Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators

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Summary

1. Voles in northern Europe have been shown to exhibit cyclic population dynamics, with a latitudinal gradient in cycle length, amplitude and interspecific synchrony.

2. Previous studies have been based on a relatively sparse network of sampling sites. In the absence of spatially comprehensive long-term records of vole dynamics, we analysed a proxy of vole density, bird-ringing data on vole-eating avian predators, Tengmalm's owl (*Aegolius funereus* L.), the Ural owl (*Strix uralensis* Pall.), the long-eared owl (*Asio otus* L.) and the rough-legged buzzard (*Buteo lagopus* Pontoppidan) to study spatial population dynamics of voles.

3. We demonstrate that the breeding success of the avian predators is highly dependent on the abundance of voles, which is also reflected in the numbers of nestlings ringed in a particular area in each year.

4. Our results show the expected increase in cycle length from south to north in Finland, but also from west to east, and in contrast to previous studies, increasing irregularity of the cyclic dynamics towards the north.

5. Fluctuations of vole populations have been synchronous over large distances, up to several hundred kilometres. Such large-scale synchrony is more likely to be caused by movements of vole-eating predators and/or by climatic perturbations than by dispersal of voles.

6. We could not conclusively verify the recent suggestion that vole population dynamics have become less regular across Finland, although certain long-term changes are apparent.

Key-words: spatial autocorrelation, synchrony, vole cycles.

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Introduction

In population ecology, there has been an increasing interest in documenting, analysing and explaining spatio-temporal variation in population densities, with a particular focus on spatial synchrony among popu-

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lations (Bjørnstad, Ims & Lambin 1999a; Koenig 1999; and references therein). In Fennoscandia, vole populations are characterized by periodic fluctuations in abundance. The length of the vole population cycle is reported to be 3–5 years with more or less synchronous fluctuations in different vole species (Hansson & Henttonen 1985, 1988; Henttonen, McGuire & Hansson 1985; Henttonen & Hansson 1986) and over large areas (e.g. Kalela 1962). The well-established gradient in vole population dynamics in Fennoscandia from non-cyclic dynamics in the south to 5-year cycles in the north, as

well as the increase in cycle amplitude and interspecific synchrony towards the north, represent important patterns that have been explained by several hypotheses (e.g. Hansson & Henttonen 1985, 1988; Henttonen & Hansson 1986; Korpimäki & Norrdahl 1989a; Hanski, Hansson & Henttonen 1991; Hanski & Henttonen 1996).

Recently, several studies have reported increasing irregularity in previously rather regular cyclic vole systems. In Finnish Lapland, vole populations have become generally more stable or fluctuated more irregularly since the mid-1980s (Henttonen *et al.* 1987; Henttonen 2000). Similar observations have been made in other parts of Fennoscandia (Lindström & Hörnfeldt 1994; Steen, Ims & Sonerud 1996; Hansson 1999; Laaksonen, Korpimäki & Hakkarainen 2002).

Previous studies on large-scale dynamics of voles have been carried out using data on vole abundance obtained with trappings (e.g. Hansson & Henttonen 1985; Mackin-Rogalska & Nabaglo 1990; Bjørnstad, Stenseth & Saitoh 1999b) or using monitoring of signs of vole (including lemming) presence (e.g. Ranta & Kaitala 1997; Erlinge *et al.* 1999; MacKinnon *et al.* 2001). Unfortunately, the analysis of the spatio-temporal patterns in population dynamics calls for a large amount of data, which are seldom available, even for Fennoscandian vole populations. Therefore, we have looked for alternative measures to direct estimates of vole population density. To study vole population fluctuations at the scale of the entire Finland, we have chosen to examine the numbers of nestlings of vole-eating birds of prey that have been ringed in each year. Since the early 1970s, the Finnish Ringing Centre has filed all the ringing records, in addition to recoveries and recaptures, and has especially encouraged the ringers to work on birds of prey (see Saurola 1987a).

Many species of avian predators rely on small mammals when they are abundant, and many of them are small mammal specialists, being dependent on small mammals for survival and especially for the success of breeding (e.g. Newton 1979; Mikkola 1983; Saurola 1995). When small mammal populations decline locally to low numbers, nomadic (and migratory) avian predators specialized in small mammals may seek better hunting grounds, while resident predators respond primarily by altering their breeding effort (Andersson & Erlinge 1977; Korpimäki 1985, 1994). Resident avian predators may even skip breeding if densities of small mammals are very low (Newton 1979; Mikkola 1983).

Vole-eating avian predators assess, in practice, numbers of voles at large spatial scales more reliably than small mammal researchers, who trap voles or search for signs of them at relatively few sites. Avian predators experience large-scale fluctuations in vole numbers, which is reflected in their breeding performance owing to variation in hunting success. However, predatory birds have rather large hunting grounds, particularly in years of low vole abundance (Wijnandts 1984; Jacobsen & Sonerud 1987), which does not make their breeding performance very susceptible to small-scale variation in vole densities.

We have used long-term ringing data of vole-eating avian predators as an indicator of vole abundance at a large spatial scale. We show first how the variables describing the predators' breeding success depend on vole density, and next we demonstrate how the breeding success of avian predators is reflected in the numbers of nestlings ringed in a particular area. We use the number of nestlings of common vole-eating avian predators ringed in different parts of Finland to study cycle length, degree of spatial synchrony and possible recent changes in the type of dynamics of voles.

Materials and methods

RINGING DATA ON AVIAN PREDATORS

We used data on the most common specialist vole-eating avian predators gathered by Finnish professional and amateur ornithologists between the years 1973 and 2000 and collated by the Finnish Ringing Centre, University of Helsinki. For the purposes of these analyses, Finland was divided into 50×50-km^2 squares (Finnish uniform grid system). We counted the annual combined numbers of ringed nestlings of Tengmalm's owl (*Aegolius funereus* L.), the Ural owl (*Strix uralensis* Pall.), the long-eared owl (*Asio otus* L.) and the rough-legged buzzard (*Buteo lagopus* Pontoppidan) for each square.

Tengmalm's owl is a small mammal specialist. Adult males exhibit high site fidelity, while juveniles and females disperse widely (Korpimäki, Lagerström & Saurola 1987; Korpimäki 1988; Hörnfeldt *et al.* 1989; Korpimäki & Norrdahl 1989b). The Ural owl has a more generalized diet than Tengmalm's owl (Korpimäki & Sulkava 1987), but its breeding performance is still highly dependent on vole availability (Pietiäinen 1989; Brommer, Pietiäinen & Kolunen 2002). The Ural owl has an almost life-long pair bond, and the pairs have high site fidelity (Saurola 1987b). The long-eared owl is usually migratory in Finland, and clearly a vole specialist, whose breeding density and success are regionally affected by vole abundance (Korpimäki 1992). All three owl species are common and the most numerous specialist vole-eating predatory bird species in the ringing data. Unfortunately, only Tengmalm's owls breed throughout Finland, though only seldom in northernmost Lapland. Owing to scarcity of owl data from northern Finland, the rough-legged buzzard, a migratory raptor with a northern distribution and specialized on small mammals (Pasanen & Sulkava 1971; Newton 1979), was included in the analyses. Similarity of the time series of the ringed nestlings of the three owl species was assessed with correlation analysis for data from 12 well-studied squares in which they were all well represented. This analysis justified (reported in the Results section) the pooling of data for the different species. The log($x + 1$)-transformed pooled data were

used in all subsequent analyses except in the coherence analysis (below).

VOLE TRAPPING DATA

The relationship between the number of ringed nestlings of the selected avian predators and the existing long-term data on vole abundance was examined to clarify the dependence of the ringing data on local vole dynamics. Generally, the vole trapping series were obtained from biannual snap-trappings conducted in spring (May–early June) and in autumn (September–October) in both open and forested habitats. The trapping indices, expressed as the number of voles caught per 100 trap-nights, included the most common vole species in the particular area (one trap-night means that one trap has been set for one night). The common species typically included the field vole (*Microtus agrestis* L.) and the bank vole (*Clethrionomus glareolus* Schreb.), in northernmost Finland, also the grey-sided vole (*C. rufocanus* Sund.), the red vole (*C. rutilus* Pall.), the root vole (*M. oeconomus* Pall.) and occasionally the Norwegian lemming (*Lemmus lemmus* L.). Less frequent species included the sibling vole (*Microtus rossiaemeridionalis* Ognev), especially in western Finland. Trapping series of vole abundances were $\log(x + 1)$-transformed in all analyses, except in the coherence analysis.

We used data from three well-studied areas to examine in greater detail how vole abundance affects the breeding success of the avian predators, and how well the breeding success corresponds to the pooled number of nestlings ringed in a particular 50×50-km^2 square. For these three study areas there are extensive data on both the breeding performance of the Ural owl (e.g. Pietiäinen 1989) and Tengmalm's owl (see, e.g., Korpimäki 1987; Laaksonen *et al*. 2002) and on vole abundance.

ANALYSES

Phase-coherence analysis and cycle length

Cycle length in the avian predator ringing data was determined with phase-coherence analysis, which has been suggested to be a better method in detecting periodicity in short and noisy time series than the more usually employed autocorrelation and spectral analyses (Lindström, Kokko & Ranta 1997). The coherence analysis is based on Poincaré mapping, in which data transformed to zero mean are examined to define the standard deviation of points that intersect the Poincaré plane. The time series is periodic if the intersection point is the same after each round or cycle. Population time series cannot be expected to fulfil the exact mathematical definition of periodicity. The phase-coherence analysis is therefore utilized to determine the amount of variation that is compatible with the identification of the time series as periodic. The analysis yields a coherence function, in which standard deviation is calculated for each subset of data corresponding to different period lengths. A distinct reduction in the standard deviation suggests periodicity at the particular length (for more details see Lindström *et al*. 1997). For assessing statistical significance, the original data series was randomized 500 times. If the standard deviation obtained for the actual data is smaller than in 95% of randomizations, the time series can be considered as periodic with that particular length at the $\alpha = 0{\cdot}05$ risk level.

To detect possible changes in vole dynamics during the study period, the coherence analysis was repeated for the ringing data for the two equally long time periods 1973–86 and 1987–2000.

Squares containing less than 50 nestlings ringed during the entire period (or less than 25 during half of the period) were excluded from the analyses. We also repeated the analysis for spatially averaged data by combining the numbers of nestlings ringed in each square with the surrounding eight squares (less than eight if the square was located at the edge of the lattice). Here also the squares with fewer than 50 observations were included.

Cluster and cross-correlation analyses and spatial synchrony

We used hierarchical cluster analysis (SYSTAT® 7·0) to classify time series in terms of their overall similarity. For the cluster analysis $\log(x + 1)$-transformed data were standardized to mean 0 and standard deviation 1. In hierarchical clustering, time series are placed in clusters by first joining two most similar time series, and then continuing, in a stepwise manner, to join a time series to another time series, a time series to a cluster, or a cluster to another cluster until all objects are combined into one cluster. Ward's minimum variance method (e.g. Romesburg 1984) was used as the joining algorithm. As a distance metric the Euclidean distance (root mean square distances) was used. Ward's method averages all distances between pairs of time series in different clusters, with adjustment for covariances, to determine how far apart the clusters are. Clustering was done for the entire data set as well as for the first (1973–86) and the second part of the time series (1987–2000).

Cross-correlations with lag zero were calculated to assess synchrony between the squares and the relationship between the degree of synchrony and distance. Cross-correlations were calculated for all of Finland as well as within particular clusters, the latter to avoid obscuring the relationship between cross-correlation and distance owing to possible differences in cycle length between clusters. For the same reason, distant squares that were not part of the main spatial area of a particular cluster were not included in the cluster-based analyses. Cross-correlations were calculated after eliminating possible trends in the time series by using

standardized growth rates ($r_t = x_t - x_{t-1}$). Detrending was necessary because the numbers of nestlings ringed tended to be lower in the beginning of the time series than towards the end of it, reflecting an increasing trend in the ringing activity.

Results

CONCORDANCE OF THE RESULTS FOR DIFFERENT AVIAN PREDATORS

The numbers of ringed nestlings of the three owl species in the same 50×50-km^2 squares ($n = 12$) were strongly correlated. The correlation was highest between Tengmalm's owl and the long-eared owl (pairwise Spearman rank correlation coefficient, mean $0.68 \pm$ SE 0.05), following by Tengmalm's owl–Ural owl relationship (0.60 ± 0.07), while the mean of the correlation coefficients for the least synchronous species pair, the long-eared owl and the Ural owl, was still 0.41 ± 0.09. The relationships between the owl species and the rough-legged buzzard could not be investigated, as these species did not occur in sufficient numbers in the same squares. However, previous studies have shown that the rough-legged buzzard is a vole specialist and its breeding performance is greatly dependent on availability of voles (Pasanen & Sulkava 1971; Newton 1979; Potapov 1997). Therefore, we do not have any reasons to assume that data on its breeding performance as an indicator of vole abundance would be substantially different

from data on other vole-eating avian predators. We use pooled data for the four species as a measure of the abundance of vole-eating avian predators.

RELATIONSHIPS BETWEEN BREEDING SUCCESS OF AVIAN PREDATORS, RINGING DATA AND VOLE ABUNDANCE

The breeding performance, measured as the mean brood size, of Tengmalm's owl in two adjacent well-studied squares in Lapua and Kauhava, western Finland (700 : 25 and 700 : 30), showed a strong positive relationship with vole abundance during the breeding season in spring (Table 1). In contrast, vole density in the previous autumn did not explain the mean brood size of Tengmalm's owl. A similar pattern was observed in the total number of nestlings produced in the two areas (Table 1).

We examined the relationship between the breeding success of the Ural owl, measured by the mean brood size, in the Päijät–Häme region of southern Finland (including data from four adjacent squares: 675 : 40, 675 : 45, 680 : 40 and 680 : 45) and the results of vole trappings conducted in square 675 : 45 from 1986 to 2000. There was a positive relationship between vole abundance, for both previous autumn and current spring, and breeding success, but unlike in Tengmalm's owl, vole density in the previous autumn explained the mean brood size statistically slightly better than vole abundance in the spring of breeding (Table 1). Vole

Table 1. Relationship between breeding success (yearly mean brood size) and the total number of nestlings vs. vole density in three long-term study populations of Tengmalm's owl and the Ural owl. Päijät-Häme region contains the Ural owl breeding data from four adjacent squares of 50×50 km^2 (the Finnish uniform grid system): 675 : 40, 675 : 45, 680 : 40, 680 : 45, while vole data are from the square 675 : 45 (Brommer *et al.* 2002; H. Pietiäinen and J. Brommer, unpublished data). In Lapua region, Tengmalm's owl breeding data and vole data were gathered from the square 700 : 25, and in Kauhava region from the square 700 : 30 (Korpimäki 1987, 1988; Korpimäki 1994; Laaksonen *et al.* 2002). The table also shows the relationships between the pooled ringing data for focal avian predators and the mean brood size from the same area. The data were log($x + 1$)-transformed before linear regression analysis

| | Tengmalm's owl | | | | Ural owl | |
| | Lapua (700 : 25) | | Kauhava (700 : 30) | | Päijät-Häme | |
	R^2	P	R^2	P	R^2	P
Mean brood size						
Vole density:						
Previous autumn	$0.03, n = 21$	0.52	$<0.01, n = 21$	0.75	$0.39, n = 14$	0.012
Current spring	$0.33, n = 21$	0.023	$0.52, n = 21$	<0.001	$0.31, n = 14$	0.031
Total number of nestlings						
Vole density:						
Previous autumn	$0.03, n = 21$	0.51	$0.07, n = 21$	0.25	$0.56, n = 11$	0.008
Current spring	$0.34, n = 21$	0.019	$0.52, n = 21$	<0.001	$0.16, n = 11$	0.23
Mean brood size						
No of nestlings ringed in the area						
700 : 25	$0.45, n = 21$	0.005				
700 : 30			$0.29, n = 21$	0.012		
675 : 40					$0.69, n = 24$	<0.001
675 : 45					$0.64, n = 24$	<0.001
680 : 40					$0.40, n = 24$	<0.001
680 : 45					$0.64, n = 24$	<0.001
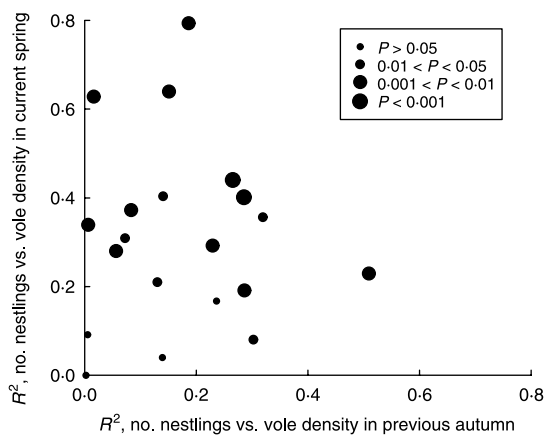
Fig. 1. Relationship between the number of nestlings ringed and vole density in the previous autumn vs. in the current spring measured by R^2. The size of the symbol shows the significance of relationship (the more significant of the two). Detailed description of the data is in Appendix.

density in the previous autumn explained best the total number of nestlings produced in the Ural owl (Table 1).

The breeding success of Tengmalm's owl and the Ural owl were compared with the pooled numbers of ringed nestlings of all four avian predators in the same areas. In both species, the mean brood size explained statistically well the pooled number of nestlings ringed (Table 1).

The existing vole trapping results were compared with the pooled ringing data of the four avian predators in all squares for which both data sets were available. In the majority (80%) of cases, there was a significant positive relationship between the density of voles and the number of nestlings ringed (Fig. 1, Appendix).

CYCLE LENGTH

Cycle length increases from south to north and to the north-east (Fig. 2). The same pattern is evident also for the early (1973–86) and the late (1987–2000) half of the time series. In south-west Finland, the dominant period is 3 years, while the frequency of 4- and 5-year cycles increases to the north and east. Most of the significant time series are from south-west Finland, where the ringing data are most abundant. In other parts of Finland, for which data are more scarce, many squares show no significant dominant cycle period, and adjacent squares often show different dominant periodicity. In the spatially averaged data, which combine data from the neighbouring squares to the focal square, the general patterns are clearer and, naturally, more squares show significant periodicity (Fig. 3) than in the original data (Fig. 2). Coastal squares (longitude 10 and 15) are exceptions in the west to east gradient. The coastal squares tend to show longer cycle period than the inland squares at the same latitudes, especially in the second half of the time period (Fig. 3).

The most striking difference between the time periods 1973–86 and 1987–2000 is the change from a 4-year

cycle to a 5-year cycle in northernmost Finland. Also, the frequency of squares showing 5–7-year cycles in the rest of Finland increased from 1973–1986 to 1987–2000 (Figs 2 and 3).

SPATIAL SYNCHRONY

In the cluster analysis, a four-cluster classification for the entire time series produced a surprisingly clear geographical pattern (Fig. 4), which is furthermore in broad agreement with the results of the coherence analyses (Figs 2 and 3). South-west Finland forms one distinct cluster (Fig. 4), in which the 3-year periodicity prevailed in the coherence analysis (Fig. 2). Another fairly distinct cluster is located in eastern central Finland, the area of 3–4-year periodicity (Figs 2 and 3). Thirdly, similar time series are found within a large area from central Finland to western Lapland, where the coherence analysis indicated rather dissimilar, though non-significant, lengths in periodicity, with 4 years being the most common period (Figs 2 and 3). Eastern Lapland exhibited highly variable dynamics with squares belonging to three different clusters, while the very north-eastern tip of Finland formed the fourth distinct cluster (Fig. 4), with a cycle length of 5 years (Figs 2 and 3).

In the analyses for the two parts of the time series, 1973–86 and 1987–2000, three clusters in the tree were more distinct (Fig. 4). The clustering for the first time period resembles the pattern for the entire time series, while in the latter period similar time series covered large areas in southern and central Finland, but excluding an area in inland south Finland (cluster 2 in Fig. 4 for 1987–2000).

Cross-correlations were calculated for the entire data set (1973–2000). The degree of synchrony declined with increasing distance (Fig. 5). In the pooled data for Finland, the mean correlation coefficient reached zero at a distance of 500–550 km. Within clusters, the mean correlation coefficients decreased with a similar slope except in the area of cluster 1, where the decrease with distance was less marked. On the other hand, there are striking differences in the overall level of synchrony in the dynamics. The degree of synchrony was clearly highest in cluster 3, which is the area in south-western Finland showing significant 3-year periodicity in the coherence analyses (Figs 2 and 3).

Discussion

VOLE POPULATION DYNAMICS IN RELATION TO RINGING DATA OF VOLE-EATING AVIAN PREDATORS

Our results confirm earlier findings of the breeding success of vole-eating avian predators being highly dependent on the availability of voles (e.g. Newton 1979; Mikkola 1983; Korpimäki 1984; Hörnfeldt *et al.* 1989; Pietiäinen 1989). Breeding success in turn
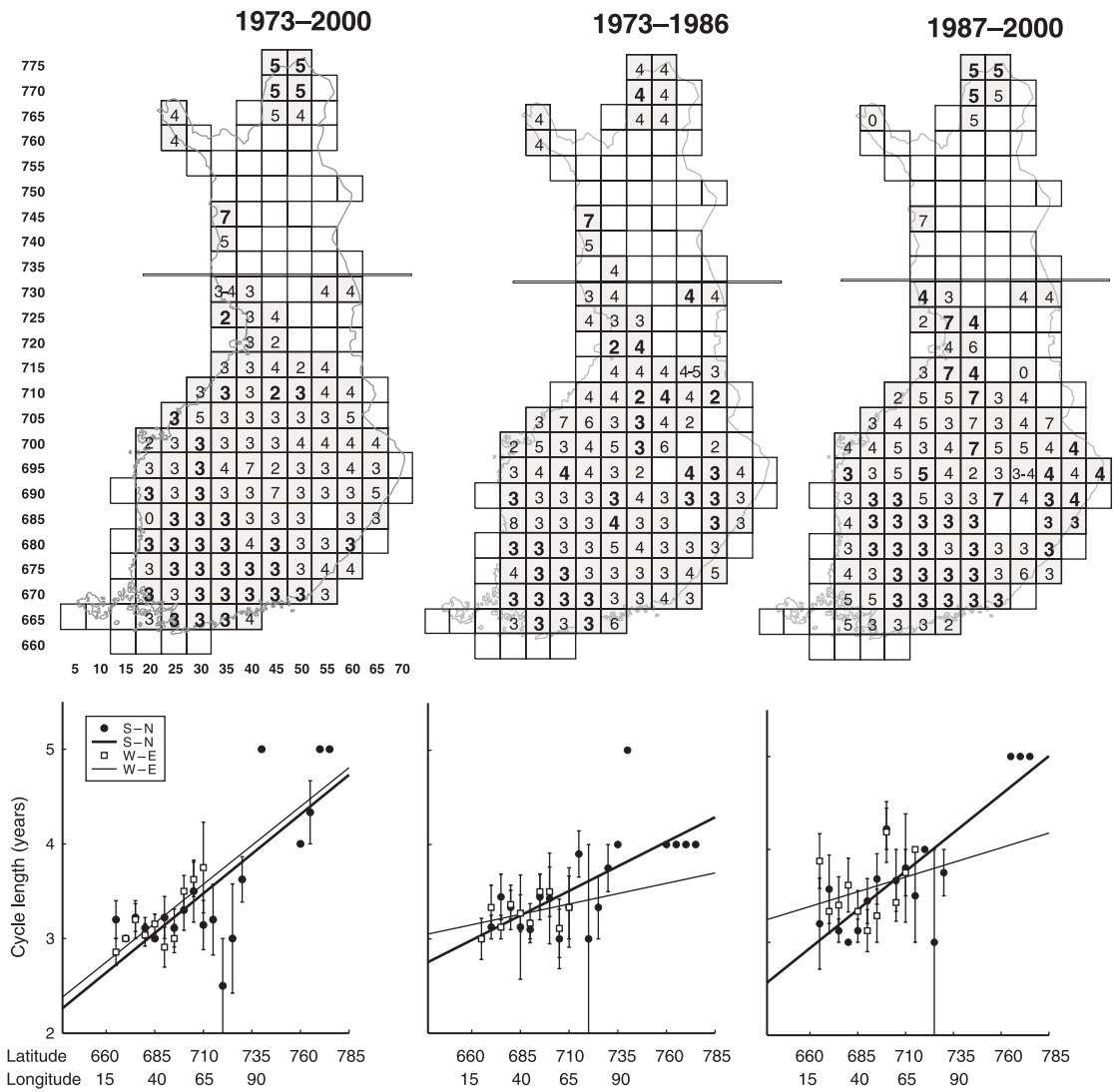
Fig. 2. Periodicity in the ringing data of nestlings of four species of vole-eating avian predators (Tengmalm's owl, the Ural owl, the long-eared owl and the rough-legged buzzard) ringed in 50×50-km^2 squares in Finland (the Finnish uniform grid system). Results are based on the coherence analysis. Analyses were repeated for three time periods (1973–2000, 1973–86 and 1987–2000). The significant results are printed in **bold** face. Squares containing fewer than 50 and 25 ringed nestlings (open squares) in the entire and divided time periods, respectively, were excluded. Zero values represent cases in which coherence analysis did not suggest any periodicity. In lower panels the cycle lengths (mean ± SE) are plotted against latitude and longitude. Squares north of the horizontal lines in maps were excluded from the plots of cycle lengths against longitude and squares having cycle length more than 5 years were excluded from both plots. Lines are simple linear regressions based on mean values.

explains well the numbers of nestlings that have been ringed, which is a measure that is available for large areas in Finland. We also showed that there are strong relationships between vole population dynamics and the ringing records of owls and raptors specializing on voles. Based on these findings, we conclude that the number of nestlings of vole-eating avian predators that have been ringed reflects well the major patterns in the density fluctuations of voles at a scale of 2500 km^2.

Our results refer to generalized vole dynamics, and there is no possibility of ascribing the results to particular vole species. During population cycles different vole species generally fluctuate in synchrony in Fennoscandia (Henttonen & Hansson 1986), even though

different species may reach peak densities at slightly different times (e.g. Henttonen *et al.* 1977; Hanski & Henttonen 1996). On the other hand, the decline years are highly synchronous across species, which should increase the generality of our results (Henttonen & Hansson 1986).

A possible source of error in our analyses might be the use of avian predator species that respond slightly differently to spring vs. autumn vole densities (Appendix). The differences in the relationships between the ringing data and vole density in the previous autumn vs. in the spring of breeding (Appendix) are mainly due to differences in the species composition of the vole-eating avian predators. For example, Tengmalm's owl dominates in the ringing data from western Finland
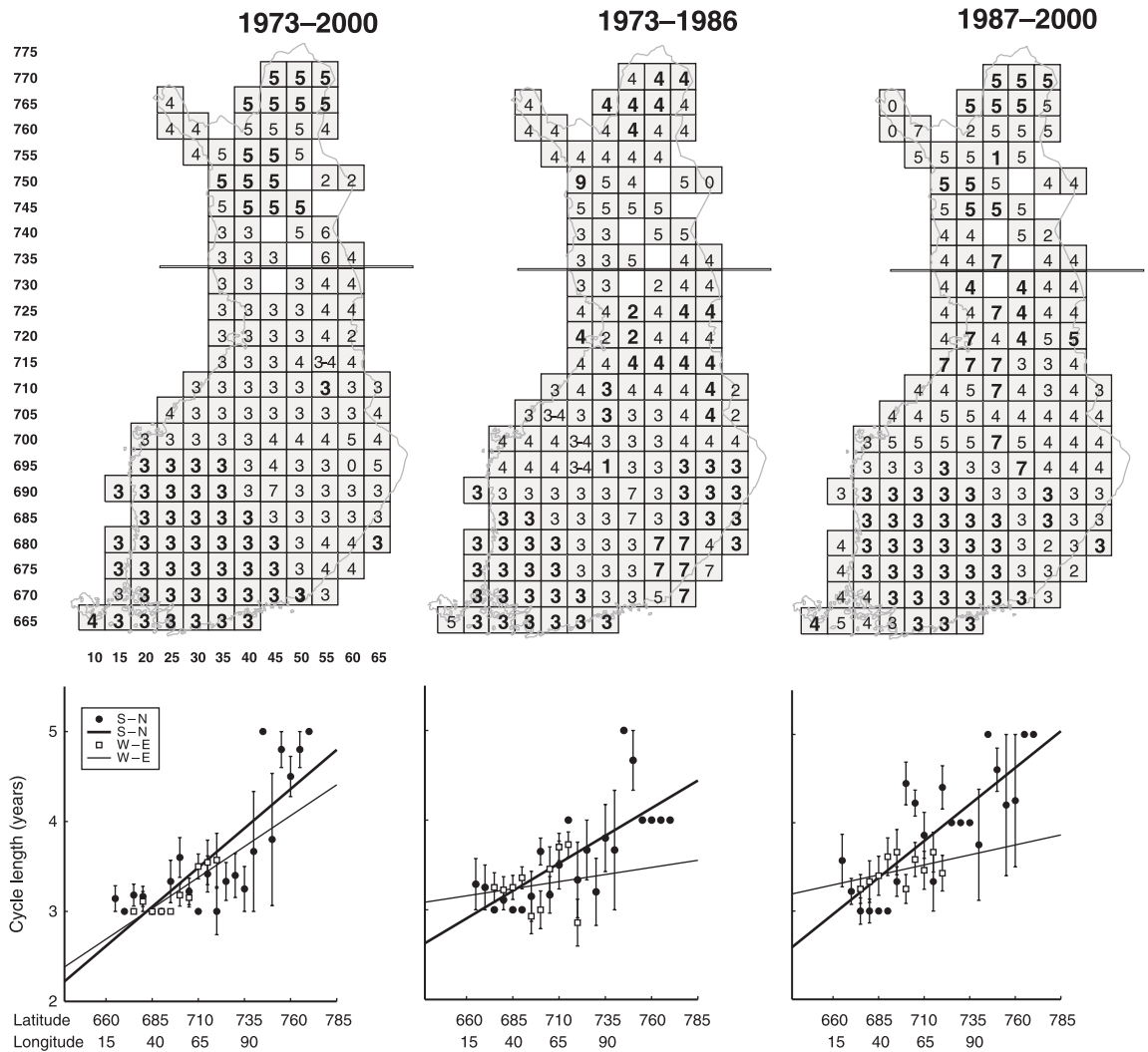
Fig. 3. Periodicity in the ringing data of nestlings of four species of vole-eating avian predators (Tengmalm's owl, the Ural owl, the long-eared owl and the rough-legged buzzard) for spatially averaged data. Data were combined in blocks of nine (at maximum, less in the edge of lattice) 50×50-km² squares (the Finnish uniform grid system). As in Fig. 2, the analysis was repeated for periods 1973–2000, 1973–86 and 1987–2000. The significant results are printed in **bold** face. Zero values represent cases in which coherence analysis did not suggest any periodicity. In lower panels the cycle lengths (mean ± SE) are plotted against latitude and longitude. Squares north of the horizontal lines in maps were excluded from the plots of cycle lengths against longitude and squares having cycle length more than 5 years were excluded from both plots. Two coastal 'columns' (10 and 15) are excluded, because these squares clearly differed from linear relationships between the cycle length and longitude. Lines are simple linear regressions based on mean values.

and southern Lapland, where the number of nestlings ringed is more dependent on the current spring density of voles. In southern and central Finland, where the Ural owl is numerically dominant, the relationship is marginally stronger with the vole density in the previous autumn (see Table 1 and Appendix). This pattern is related to differences in site fidelity between these species. Both sexes of the Ural owl tend to live in the same territory all year round (Saurola 1987b), and thus the condition of the female and her breeding success are affected by food availability during the winter, which in turn is better reflected by the vole trapping results for the previous autumn than for the spring of breeding. In contrast, in Tengmalm's owl adult females as well as young birds tend to change territory between successive years and may move long distances between successive breeding attempts, whereas adult males are site-tenacious (Korpimäki *et al.* 1987; Korpimäki 1988). Therefore, the breeding success of Tengmalm's owl is most affected by the spring density of voles in their current territory. Pooling the data for avian predators with somewhat different responses to changes in vole density may affect the clustering of the time series but not the estimated length of cycles. We expect that even the former effect is small.

Our results were based on the breeding success of vole-eating avian predators. We appreciate that the vole cycle also affects the status (breeding vs. non-breeding) and demography of the predator population, but this is difficult to study, in particular because the non-breeding population cannot be estimated without unrealistically massive radio-tracking operations.
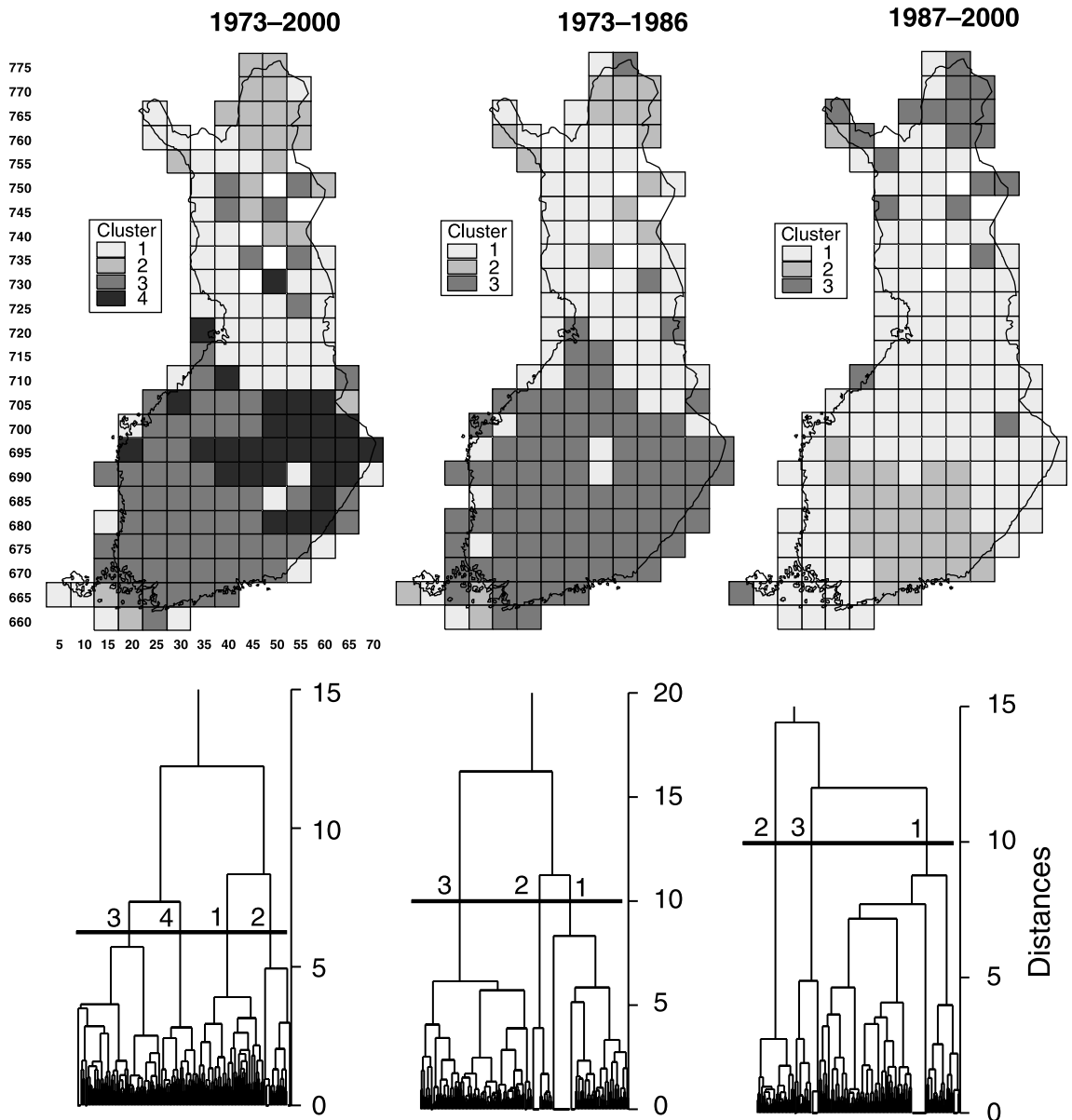
1973–2000 **1973–1986** **1987–2000**

Fig. 4. Results of cluster analysis showing four or three clusters of vole-eating avian predators in time periods 1973–2000, 1973–86 and 1987–2000. The same fill colours of 50×50-km^2 squares represent similar time series within each map. Lower panels show trees describing the similarities in the time series. Numbers beside the branches of cluster trees represent cluster numbers in corresponding maps. Ward's minimum variance method was used as the joining algorithm to define how distances between clusters are measured. As a distance metric the Euclidean distance (root mean square distances) was used.

CYCLE LENGTH

The vole population dynamics revealed by the breeding success of vole-eating avian predators showed an increase in cycle length from south to north and north-east, the period being 3 years in the south and increasing to 5 years in the northernmost part of Finland. This is in accordance with earlier results based on a limited number of local vole studies (Hansson & Henttonen 1985, 1988; Henttonen *et al.* 1985; Hanski *et al.* 1991).

In previous studies on the spatial population dynamics of voles (Hansson & Henttonen 1985, 1988), southern Finland was categorized as a 'semicyclic' area with more irregular dynamics than in the northern 'truly cyclic' areas. Instead, we found the vole cycles as

inferred from the avian predator ringing data to be actually more regular in southern Finland than in the northern part of the country. It should be noted, however, that the suggestion by Hansson & Henttonen (1985, 1988) was based on the amplitude of cycles, not on cycle length itself, which was analysed by Hanski *et al.* (1991). Additionally, our results from the north should be interpreted cautiously because of limited ringing data in many areas.

SPATIAL SYNCHRONY

The degree of spatial synchrony tended to be high over large distances in Finland, up to 500 km, which is in accordance with previous suggestions about spatial
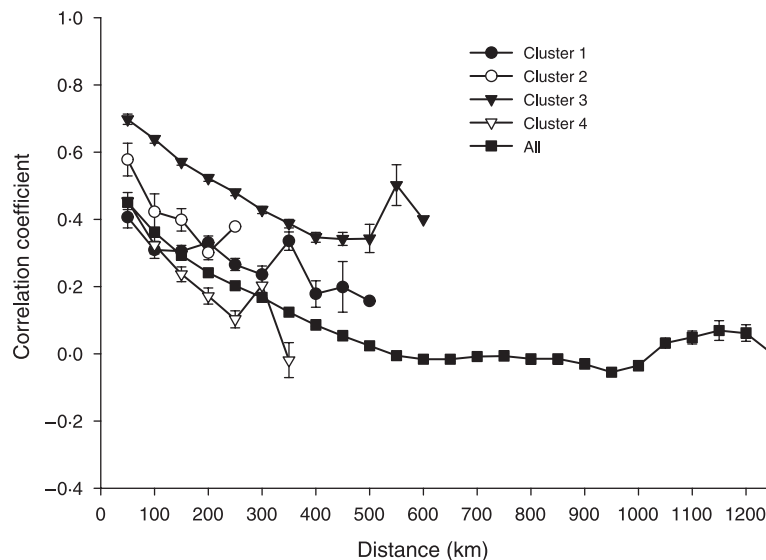
Fig. 5. Cross-correlation (mean ± SE) with lag zero against distance within each cluster in Fig. 4 (left-hand panels) and for entire Finland.

synchrony of cyclic peaks in Finland (Henttonen *et al.* 1977), but in contrast to the results of several previous studies from more southern localities reporting a much smaller spatial scale of synchrony: 30–40 km in bank vole populations in southern Norway (Steen *et al.* 1996), *c.* 50 km in grey-sided voles in Hokkaido, Japan (Bjørnstad *et al.* 1999b) and only 4 km (Lambin *et al.* 1998) or 8–10 km (MacKinnon *et al.* 2001) in Scottish field voles. It should be noted that these estimates of spatial synchrony were obtained with somewhat different methods from those used here and were based on data from very different spatial scales.

There are three main mechanisms that have been proposed to explain spatial synchrony in animal population fluctuations in general (Bjørnstad *et al.* 1999a). The first one, operating usually at the smallest scale, is dispersal of the focal organism itself (here voles). The second mechanism consists of community processes such as predation, operating at an intermediate scale if predators (or parasites) are more mobile than the focal species. The third mechanism includes density-independent processes such as climatic perturbations, which are capable of causing large-scale synchrony in conspecific populations with similar structure of density dependence. This process is known as the Moran effect (Royama 1992).

Predation by nomadic avian predators has been proposed to be the main factor leading to geographical synchrony of vole populations in Fennoscandia (Ydenberg 1987; Korpimäki & Norrdahl 1989b; Ims & Steen 1990). There is also some experimental evidence for this hypothesis (Norrdahl & Korpimäki 1996; Ims & Andreassen 2000). The small-scale synchrony observed in the field vole populations in Scotland is likely to be the result of predation by resident predators, such as weasels, and/or dispersal of field voles (Lambin *et al.* 1998; MacKinnon *et al.* 2001). For Hokkaido, Bjørnstad *et al.* (1999b) concluded that the grey-sided

vole populations were synchronized by predators, because the observed spatial synchrony of populations was so large that it could not be attributed to dispersal by voles only.

What might be the most likely explanation of the spatially correlated vole population fluctuations in Finland? The current study on avian predators cannot reveal the causes of the observed geographical patterns, but the observation of synchrony over very large areas suggests some explanations are more likely than others. Interestingly, the scale of synchrony (500–600 km) is about the same within which young and adult female Tengmalm's owl have been reported to move between birth site and first breeding site and between successive breeding attempts (Korpimäki *et al.* 1987). Therefore, nomadic avian predators can operate as synchronizing agents at the scale that was detected in this study, although it is also possible that different synchronizing mechanisms act simultaneously but at different scales (Bjørnstad *et al.* 1999a). For voles, we can confidently reject dispersal of voles as an explanation of the large-scale synchrony described in this study. The remaining explanations are the Moran effect and trophic interactions, most likely predation by mobile avian predators. Our data do not reveal anything new about the mechanisms of periodic fluctuations in voles, though we do not exclude the possibility that synchronizing factors may also contribute to the cyclicity itself.

TEMPORAL CHANGES IN VOLE POPULATION DYNAMICS

The recent changes in the type of dynamics of vole populations that have been proposed to have occurred in Finland (e.g. Henttonen 2000; see also changes observed in predatory birds, Laaksonen *et al.* 2002) were not very apparent in our analyses. Results of vole trappings suggest that vole cycles have become more irregular

since 1985 in northern Finland, since 1990 in the north-westernmost part of Finland, and in the late 1990s in southern and central Finland (Henttonen *et al.* 1987; Hanski & Henttonen 1996; Henttonen 2000; Henttonen & Wallgren 2001; Sundell 2003). In this study, the most obvious change was detected for the northernmost part of Finland, where 4-year cycles have been replaced by 5-year cycles. It is possible that the proposed changes in central and southern Fennoscandia are so recent that the data and methods used here are not sufficient to detect them. One indication of increased irregularity in our results is that more squares show spurious periodicity of 7 years in the time period 1987–2000 than in the period 1973–86. We consider the 7-year cycles spurious because no study of voles has suggested the existence of such long cycles in Fennoscandia. The apparent period of 7 years can arise due to truncated peak(s) in 3- or 4-year cyclic dynamics.

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Appendix

Relationship between the number of ringed nestlings of vole-eating avian predators and vole abundance. Significant results are printed in bold (not corrected for multiple comparisons). Data were $\log(x + 1)$-transformed before linear regression analysis. The coordinates of squares are based on the Finnish uniform grid system (see Figs 3–5). The cycle length of the vole populations obtained with coherence analysis and by using autumn abundances is also shown

Square	Previous autumn			Current spring			Cycle length	Period	Reference
	R^2	P	n	R^2	P	n			
Kirkkonummi									
665 : 30	0·072	0·266		0·309	**0·011**				
665 : 35	0·140	0·115	19	0·403	**0·033**	20	**3**	1981–2000	Kimpari Bird Project, unpublished
Sipoo									
670 : 40	0·319	**0·035**	14	0·356	**0·019**	15	**3**	1986–2000	Solonen (2001)
Loppi									
670 : 30	0·286	**0·004**		0·191	**0·020**				
670 : 35	0·229	**0·012**	27	0·292	**0·003**	28	**3**	1973–2000	A. Kaikusalo & H. Henttonen, unpublished
Hauho									
675 : 35	0·139	0·189	14	0·040	0·455	16	5*	1981–1998	A. Kaikusalo & H. Henttonen, unpublished
Heinola									
675 : 45	0·509	**0·004**	14	0·229	0·083	14	**3**	1986–2000	Brommer *et al.* (2002), H. Pietiäinen & J. Brommer, unpublished
Korpilahti									
685 : 40	0·302	**0·018**	18	0·080	0·254	18	**	1979–2000	A. Kaikusalo & H. Henttonen, unpublished
Karvia									
685 : 25	0·005	0·822		0·091	0·273				
690 : 25	0·002	0·896	13	0·000	0·950	15	5*	1985–2000	A. Kaikusalo & H. Henttonen, unpublished
Suupohja									
700 : 25	0·151	0·189	13	0·639	**0·001**	13	**4**	1975–1987	Viitasaari (1988)
Lapua									
700 : 25	0·285	**0·004**	19	0·401	**<0·001**	21	**3**	1980–2000	Korpimäki (1984, 1987), Klemola *et al.* (2000), Laaksonen *et al.* (2002)
Kauhava									
700 : 30	0·265	**0·012**	19	0·440	**<0·001**	21	**3**	1980–2000	Korpimäki (1984, 1987), Klemola *et al.* (2000), Laaksonen *et al.* (2002)
Koli									
700 : 60	0·016	0·691	12	0·628	**0·001**	14	4*	1987–2000	A. Kaikusalo & H. Henttonen, unpublished
Sotkamo									
705 : 55	0·056	0·244		0·280	**0·004**				
710 : 55	0·083	0·153	26	0·372	**0·001**	28	**4**	1973–2000	A. Kaikusalo & H. Henttonen, unpublished
Muhos									
715 : 45	0·236	0·222	8	0·167	0·213	11	3*	1991–2000	A. Kaikusalo & H. Henttonen, unpublished
Kolari									
745 : 35	0·006	0·702	25	0·339	**0·002**	25	5	1973–2000	A. Kaikusalo & H. Henttonen, unpublished
Pallasjärvi***									
755 : 35	0·133	**0·023**	28	0·209	0·057	28	**5**	1973–2000	Henttonen (2000), H. Henttonen, unpublished
Kilpisjärvi									
765 : 25	0·186	**0·031**	25	0·793	**0·003**	8	5	1973–2000	A. Kaikusalo & H. Henttonen, unpublished

*Analysis on cycle length is based on the spring abundances of voles.
**Analyses on cycle lengths were not performed owing to gaps in the time series.
***Only bank voles are included in vole abundances.