of whether spatial synchronization occurs primarily during the winter or during the summer season and whether this is affected by the structure of the landscape.

First, we calculated coefficients of spatial variation (see formula above) for all separate spring and autumn trapping indices across trapping sites, separately for both areas. We predict that if spatial synchronization were to take place primarily during winter seasons, the spatial variation in the trapping indices would be smaller in the spring trapping sessions than in the autumn trappings, and vice versa. In addition, seasonal effects on synchronization may have impacts of different magnitudes in the two landscape types. Second, we calculated population growth rates r_t for each biannual trapping interval (summer and winter) for each trapping series using the formula $r_t=\ln (N_{t+1}/N_t)$, where N_t is the trapping index at time t. Similar to our first approach, we then calculated an index of variation V_r for all separate summer and winter growth rates across trapping sites, separately for both areas. Since the mean population growth rate per area was negative between several trapping sessions, and zero between a few, we calculated V_r using the formula $V_r = [SD/(|\bar{X}| + 1) \times 100]$, to avoid obtaining negative indices of variation and to avoid division by zero. Again, we predict that if spatial synchronization were to take place primarily during winter seasons, the spatial variation in population growth rates would be smaller in winter than in summer. In both approaches, differences in the indices of variation were analyzed using an ANOVA with season and area as explanatory variables.

For the analysis of landscape effects on spatial synchrony, we used the biannual population growth rate (r_t; see above for formula) data calculated from the ln (x+1)-transformed trapping series which were standardized to mean = 10 and SD=1. Pairwise cross-correlation analyses (Chatfield 1989) were performed on these series of growth rates between sites, in both areas separately (procedure ARIMA, SAS). The procedure calculates cross-correlation coefficients at various time lags, with high positive values at lag = 0 indicating synchronously fluctuating populations (Ranta et al. 1995b). Although pairwise cross-correlation coefficients calculated from a group of populations are commonly considered statistically non-independent of each other (Ranta et al. 1995b; Koenig 1999), we chose to include all cross-correlation coefficients at lag zero into analyses of covariance, with distance between sites and area as explanatory variables, for descriptive purposes. The assumptions of all analyses of covariance were met, as no interactions were observed between the inter-site distance and area.

Results

The mean (±SE, n=6) field-forest ratio was nearly four times higher in the trapping municipalities of the western area (0.33±0.05) than in those of the eastern area (0.09±0.02) (t-test: t=4.5, P=0.001). The difference in field-forest ratio was even greater on a regional scale, within the area of the circles (west: 0.68, east: 0.14). The mean ratio of trapped *Microtus* voles over bank voles was roughly 3:1 in the field habitats in the western area and roughly 1:1 in the eastern area. Bank voles were slightly more numerous in forest trappings in the east than in the west (Table 3). No differences were found in the coefficients of variation of the trapping series of either species between the eastern and the western areas (F<2.3, and P>0.2 in all cases), indicating that the amplitude of small rodent cycles was essentially the same in both areas (Table 3).

Microtus voles in field habitats exhibited substantially less spatial variation in trapping indices in the western area than in the eastern area, in both the spring and

Table 3 Mean (±SE) coefficients of variation (*CV*) of vole trapping series from field and forest habitats in the western and eastern region of the study area. No. voles is the mean (±SE) number of voles (per 100 trap nights) trapped at one trapping site during one biannual trapping session, calculated from area- and habitat-wise pooled trapping series

Species	Habitat	West			East		
		n	*CV*	No. voles	*n*	*CV*	No. voles
Microtus	Field	7	90.9±32.2	5.4±1.0	6	95.6±34.3	2.8±0.4
Bank vole	Field	7	99.9±37.0	1.8±0.3	6	128.4±46.8	2.7±0.8
	Forest	6	74.1±26.9	4.5±0.6	6	64.2±22.7	6.0±0.9

Table 4 ANOVA table for the effects of area (West/East) and season (spring/autumn) on coefficients of spatial variation in vole trapping indices

Species	Habitat	Effect	NDF	DDF	F	P
Microtus	Field	Area	1	75	19.37	<0.0001
		Season	1	75	2.26	0.14
		Area×Season	1	75	2.49	0.12
Bank vole	Field	Area	1	75	0.20	0.66
		Season	1	75	28.88	<0.0001
		Area×Season	1	75	0.90	0.35
Bank vole	Forest	Area	1	79	0.42	0.52
		Season	1	79	0.32	0.57
		Area×Season	1	79	0.15	0.70
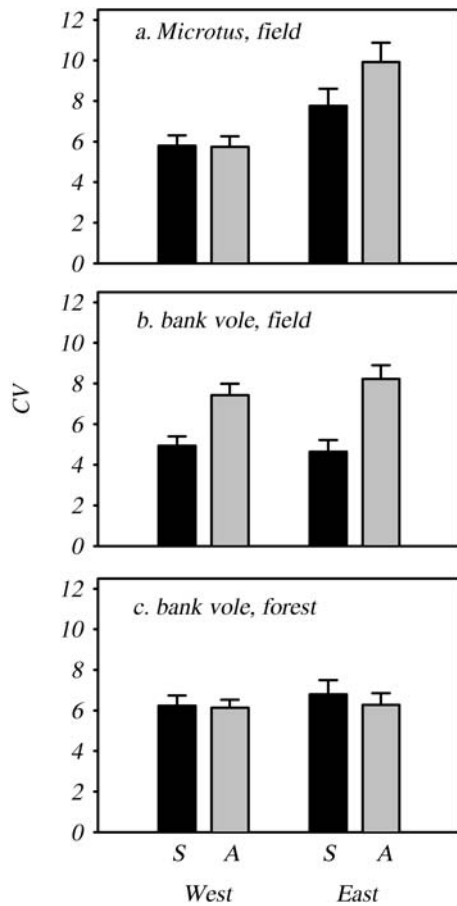
Fig. 3 Mean (+SE) coefficients of spatial variation of trapping indices (*CV*) for **a** *Microtus* voles in field habitats, **b** bank voles in field habitats, and **c** bank voles in forest habitats. *Black bars* denote spring (S) values, and *gray bars* denote autumn (A) values

Fig. 4 Mean (+SE) coefficients of spatial variation of population growth rates (V_r) for **a** *Microtus* voles in field habitats, **b** bank voles in field habitats, and **c** bank voles in forest habitats. *Black bars* denote winter (W) values, and *gray bars* denote summer (S) values

autumn trapping sessions (Table 4, Fig. 3a). Bank voles in field habitats, on the other hand, exhibited less spatial variation in trapping indices in the spring than in the autumn, regardless of landscape type (Table 4, Fig. 3b). Additionally, the growth rates of *Microtus* populations in field habitats varied spatially much less in the western than in the eastern area during both seasons (Table 5, Fig. 4a). The spatial variation in the growth rates of bank vole populations in field habitats, on the other hand, did not differ between areas or seasons (Table 5, Fig. 4b). No effects of area or season were detected on the spatial
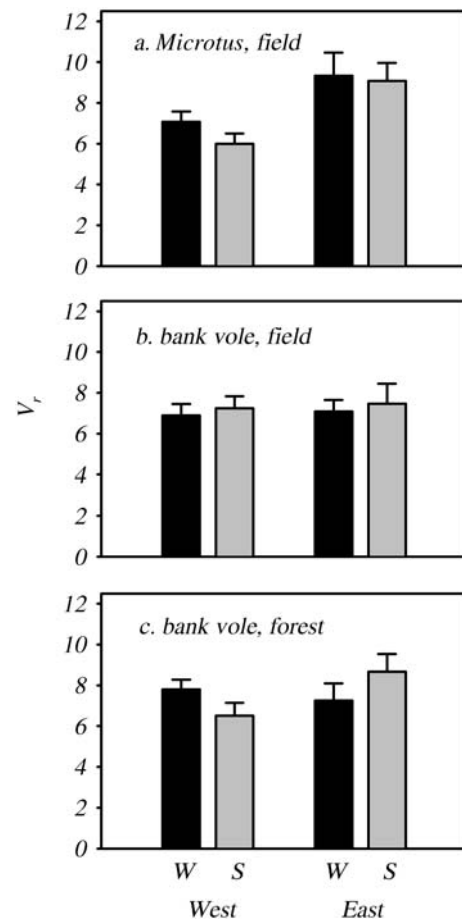
variation in bank vole population indices (Table 4, Fig. 3c) or population growth rates (Table 5, Fig. 4c) in the forest habitats.

The spatial synchrony, as calculated by cross-correlation without time lag, in population fluctuations of *Microtus* voles in field habitats was higher in the agriculturally more uniform western area than in the more fragmented eastern area ($F^{area}_{1,33}=78.7$, $P<0.0001$) (Fig. 5a). The degree of synchrony in both areas tended to decline with increasing distance between sites

Table 5 ANOVA table for the effects of area (west/east) and season (winter/summer) on co-efficients of spatial variation in vole population growth rates

Species	Habitat	Effect	NDF	DDF	F	P
Microtus	Field	Area	1	71	13.32	<0.001
		Season	1	71	0.81	0.37
		Area×Season	1	71	0.32	0.57
Bank vole	Field	Area	1	71	0.09	0.77
		Season	1	71	0.28	0.60
		Area×Season	1	71	<0.01	0.98
Bank vole	Forest	Area	1	76	1.33	0.25
		Season	1	76	0.01	0.93
		Area×Season	1	76	3.71	0.06
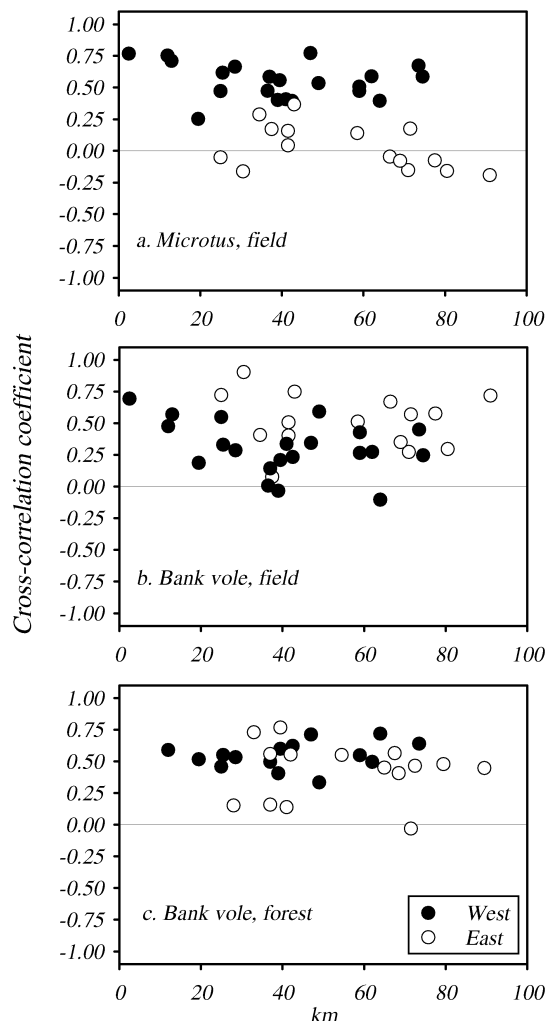
Fig. 5a–c The degree of synchrony among vole population fluctuations in relation to the pairwise distance between trapping sites in two regions of western Finland. The degree of synchrony between two populations is expressed as a cross-correlation coefficient (with time lag = 0), calculated from biannual population growth rates obtained from ln (x+1)-transformed trapping series, which were standardized to mean=10 and SD=1

range of observations ($t=0.6$, $P>0.5$) (Fig. 5a). In contrast to *Microtus* voles, bank vole populations in field habitats exhibited a higher degree of spatial synchrony within the more forested eastern area, as compared to the agricultural western area ($F^{area}_{1,33}=10.7$, $P=0.003$) (Fig. 5b). The occurrence of bank voles in field habitats did not differ between the areas; one or more bank voles were trapped in exactly 50% of all trapping sessions in both the eastern and the western areas. The degree of spatial synchrony in bank vole populations in forest habitats was clearly positive throughout the spatial range of observations and did not differ between areas (bank voles: $F^{area}_{1,27}=3.3$, $P=0.08$, $F^{distance}_{1,27}<0.1$, $P=0.84$) (Fig. 5c).

Discussion

We found the amplitude of vole cycles to be essentially the same in two areas of western Finland: one area composed of large interconnected areas of agricultural farmland interspersed by forests and the other highly dominated by forest areas, containing more isolated patches of agricultural land. The degree of spatial variation and synchrony in the fluctuations of vole populations in field habitats differed markedly between the landscapes. Populations of *Microtus* voles in their preferred habitats, grassy open areas (Hansson 1971), exhibited substantially less spatial variation in their numbers and dynamics in the western, more continuous agricultural area than in the eastern, more fragmented agricultural area. Bank voles in field habitats exhibited a similar degree of spatial variation in population numbers and growth rates in both areas. However, bank vole populations, being generally more confined to forest habitats (Hansson 1971), fluctuated spatially more synchronously within field habitats in the eastern area than in the western area. Bank voles within forest habitats fluctuated spatially relatively synchronously and similarly in both areas.

Amplitude of vole cycles

We found no differences in the amplitude of vole cycles between the western agricultural area and the eastern forested area. Agriculturally dominated landscapes have previously been shown to exhibit more stable vole

($F^{distance}_{1,33}=4.0$, $P=0.053$). Pairwise cross-correlation coefficients in the western area, however, remained clearly positive at distances of more than 75 km, whereas those in the eastern area did not differ from zero throughout the

dynamics than forest-dominated landscapes because of higher numbers of generalist predators, which may subsist year-round in agricultural habitats on abundant alternative prey types (Erlinge et al. 1983; Angelstam et al. 1984; Andrén et al. 1985; Martinsson et al. 1993). The fact that the agricultural landscape in this study did not exhibit more stable vole dynamics than the forested landscape cannot be explained by a lack of generalist predators in the western area. The species composition in communities of owls, commonly classified as functionally generalized predators (Hanski et al. 1991; see also Korpimäki and Krebs 1996), has been found to differ between the areas, such that the proportion of species within the community that feed primarily on voles [e.g., the long-eared owl (*Asio otus*), the short-eared owl (*A. flammeus*), and Tengmalm's owl (*Aegolius funereus*)], as well as the total number of their nesting pairs, increases from east to west (Korpimäki 1987). The agricultural landscape also supports substantial populations of other generalist-type predators, such as Eurasian kestrels (*Falco tinnunculus*), corvids (magpies [*Pica pica*]), hooded crows (*Corvus corone*), and, although not highly numerous, red foxes (Korpimäki and Norrdahl 1991; Norrdahl and Korpimäki 2002). Nonetheless, the abundance of generalist predators was apparently not sufficient enough to prevent the cyclic dynamics exhibited by vole populations in the western area (Fig. 2)

Although meteorological data indicate a decrease in snow depth and duration of snow cover from the eastern area to the western area (FMI 1994; Solantie et al. 1996; Solantie 2000), we believe that the sheltering effect of snow for voles is not markedly different between the two areas. The most stable year-round prime habitats for small rodents in agricultural landscapes are grassy edges of ditches and barns, which are spared from annual plowings (Norrdahl and Korpimäki 1993). In vast open landscapes, such as in the western study area, wind-driven snow rapidly fills these open ditches and the edges of barns during the onset of the winter season, while little snow cover accumulates on the agricultural fields themselves or on sites where snow-depth data is collected. The snow cover in ditches often accumulates to the brim, and very rarely melts away during warmer spells, when most field areas become bare. This holds also for spring, as ditches may retain their snow cover for up to a few weeks longer than the surrounding field areas. Furthermore, due to the effect of wind, the snow cover in the ditches has a very hard crust for the greatest part of the winter, making predation on voles by supranivean, especially avian, predators virtually impossible. In effect, voles are as, if not more, sheltered from predation in the western, more agricultural landscape than in the forested east, regardless of the relative numbers of generalist and specialist predators present.

Spatial variation in population sizes and growth rates

The spatial dynamics of *Microtus* voles in field habitats were consistently, throughout the year, more uniform in the western agricultural landscape than in the eastern forested landscape. We could not, therefore, identify either summer or winter as the main season of synchronization for *Microtus*. The observed inter-areal differences in the degree of spatial variation were more likely related to landscape composition than to differences in climate. Based on meteorological data alone, we might have expected stronger wintertime synchronization of *Microtus* population fluctuations within the western area, with less snow, than in the eastern area. However, for reasons mentioned above, vole populations in both areas appeared to be relatively equally sheltered by snow cover during the winter from the synchronizing impact of either recurrent environmental perturbations or mobile predators. We therefore suggest that the smaller degree of spatial variation in *Microtus* population dynamics in the western area is to a great extent brought about by a higher degree of connectivity between trapping sites, enabling more effective and regular movements of both the voles and their predators (Holyoak and Lawler 1996; Blasius et al. 1999).

Bank vole populations in field habitats exhibited a higher degree of spatial variation in autumn trapping indices than in spring trapping indices in both areas. No inter-areal or seasonal differences were observed in the spatial variation of population growth rates. This may imply that bank vole populations in field habitats become primarily synchronized during winter months. If so, this effectively precludes mobile avian predators as the main synchronizing agent of these populations, as the majority of vole-eating birds of prey migrate out of Northern Europe for the winter months (Mikkola 1983; Sonerud 1986; Korpimäki 1992) and vole populations become protected by snow cover. If synchronization of bank vole populations were to take place primarily during the winter, also dispersal as a causal mechanism would have to be largely dismissed (Lomolino 1989; see also Mihok 1984), thus indicating either a Moran effect or mammalian predation in action as a synchronizing mechanism. The most important mammalian predators of voles in the study area, least weasels (*Mustela nivalis*) and stoats (*M. erminea*) (Norrdahl and Korpimäki 1995), have been shown to concentrate their hunting efforts into agricultural habitats (Klemola et al. 1999), and their potential influence on bank vole populations during winter can be considered substantial.

The observations of the seasonal differences in bank vole synchronization must, however, be treated with caution, as autumn trappings were generally carried out towards the end of their breeding season, when territorial behavior begins breaking down before winter (Ylönen and Viitala 1985, 1991). An increase in movement associated with this process predisposes bank voles to snap traps, possibly resulting in inflated population indices. If the breakdown in territoriality occurs asyn-

chronously within an area, depending, for instance, on vole density, the spatial variation in autumn bank vole indices would become temporarily abnormally elevated. However, this explanation is challenged by the fact that bank vole populations in forest habitats, where the breakdown in territoriality occurs equally, did not exhibit the aforementioned seasonal difference in spatial variation.

Spatial population synchrony

Populations of *Microtus* voles in field habitats fluctuated in closer synchrony in the western agricultural landscape than in the eastern forested landscape. Pairwise cross-correlation coefficients for the western area remained above roughly 0.5 through the range of observations, at distances of up to 80 km (Fig. 5). Synchrony between populations in the eastern area, on the other hand, was effectively nonexistent. Both areas exhibited a slight tendency for the degree of synchrony to decline with increasing distance between sites (Fig. 5a). Previously, the degree of synchrony among vole populations in Finland has been suggested to be high over distances of even hundreds of kilometers (Kalela 1962; Henttonen et al. 1977), which suggests a Moran effect as a likely synchronizing mechanism (Ranta et al. 1995a). Elsewhere, more detailed studies at a smaller scale have indicated that synchrony among populations of arvicoline rodents may prevail at distances of up to only 50 km between sites (Steen et al. 1996; Lambin et al. 1998; Bjørnstad et al. 1999b; MacKinnon et al. 2001). Such an extent of synchrony most strongly supports dispersal as a causal agent (Steen et al. 1996).

Our results suggest that neither a Moran effect nor dispersal is alone adequate for causing the observed patterns of spatial synchrony between *Microtus* populations in field habitats. Based on the degree and extent of synchrony in the western area, a Moran effect would be a plausible causal agent, as synchrony remains remarkably high at distances nearing 80 km between sites, with only a slight decrease in strength with increasing distance. This extent clearly exceeds previous estimates of the potentially synchronizing effect of dispersal movements in arvicoline rodents (30–50 km) (Steen et al. 1996; Bjørnstad et al. 1999b). In the eastern area, however, at comparable distances, *Microtus* populations in field habitats did not fluctuate synchronously (Fig. 5a). Although the two areas were defined partly on the basis of climatic features, we do not believe that the areas differ to such a great extent in the frequency and magnitude of environmental perturbations as the differences in synchrony might suggest. In the case of a pure Moran effect synchronizing populations in our study area, we would expect to observe more similar patterns of synchrony between the western and the eastern areas. Because we do not, we believe that landscape composition, and the degree of connectivity between trapping sites, plays a

major role in producing the observed patterns in spatial synchrony.

Avian predators have been suggested to be capable of inducing regional synchrony among small rodent populations (Ydenberg 1987; Korpimäki and Norrdahl 1989; Ims and Steen 1990; see also Petty et al. 2000); this suggestion also has received experimental support (Norrdahl and Korpimäki 1996; Ims and Andreassen 2000). Heikkilä et al. (1994) also suggested that stoats might be capable of synchronizing vole population fluctuations. The synchronizing effect of these predators is naturally dependent upon their scale of operation, as well as on their preferences of habitat. Furthermore, landscape composition may influence synchronizing effects. In a spatially relatively homogeneous environment, such as one comprised of agricultural fields, landscape structures cannot be considered to greatly hinder movements of predators between hunting grounds. In effect, the costs of travel for predators in this kind of environment are small (Bernstein et al. 1991). In a spatially heterogeneous environment, predators would be expected to forage in prey patches and subsequently migrate between patches whenever the energetic gain in their current patch declines to a level lower than that of the region-wide average (Bernstein et al. 1999). Bernstein et al. (1991) have shown that when the costs of between-patch travel for predators are increased, e.g., in the form of increasing distance between patches or increasing unsuitability of the habitat in between prey patches, predators tend to become more sedentary and unwilling to leave their current patch, resulting in an uneven distribution of predators in relation to prey abundance.

We suggest that this may be a plausible explanation for the observed inter-areal differences in synchrony among field-habitat *Microtus* populations in our study area. As shown earlier (Korpimäki and Norrdahl 1991; Klemola et al. 1999), most vole-eating predators in our study area prefer agricultural farmland habitats for hunting. The western continuous agricultural landscape enables predators to distribute their hunting efforts relatively evenly among field habitats, thus yielding substantial potential for synchronization. The eastern landscape, however, confines predators more rigidly to the individual isolated agricultural fields, with high travel costs between patches. This applies to both mustelids and birds of prey, particularly during the reproductive season, when the predators must act as central place foragers. This spatial aggregation in turn may result in spatially more independent predator-prey interactions and, consequently, the observed lower degree of synchrony between sites in the eastern area.

Bank vole populations in field habitats exhibited a higher degree of spatial synchrony in the eastern, forest-dominated landscape than in the western, more agricultural area. Field trapping sites in the eastern area are surrounded by a matrix of forests, the main habitat of bank voles (Hansson 1971), which harbor few *Microtus*, the dominant competitor of the bank vole (Hansson 1983; Hanski and Henttonen 1996). Field trapping sites in the

west, on the other hand, are part of, and to a great extent surrounded by, vast expanses of agricultural farmland, mostly inhabited by *Microtus* voles. This effectively decreases the connectivity of the trapping sites for bank voles. Furthermore, due to the cyclic nature of vole populations in our study area (e.g., Korpimäki et al. 1991, 2002), bank voles often become periodically extirpated from field habitats. Although bank voles occurred equally frequently in field trappings in both areas, recolonization by voles into fields following these extirpations is most likely both temporally and spatially more irregular in the western area. This may be due to either the competitive effect of the presence of *Microtus* or a high risk of predation in the fields (Klemola et al. 1999). Recolonization by bank voles into fields in the eastern area is conversely expected to be more predictable due to larger source populations in the surrounding forests and relatively low numbers of competing resident *Microtus*.

The spatial synchrony among bank vole populations in forest habitats was positive throughout the range of observations but did not differ between the two landscapes. The overall level of bank vole synchrony in the forests was similar to the eastern field sites. Judging from the extent of synchrony (strong positive correlations at distances of up to 90 km), bank vole populations in forests throughout our study area may be synchronized by the action of a Moran-type effect, such as weather.

Conclusions

We found that the composition of the landscape greatly affects the spatial, but not the temporal, properties of vole cycles. The cyclic dynamics of vole population fluctuations did not appear to become more stable with increasing amounts of agricultural habitat in the landscape, as has previously been suggested. However, the spatial dynamics of these fluctuations showed clear landscape-related differences between the areas. *Microtus* voles exhibited a higher degree of spatial synchrony in a more agricultural landscape, as compared to a forested landscape. The spatial dynamics of bank voles displayed an opposite pattern. Bank voles also exhibited a seasonal difference in the timing of synchronization, with winters having a stronger effect than summers. The observed inter-areal differences in spatial population dynamics can most likely be attributed to the structure of the landscape and, through this, the degree of connectivity between habitat patches. Our results therefore indicate that landscape composition needs to be taken into account when describing patterns and causes of spatial synchrony in animal population fluctuations. More research, aimed specifically at untangling the relative influences of predators, dispersal, and climate on synchrony, is needed. This can be achieved by large-scale monitoring schemes in various environments that enable the controlling of each possible mechanism separately.

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