SYNCHRONY AND SCALING IN DYNAMICS OF VOLES AND MICE IN NORTHERN JAPAN

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Abstract. One hundred and seventy-six time series of the Japanese wood mouse (*Apodemus speciosus*) and 185 time series of the grey-sided vole (*Clethrionomys rufocanus*) spanning 31 years (1962–1992) were studied with respect to synchrony and spatial correlation in population dynamics. The time series were collected at fixed sites as part of the rodent census program of the Japanese Forestry Agency. The survey locations cover a region of 115 by 270 km in northern Hokkaido, Japan. The average correlation between the time series was 0.34 ($CI_{95\%}$ = [0.31, 0.36]) for the grey-sided vole and 0.16 ($CI_{95\%}$ = [0.13, 0.18]) for the Japanese wood mouse. This average correlation was decomposed spatially using spatial autocorrelation techniques and the nonparametric covariance function. The lower region-wide correlation in the latter species was found to be due to the spatial covariance dropping more rapidly with distance. The spatial scale of the dynamics was measured by the L_0 correlation length (the distance at which the covariance is equal to that between two randomly chosen sites within the region). This distance was estimated to be ~50 km for the grey-sided vole and 20–30 km for the Japanese wood mouse. The L_0 correlation length was linked to the scaling of the underlying ecological processes through a simple epiphenomenological model motivated by diffusion theory (the exponential covariance model). A review of the ecology of the rodent species indicates that the spatial scale of the pattern of fluctuation of the grey-sided vole is more extensive than can be accounted for by a process of dispersal of voles. Predator movement and regulation of the vole by predators are possible causes of the pattern of spatial covariance. The Japanese wood mouse has a scale of dynamics slightly larger than what may be accounted for by the movement of individuals. This species constitutes a negligible part of predators' diet. Food resource dynamics may be an important regulatory factor and a source of spatial covariance. We interpret the results as indicating that the natural scales of regulation are species specific and can be large relative to the scale of local populations.

Key words: Apodemus speciosus; *bootstrapping;* Clethrionomys rufocanus; *Hokkaido; nonparametric covariance function; rodents; scale of regulation; spatial correlogram.*

INTRODUCTION

An isolated population in a homogenous environment will have a spatial scale of dynamics determined by its movement pattern (de Roos et al. 1991, Holmes et al. 1994, Molofsky 1994, Neubert et al. 1995). In its simplest form with diffusive movement, covariance between samples will decay exponentially or somewhat faster than exponentially with spatial distance. The rate of decay is proportional to the average movement distance (see, for example, Okubo 1980, Sokal and Wartenberg 1983, Lande 1991, Turchin and Thoeny 1993, Myers et al. 1995, 1997). For a wide range of taxa it has been demonstrated that the dynamics covary across much larger regions than the scale of the local population (Moran 1953, Myrberget 1973, Smith 1983, Ydenberg 1987, Myers 1988, Shepherd et al. 1988, Barbour 1990, Pollard 1991, Hanski and Woiwod 1993, Sinclair et al. 1993, Swetnam and Lynch 1993, Myers and Rothman 1995, Ranta et al. 1995*a*, Steen et al. 1996, Sutcliffe et al. 1996). It appears that the demography of many natural populations are regionalized (sensu Myers and Rothman 1995).

Here we address the issue of spatial scaling of population dynamics of two sympatric rodent species in Hokkaido, Japan: the grey-sided vole (*Clethrionomys rufocanus* [Sundevall 1846]) and the Japanese wood mouse (*Apodemus speciosus* [Temminck 1844]). Building on Bjørnstad and Falck (1997) we introduce a method to estimate the spatial covariance function and a measure of the scale of the spatial pattern of dynamics. We apply the method to the data in order to demonstrate that their natural scalings are consistently and significantly different. A possible angle from which to in-

terpret spatial scaling in natural populations is through a community perspective on population dynamics (e.g., Hansson and Henttonen 1988). As an integrated part of this paper we therefore provide a review of the population and community ecology of the two Japanese small rodent species.

A population's dynamics are determined by three classes of processes: those of reproduction, mortality, and movement. Several factors are known to affect each of these classes. Focusing on small rodents, these are known to include competition (e.g., Batzli et al. 1977, Boonstra 1978, Rodd and Boonstra 1988, Löfgren 1995a, b), predation (e.g., Lin and Batzli 1995, Norrdahl and Korpimäki 1995, Reid et al. 1995, Steen 1995), climatic forces (e.g., Pucek et al. 1993), and habitat characteristics such as food availability and vegetation (e.g., Cole and Batzli 1978, 1979, Alibhai 1985, Hansson 1985a, Saitoh 1989, Montgomery et al. 1991, Selås 1997). Each of the influential factors is likely to be operating across a finite spatial domain (Addicott et al. 1987, Wiens 1989, Levin 1992, Dutilleul and Legendre 1993, Holt 1994). With a multitude of influential factors, there may be no single scale of regulation; the spatial variability may thus be a continuous function of scale (e.g., Allen and Starr 1982, O'Neill et al. 1991). Some features of the dynamics (those associated with, say, mortality or predation) may exhibit a distinct scale of determination, and others (those associated with, say, migration or extinction) may exhibit another (see, for example, Moloney et al. 1992, Thomson et al. 1996). However, when some process is more influential than the others are, population dynamics may be conjectured to possess a "characteristic spatial scale" of regulation (Jumars 1976, Carpenter and Chaney 1983, Addicott et al. 1987, Morris 1987, Carlile et al. 1989, de Roos et al. 1991). Several constraints on the demography may make one set of processes dominant, and this set may determine the global scale of regulation. For instance, strong intraspecific interactions may render mortality caused by predation to be compensatory (Errington 1946), and in that way cause predation to be unimportant as a global regulatory factor. In case such a regulation will take place at the scale of the local population. Alternatively, predation may exert such strong disturbance on the populations that all regulation will be due to the trophic interactions (cf. Huston 1979, Sousa 1984), and regulation will be at the scale of the movement of predators.

A characteristic spatial scale implies similarity of the dynamics within the area of influence. More distant populations, in contrast, are likely to be no more similar than that expected by chance alone in the region. In this way, it is useful to distinguish region-wide similarity and local above-average similarity (e.g., Sutcliffe et al. 1996). The region-wide covariance is typically determined by wide-scale climatic factors or common underlying seasonal cycles (Royama 1992, Ranta et al. 1995b). The local covariance, in contrast, may well be induced by movement and local interactions (de Roos et al. 1991, Holmes et al. 1994, Molofsky 1994, Neubert et al. 1995). Using a perspective of spatial covariance, the scale of the spatial pattern may be defined as the distance at which the covariance between two sites is no greater than two randomly chosen sites within the region. This distance is estimated by the L_0 correlation length (see Bayly et al. 1993).

MATERIALS AND METHODS

The data

The Forestry Agency of Japan (FAJ) standardized their census program on woodland rodents in 1954. The focal species of the census is the grey-sided vole, *C. rufocanus*, a species that may periodically reach pest-like abundance in Japanese forests (Tanaka 1957, Ota 1984, Saitoh 1987, Stenseth et al. 1996). Data on one congener of the grey-sided vole (*C. rutilus*) and two murine rodents (*Apodemus speciosus* and *A. argenteus*) is also routinely collected, as all four species are sympatric. A large proportion of northern Hokkaido is covered by the forest that comprises the main habitats of these rodents (Fig. 1). The forests managed by FAJ form relatively large continuous areas surrounded by private forest plantations, cultivated areas (pastures and farms), and fields. The continuous forested areas are divided into ranger offices (Fig. 1). Rodents may readily move through the forested areas. The grey-sided vole is a habitat generalist that is also found in nonforested areas. The wood mice are generally confined to forests.

Since the initiation of the survey, the personnel of FAJ have conducted snap-trapping censuses three times every year (spring, summer, autumn) (although the autumn records for *Apodemus* are missing for 1970 and 1974) in numerous fixed sites across the whole of Hokkaido (the northernmost island of Japan; 41°24′–45°31′ N, 139°46′–145°49′ E). The protocol has been identical throughout (0.5 ha monitored using either 150 or 250 trap nights per census period; standardized according to Stenseth et al. [1996] and Saitoh et al. [1997]). The most complete data set stems from the Asahikawa region of northern Hokkaido (42°50′–45°31′ N, 141°30′–143°15′ E) (Fig. 1). Each of the 151 ranger offices of the FAJ in northern Hokkaido was asked to census at least one stand of natural, indigenous forest and at least one stand of man-made forest plantation. Whenever any ranger office monitored more than one stand of each in a year, we used average values. The target distance between the two stands was set to be ~0.5 km. Some ranger offices did not complete the survey in all years.

We analyzed the time series that are complete (except for the 1970 and 1974 gap) from the natural forest stands and forest plantations in the 31-yr period spanning 1962–1992. We concentrated on the autumn count (late September/early October for which nearly all in-
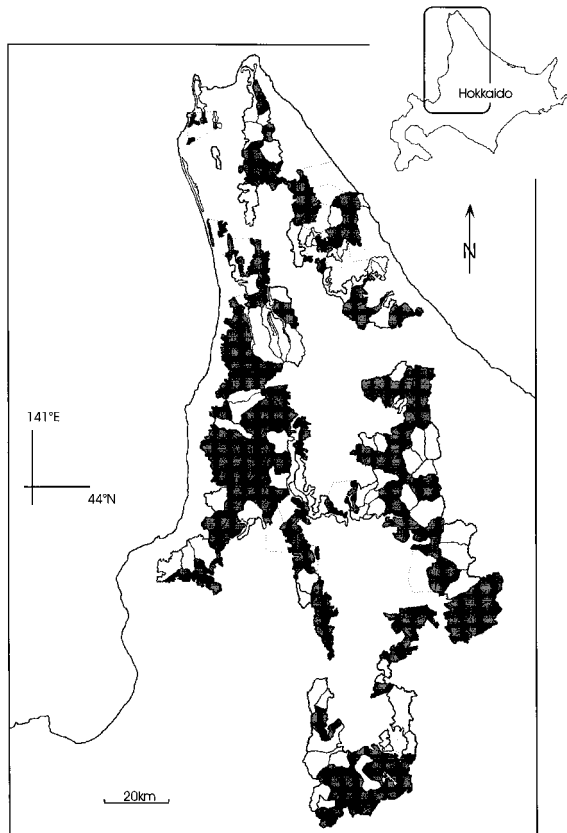
FIG. 1.   Map of the sample stations in the Asahikawa region of northern Hokkaido. The sampling stations are marked by shaded regions. Each station represents four time series (except in the few cases where some data are missing): two of the grey-sided vole (*C. rufocanus*) (one from a natural forest and one from an adjacent forest plantation) and two of the Japanese wood mouse (*A. speciosus*). The series span the period 1962–1992 and are complete for the vole; data are missing for the years 1970 and 1974 for the wood mouse. The enclosed areas on the background map show the forest areas managed by the Japanese Forest Agency. The boundaries identify the local administrative structures (the ranger offices) responsible for the sampling. The forests of adjacent ranger offices are continuous, and rodents can move between them. Nonenclosed areas represent private forests (plantations), towns, cultivated areas (pasture or farms), or fields, on which the grey-sided vole is usually uncommon and the wood mouse is only transient. The grey-sided vole may, however, be quite common in plantations and fields covered by bamboo grass.

dividuals are year-born; Fujimaki 1969, Abe 1976*a*, *b*, Kuwahata 1984) of two species: the grey-sided vole and the Japanese wood mouse (*Apodemus speciosus*). In this way, the data sets are comprised of 185 series and 109 713 trapped individuals of the former species (58.6% of total catch), and 176 series and 31 319 individuals of the latter (16.3% of total catch) (Fig. 2). The lower number of series of the latter species is caused by underreporting due to the focus on the grey-sided vole as a pest species. Ninety-seven of the ranger offices thus contributed to the data set (shaded areas

in Fig. 1) and these offices provided 175 time series that are complete for both the vole and the wood mouse.

The average counts in the time series were 5.6 (SD = 2.3, range = [2.6, 16.9]) and 1.7 (SD = 0.9, range = [0.3, 5.4]) for the vole and the wood mouse, respectively (Fig. 3). There was a negative correlation between the mean numbers of the two species (Spearman rank correlation = −0.45; based on the averages of the 175 parallel series). This is most likely to reflect divergence in habitat preference and not competitive displacement.

For the analyses of scale of population dynamics we investigated three descriptors of the population dynamics. The most obvious is the time series themselves (measured on a logarithmic scale, with a constant of unity added prior to transformation), LN (=ln(Count + 1); see Stenseth et al. 1996, Saitoh et al. 1997). The variability of each population time series was measured by the S-index (=SD[$\log_{10}$(Count + 1)]) favored in small rodent ecology (e.g., Stenseth and Framstad 1980, Ostfeld 1988, Saitoh et al. 1997). Finally, the sequence of annual rates of change (the sequences of first differenced log-abundances), R (R_t = ln(Count$_t$ + 1) − ln(Count$_{t-1}$ + 1)) was calculated (e.g., Hanski and Woiwod 1993, Steen et al. 1996, Sutcliffe et al. 1996). Each office is, thus, described by 31, 1, and 30 numbers, repectively, for these three descriptors.

The distances between the range offices constrain the spatial scope of the analysis. The distance to the nearest neighbor defines the grain (sensu Wiens 1989) and the distance to the "farthest neighbor" the spatial extent. The distance to the nearest neighboring sampling station is ~500 m because this was the target distance between adjacent natural forest and forest plantation trap stations. The average distance to the second nearest neighbor (the trapping stations of the nearest ranger office) is 8.2 km (minimum 3.3 km, maximum 23.5
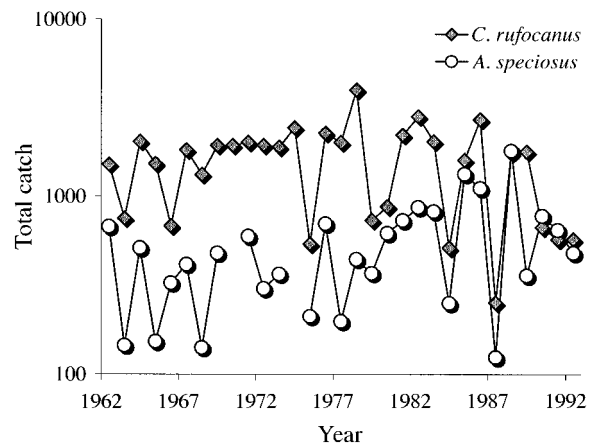

FIG. 2.   The number of individuals of the grey-sided vole (*C. rufocanus*) and the Japanese wood mouse (*A. speciosus*) captured in each year. The numbers represent the sum across all the time series (185 for the vole and 176 for the wood mouse).

FIG. 3. The mean number of individuals in each ranger office. The counts are averaged across the series of natural forests and forest plantations. Symbols represent deviations from the grand mean (on a logarithmic scale). Open squares represent values that are lower than the grand mean, and filled circles represent values that are greater. The size of the symbols represents the absolute deviation from the mean (note the logarithmic scale). (A) The grey-sided vole, *C. rufocanus.* (B) The Japanese wood mouse, *A. speciosus.*
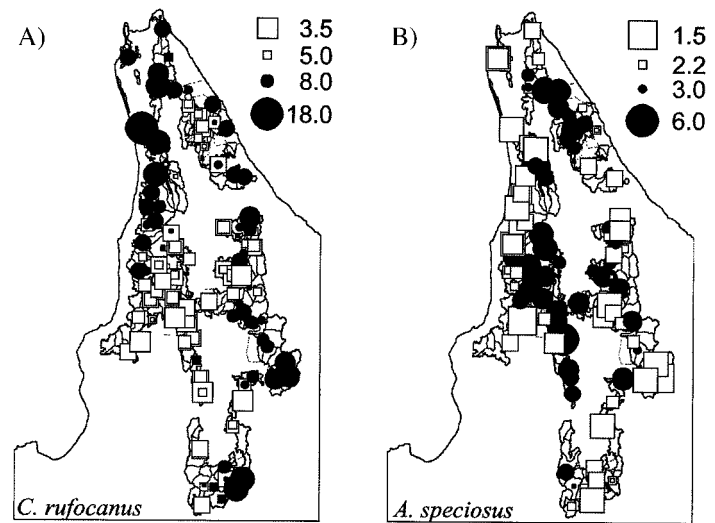
km). The average distance to the most distant population is 189.6 km (minimum 140.2 km, maximum 272.6 km). The average distance between all sampling stations is 85.5 km.

The species

Here, we review relevant information on reproductive and social biology of the two species, their diet, habitat preferences, enemies, competitors, and population fluctuations as needed to interpret the spatial dynamics. The review will be relatively comprehensive because most of the original sources are in Japanese.

Intraspecific processes.—The grey-sided vole (*C. rufocanus*) is a small-sized (30–40 g), short-tailed (~40% of body length [head and body]) microtine rodent that has a Palearctic distribution. The Japanese wood mouse (*A. speciosus*) is an endemic species to Japan. It is larger (40–60 g) than the grey-sided vole. Considering that it is a murine rodent, its tail is relatively short (75%–100% of body length). The Japanese wood mouse mainly uses the forest floor, though it may climb in the vegetation. The grey-sided vole is the most strictly ground-dwelling among rodent species in Hokkaido (Abe 1986, Abe et al. 1989).

The main reproductive season in both species is from April/May to September/October in Hokkaido and the litter size is typically 4–7 individuals in both species (Murakami 1974, Fujimaki 1975, Kondo and Abe 1978, Kuwahata 1984, Nakata 1984, 1989). Some subnivean reproduction has been recorded in the vole (Nakata 1989, Saitoh 1991), but not in the wood mouse. Although the Japanese wood mouse does not hibernate, it spends most of its time in the nest during winter (Kondo 1980). Generally speaking, the lifetime of free-ranging individuals is <1 yr (Fujimaki 1969, Abe 1976a, b, Fujimaki et al. 1976, Kuwahata 1984). Maturation may commence at 30 d under benign conditions for the grey-sided vole (Abe 1968, 1976a) and at 60 d

for the Japanese wood mouse (Kondo and Abe 1978, Ota 1984). Density-dependent reduction in reproduction is frequently demonstrated in the grey-sided vole in Hokkaido (Abe 1976a, Saitoh 1981, 1990, Kawata 1987, Nakata 1989), and is believed to occur in the Japanese wood mouse (Kondo and Abe 1978).

Female grey-sided voles defend exclusive territories with size ranging from 200 to 600 m² (Saitoh 1991). Males have overlapping home ranges about twice the size of those of females (Ota 1984). The spatial organization of the Japanese wood mouse appears similar to that of the vole but with larger spatial requirements (home range of males: 800–2000 m²; females: 600–1000 m²) (Kondo 1982, Oka 1992). Dispersal is male-biased in small rodents and associated with the late juvenile stages (e.g., Stenseth and Lidicker 1992). In the grey-sided vole the main migratory event is related to the onset of maturation (Saitoh 1983, 1995). Typical dispersal distances may be in the order of 100 m for males and 0–50 m for females (Saitoh 1995). These estimates may be biased downwards, though, due to constraints imposed by the extent of the study; dispersal distances in the order of 1 km have been reported for various European microtines (Stoddart 1970, Szacki et al. 1993, Steen 1994). Even longer distances, up to 2–4 km, have been reported for European *Apodemus* spp. (Wolton and Flowerdew 1985, Szacki et al. 1993).

Habitat and diet.—The grey-side vole and the Japanese wood mouse live in sympatry in mixed broad-leaved and coniferous forest and forest plantations in Hokkaido (Ota 1984, Abe 1986). The vole is a habitat generalist that prefers forests but also inhabits fields and pastures. The wood mouse is more strongly confined to woody habitats and prefers natural forest stands. A dominant understory plant in the forests is the bamboo grass (*Sasa* spp.) (Wada 1993). Snow cover is abundant during the four months from mid-December to mid-April in northern Hokkaido (SDMO 1991,

1992), whereas cover and density of understory vegetation is high from mid-June to late November (Yoneda 1983).

The main dietary items are seeds, green plants, and invertebrates for these small rodents. While the grey-sided vole in Hokkaido is predominantly folivorous (80% occurrence in stomach analyses) and subdominantly granivorous (15%), the Japanese wood mouse is predominantly granivorous (45%) and insectivorous (45%) (Ota et al. 1959, Ota 1984, see also Hansson 1985b). Although sympatric, there is no published evidence of competition between the grey-sided vole and the Japanese wood mouse (Abe 1986).

Abundance of forbs and leaves is likely to vary at a local (microhabitat) scale (Nakata 1995). This resource is not strongly depleted through rodent foraging (Hansson 1985b). The availability of seeds, in contrast, varies at a broader scale in the form of masting (Tanaka 1956, 1957, Janzen 1976, Wada 1993). The bamboo grass (*Sasa* spp.) as well as many of the tree species (such as *Quercus* and *Acer*) have mast years (Wada 1993). Occasionally the bamboo grass have region-wide masting (Numata 1970, Janzen 1976), but the usual pattern of seed masting is at the scale of the forest stand (i.e., in the order of a few kilometers; Tanaka 1956, H. Abe, *personal communication*). Seeds are known to be depleted by rodents (Hansson 1985b).

Predators.—Five mustelid species are the main predators of small rodents in Hokkaido (in order of importance): *Mustela nivalis, M. itatsi, M. vison, Martes zibellina,* and *Mustela erminea.* In addition, the red fox (*Vulpes vulpes*), two owls (*Strix uralensis* and *Asio otus*), and four species of snakes (*Elaphe climacophora, E. conspicillata,* and *E. quadrivirgata, Agkistrodon blombhoffii*) are important predators of rodents. Where known, the proportion of the vole in the predators' diets is much higher than that of the Japanese wood mouse. The reported percentages of occurrence in droppings or stomach contents of the two are: 30 vs. <1%, respectively, in *M. vison* (Uraguchi et al. 1987), 30–60% vs. 1% in *V. vulpes* (Abe 1975, Misawa 1979, Kondo et al. 1986), 25–50 vs. 5–25% in *S. uralensis* (Matsuoka 1977, Yoneda et al. 1979) and 98–100 vs. 1–4% in *A. otus* (Matsuoka 1974). Analogously, *M. itatsi* has been reported to have small rodents as a major food item (50–60%) in Hokkaido, where *C. rufocanus* is present (Inukai 1934, 1935), whereas rodents comprise <15% of diet on the more southern islands where *C. rufocanus* is not present (Yukawa 1968). There is little data on the mortality factors of rodents themselves from Hokkaido. Yoneda (1979) calculated that mammalian predators accounted for 30–65% of deaths of the grey-sided vole. This agrees well with more detailed studies of *Clethrionomys* in northern Europe (Norrdahl and Korpimäki 1995). Thus, the grey-sided vole appears to be tightly interacting with predators, whereas the Japanese wood mouse does not. The conspicuously lower vulnerability of the wood mouse to predation may be due to its greater mobility.

Home ranges of the predators are generally much larger than those of the rodents. Typical home-range size of *V. vulpes* in Japan is estimated at 500–800 ha (Misawa et al. 1987, Cavallini 1992, Takeuchi and Koganezawa 1992). Home range sizes of mustelids have not been reported from Hokkaido; studies from elsewhere report home range sizes of 1–200 ha (King 1983, Sheffield and King 1994). The home range of *A. otus* is 40–60 ha (range 4–400 ha) in North America (Belthoff et al. 1993). Home ranges of *S. uralensis* are likely to be of the same order of magnitude.

The median juvenile dispersal of foxes in American woodlands is 25 km for males and 10 km for females (range 1–300 km) (Allen and Sargeant 1993). Typical dispersal distances of mustelids appear to be 2–10 km (range 0–35 km) (King 1983, Sheffield and King 1994). We have no data on dispersal distances of the two owl species.

Population fluctuations.—The grey-sided vole, but not the Japanese wood mouse, has regularly been reported to reach pest-like abundance in larch (*Larix leptolepis*) and todo-fir (*Abies sachalinensis*) plantations (Tanaka 1956, 1957, Ota 1984, Stenseth et al. 1996). Bjørnstad et al. (1996), Stenseth et al. (1996), and Saitoh et al. (1997) have studied the population dynamics of the grey-sided vole from northern Hokkaido (based on a subset of the present data). They demonstrate that the abundance of the vole is governed by both direct and delayed density dependence (Stenseth et al. 1996, Saitoh et al. 1997). No similar pattern has been reported for *Apodemus.* The European *Apodemus* species appear to have dynamics dominated by irregular outbreaks related to years of abundant seed production (Flowerdew 1985). Saitoh et al. (1999) demonstrate that there is essentially no delayed density dependence in the time series of the Japanese wood mouse from Hokkaido.

A synoptic summary.—Current research indicates that the grey-sided vole and the Japanese wood mouse have similar reproductive biologies in Hokkaido, but the wood mouse is more mobile (movement at a scale of 1–2 km) than the vole (movement at a scale of <1 km). The diet of the wood mouse is comprised of depletable resources (notably seeds) that vary at the scale of the forest stand (scale of a few kilometers). The diet of the vole is less likely to be depleted and can vary locally in space (microhabitat scale). The grey-sided vole is a dominant prey for many predators, while the wood mouse is not. Typical movement distances of the predators are at scales up to 25 km.

Statistical analyses

Spatial scaling and synchrony may be studied through the pattern of spatial covariance in dynamics. The challenge is to find a method that enables statistical inference regarding the following questions: (1) Do populations in close spatial proximity covary in dy-

namics? (2) At what distance does the covariance among populations drop to the region-wide average? (3) Are the spatial covariance functions of alternative demographic descriptors different in a statistical sense? We propose that a suitable tool for making this inference is the spline correlogram (Bjørnstad and Falck 1997), a modification of the nonparametric covariance function developed by Hall and coworkers (Hall and Patil 1994, Hall et al. 1994).

The region-wide correlation is calculated as the average Spearman rank correlation between the log-transformed time series (or their first differences) for each species (e.g., Hanski and Woiwod 1993, Sutcliffe et al. 1996). A bootstrap confidence interval for these averages is provided by sampling with replacement among the stations (deleting cross-correlations arising from comparing a station with itself). One thousand bootstrap iterations are employed, and the confidence intervals are erected using the percentile method (Efron and Tibshirani 1993). The correlation between adjacent stands of natural forest and forest plantations is quantified in the same way, based on the ranger offices that provide complete records of both (88 ranger offices for the vole and 84 offices for the wood mouse).

To investigate how the covariance in the different population dynamic descriptors is a function of spatial distance (δ) we use spatial autocorrelation techniques (Sokal and Oden 1978, Sokal 1979, Sokal and Wartenberg 1983, Oden 1984). We measure the geographic distance, δ_{ij}, between populations i and j by the metric Euclidean distance between their respective x- and y-coordinates:

$$\delta_{ij} = \delta_{ji} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}. \qquad (1)$$

Among n populations there are $n(n - 1)/2$ unique distances corresponding to the upper (or lower) triangle of the distance matrix (that is, δ_{ij} for $i = 1, \ldots, n, j = i + 1, \ldots, n$).

The corresponding covariance between the samples z_i and z_j at these sites is quantified by

$$\text{Cov}(z_i, z_j) = (z_i - \bar{z})(z_j - \bar{z}) \qquad (2a)$$

where $\bar{z} = (1/n) \sum_{l=1}^{n} z_l$. The sample autocorrelation, ρ_{ij}, is

$$\hat{\rho}(z_i, z_j) = \hat{\rho}_{ij} = \frac{(z_i - \bar{z})(z_j - \bar{z})}{\frac{1}{n} \sum_{l=1}^{n} (z_l - \bar{z})^2}. \qquad (2b)$$

In the case where z is multivariate (a time series recorded at each location), the product in Eq. 2a, b is the vector product (Oden and Sokal 1986, Bjørnstad and Falck 1997). In the cases where z is univariate (just one observation at each location) the product is the scalar product.

The spatial correlogram is calculated as the k step function, $C_k(d_k)$, obtained through local averages of ρ around some focal distance d:

$$C_k(d_k) = \text{mean}_k(\hat{\rho}_{ij} \mid L_k < \delta_{ij} \leq U_k) \qquad (3)$$

where L_k and U_k signify the lower and upper tolerance limit (usually set such that each pairwise similarity is only used once) around the k focal distances (see, for example, Journel and Huijbregts 1978, Deutsch and Journel 1992, Bjørnstad and Falck 1997). Note that Eq. 3 is usually called the Mantel correlogram when z is multivariate (Oden and Sokal 1986, Legendre and Fortin 1989, Legendre 1993, Bjørnstad and Falck 1997).

The correlogram is frequently employed to investigate pattern and spatial scaling in ecological data (Legendre and Troussellier 1988, Simard and Savard 1990, Moloney et al. 1992, Brown et al. 1995, Steen et al. 1996, Thomson et al. 1996) and population genetic studies (reviewed in Epperson 1993). The scale of the pattern may be quantified by the x-intercept (Sokal and Wartenberg 1983, Legendre and Fortin 1989, Epperson 1990, 1993, Bjørnstad and Falck 1997) defined as the shortest distance d_0 at which the correlogram, $C(d)$, crosses the x-axis. Because the measure z is centered by the sample mean (Eq. 2b) prior to calculations, d_0 will estimate the average distance at which the similarity between any two populations is equal to the region-wide similarity. It thus provides an estimate of the L_0 correlation length (e.g., Bayly et al. 1993) although it gives a relatively unstable estimate (Sokal and Wartenberg 1983, Bjørnstad and Falck 1997). We calculate correlograms with a distance class width of 12 km (giving 24 distinct distance classes) for all three dynamic descriptors. Complete spatial randomness implies that the correlogram is nonsignificantly different from zero for all distance classes (see, for example, Oden 1984).

The correlogram gives an estimate of the underlying spatial covariance function in the form of a step function. Furthermore, it does not provide a confidence region for the spatial covariance. Thus, it cannot fully address the presence of statistical difference between the correlograms of different descriptors or species. To alleviate this, we employ the spline correlogram (Bjørnstad and Falck 1997), which is an adaptation of the nonparametric covariance function of Hall and coworkers (Hall et al. 1994, Hall and Patil 1994). This method provides a direct estimate of the covariance function itself. A bootstrap algorithm has been developed to provide a confidence envelope for the function (Hall and Patil 1994, Bjørnstad and Falck 1997). Hall and Patil's (1994: Eq. 2.1) kernel estimator of the relationship between the autocorrelation and the geographic distance is given by

$$\tilde{\rho}(\delta) = \frac{\sum_{i=1}^{n} \sum_{j=i+1}^{n} K(\delta_{ij}/h)\hat{\rho}_{ij}}{\sum_{i=1}^{n} \sum_{j=i+1}^{n} K(\delta_{ij}/h)} \qquad (4)$$

where K is a kernel function (e.g., Härdle 1990, Hastie and Tibshirani 1990) and $h > 0$ is the bandwidth. The

FIG. 4.   The annual rates of change (the difference in log abundance) in the time series for the four years 1976–1979. Top row: Grey-sided vole (*C. rufocanus*). Bottom row: Japanese wood mouse (*A. speciosus*). Symbols represent negative (□) and positive (●) growth rates. The size of the symbol represents the absolute magnitude of change.

spline correlogram (Bjørnstad and Falck 1997) uses a cubic B-spline as an equivalent kernel smoother (Nychka 1995) because this adapts better to irregularly spaced data than other kernels (see, for example, Jones et al. 1994). The asymptotic kernel function for the cubic B-spline is (Green and Silverman 1994)

$$K(u) = \frac{1}{2}\exp\left(-\frac{|u|}{\sqrt{2}}\right)\sin\left(-\frac{|u|}{\sqrt{2}} + \frac{\pi}{4}\right). \quad (5)$$

The spline correlogram provides a direct estimate of the spatial covariance function, and also a direct estimate of the L_0 correlation length. The local autocorrelation may be measured by the extrapolation of the spline correlogram to $\rho(0)$ (Hall et al. 1994). A detailed development of the spline correlogram is provided by Bjørnstad and Falck (1997). We apply the spline correlogram to the three population dynamic descriptors of the two species (the log-series LN, the annual rate of change R, and the population variability S) using 25 degrees of freedom for the spline (in a loose sense corresponding to 25 distance classes for the spatial correlogram). We use 1000 bootstrap resamples for the confidence intervals. The bootstrap resampling algorithm for the spline correlogram is the same as that

used for the region-wide correlation (i.e., sampling with replacement among the stations prior to calculating δ_{ij} and $\hat{\rho}_{ij}$ and evaluating Eq. 4).

Sampling error may impair or bias comparison of the spatial profiles if the sampling variances differ between the species. The "nugget covariance" measured by $\rho(\delta = 0)$ quantifies the measurement variance (error) (e.g., Cressie 1993:127–135; see also Isaaks and Srivastava 1989). This local autocorrelation, thus, both quantifies whether local structuring is present and the sampling effects. The estimation was conducted using the "blomster algorithm" (Bjørnstad and Falck 1997) coded in S-plus version 3.3 (Statistical Sciences 1995).

RESULTS

The average correlation between the 185 log-transformed series of the grey-sided vole was 0.34 (SD = 0.19, min = −0.37, max = 0.96, CI$_{95\%}$ = [0.31, 0.36]). The corresponding correlation in the annual rates of change (the first differenced series) was 0.36 (SD = 0.20, min = −0.53, max = 0.97, CI$_{95\%}$ = [0.33, 0.38]). Mean correlation between the 180 log-transformed series of the Japanese wood mouse was 0.16 (SD = 0.22, min = −0.68, max = 0.98, CI$_{95\%}$ = [0.13, 0.18]). The
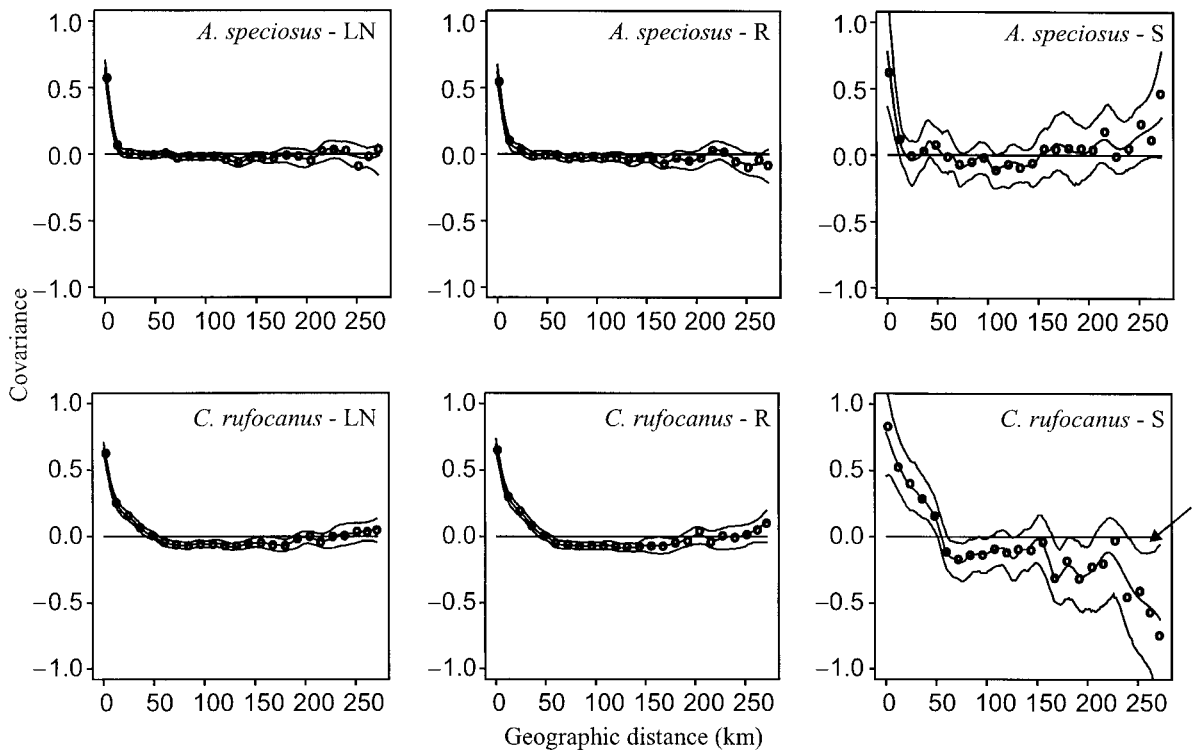
FIG. 5. The nonparametric covariance function of the three population dynamic descriptors for the Japanese wood mouse, *A. speciosus*, and the grey-sided vole, *C. rufocanus*. The abbreviations are as in the text (LN = log-transformed time series; R = the annual population growth; S = the standard deviation of the $\log_{10}$ time series). The *x*-axes represent the geographic distance between the samples (in kilometers), the *y*-axes represent the correlation. The thin lines represent the estimated functions and 95% bootstrap confidence intervals as estimated using spline correlograms with 25 degrees of freedom. The spatial (or Mantel) correlograms based on 12-km distance classes are shown as open circles.

correlation in the rates of change was 0.25 (SD = 0.23, min = −0.61, max = 0.95, $CI_{95\%}$ = [0.21, 0.27]). The confidence intervals for the mean correlation are all strictly positive, indicating that the dynamics of both species are significantly regionalized. The overall level of spatial synchrony is, however, significantly greater in the grey-sided vole. The synchrony may be visualized by plotting the annual rates of change on the map (Fig. 4 shows this for the period 1976–1979 for the

two species). Population growth and decline tend to occur in a similar fashion across large areas.

The mean correlation between populations in adjacent stands of natural forest and forest plantations (separated by ~500 m) was very high in both species. For the log-transformed series of the grey-sided vole it was 0.80 (SD = 0.09, min = 0.49, max = 0.96, $CI_{95\%}$ = [0.79, 0.82]). The corresponding correlation in the annual rates of change was 0.82 (SD = 0.09, min = 0.51,

TABLE 1. The estimates of the *x*-intercept (km) and the local autocorrelation $\rho(\delta = 0)$, with 95% bootstrap confidence intervals (in brackets based on the spline correlogram with 25 degrees of freedom and 1000 bootstrap iterations), for the three demographic descriptors for the grey-sided vole (*Clethrionomys rufocanus*) and the Japanese wood mouse (*Apodemus speciosus*).

Descriptor	*Clethrionomys rufocanus*		*Apodemus speciosus*	
	$\rho(0)$	*x*-intercept (km)	$\rho(0)$	*x*-intercept (km)
LN	0.67	50.7	0.65	31.8
	[0.63, 0.71]	[42.0, 54.7]	[0.59, 0.71]	[14.5, 53.9]
R	0.70	50.6	0.62	31.0
	[0.65, 0.74]	[42.6, 55.5]	[0.56, 0.68]	[22.8, 59.1]
S	0.79	55.1	0.78	18.3
	[0.45, 1]	[50.9, 60.4]	[0.37, 1]	[11.7, 66.9]

Note: The abbreviations are as in the main text (LN = log-transformed time series; R = the annual population growth; S = the standard deviation of the $\log_{10}$ time series).
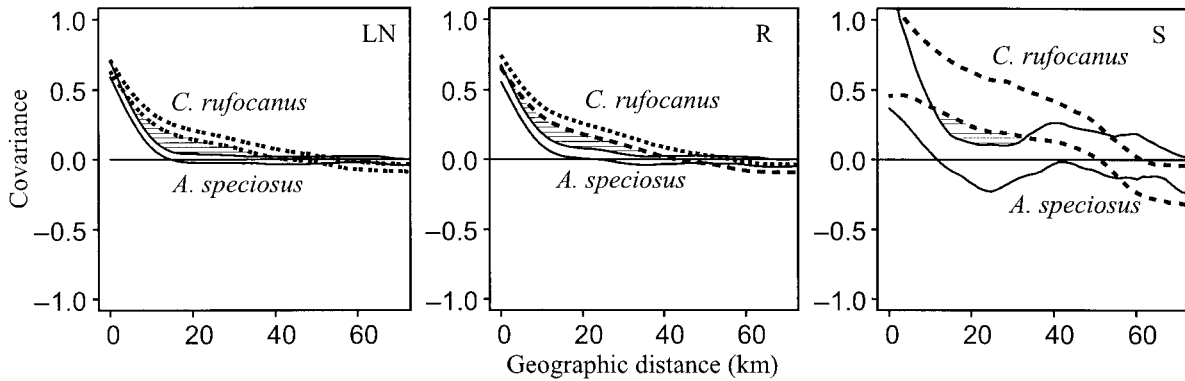
FIG. 6. The 95% confidence envelopes (see Fig. 5) for the spatial covariance function for the grey-sided vole, *C. rufocanus* (dotted lines), and the Japanese wood mouse, *A. speciosus* (black lines), overlaid for distances up to 80 km for the three different descriptors. Significant discrepancies are highlighted by hatching.

max = 0.97, $CI_{95\%}$ = [0.80, 0.84]). For the log-transformed series of the Japanese wood mouse it was 0.76 (SD = 0.12, min = 0.44, max = 0.98, $CI_{95\%}$ = [0.74, 0.79]). The corresponding correlation in the annual rates of change was 0.75 (SD = 0.14, min = 0.25, max = 0.95, $CI_{95\%}$ = [0.71, 0.77]). The mean correlation between a population and its most distant population (on average separated by 190 km) was positive in both species. For the log-transformed series of the grey-sided vole it was 0.35 (SD = 0.16, $CI_{95\%}$ = [0.33, 0.37]), and for the Japanese wood mouse it was 0.08 (SD = 0.20, $CI_{95\%}$ = [0.05, 0.11]).

Despite the negative correlation in mean abundance between the two species (Fig. 3 and above), there was significantly positive correlation in the annual rates of change in sympatric populations of the two species (mean correlation = 0.32; SD = 0.21, min = −0.34, max = 0.81, $CI_{95\%}$ = [0.29, 0.35]). The difference in mean abundance is therefore likely to reflect differences in habitat preference rather than competitive displacement.

The spatial and the spline correlograms estimate how the covariance is a function of spatial distance (Fig. 5). Significant local positive autocorrelations are apparent for all descriptors for both species (Table 1). None of the estimates of local autocorrelation are significantly different from the others, indicating that the sampling variability is comparable for the two species. The spatial scaling is, however, different for the two species. The Japanese wood mouse has 20–30 km L_0 correlation length (*x*-intercept), whereas the correlation length is 50–55 km in the grey-sided vole (Table 1). The nonparametric covariance functions for the three descriptors of each species (with confidence envelopes) are depicted in Fig. 5. The profiles for the log-transformed time series (LN) and the annual growth rates (R) exhibit a characteristic decrease of similarity (spatial autocorrelation) with distance. No strong negative autocorrelation is evident, and significantly positive autocorrelation is found at short spatial distances. The

functions for the population variability (S) exhibit a similar degree of local autocorrelation, and a similar correlation length (Table 1). However, for the grey-sided vole there is a conspicuous and significant dissimilarity at large distances. This is indicative of clinal variation.

The more narrow correlation length in the dynamics of the Japanese wood mouse is evident from the superimposed confidence intervals for the covariance functions (Fig. 6). While there is no significant difference between the different descriptors for each individual species, there are significant differences between the species. The spatial covariance drops significantly more quickly for the dynamics of the Japanese wood mouse. Thus, the significantly lower region-wide correlation in this species is due to correlation dropping more quickly with distance, and not due to the local correlation being lower or the sampling variance greater.

The results may be summarized as follows: both species exhibit significantly regionalized dynamics. The correlation is very high between adjacent populations. The L_0 correlation length was between 20 and 30 km for the dynamics of the Japanese wood mouse and ~50 km for the grey-sided vole (Table 1, Fig. 5). The spatial covariance drops significantly more quickly in the former species (Fig. 6). All available evidence thus suggests that the spatial scale of the population dynamics of the grey-sided vole is significantly larger than that of the Japanese wood mouse in northern Hokkaido.

DISCUSSION

Region-wide synchrony in dynamics is common in fluctuating populations (Smith 1983, Ydenberg 1987, Myers 1988, Shepherd et al. 1988, Barbour 1990, Pollard 1991, Hanski and Woiwod 1993, Sinclair et al. 1993, Swetnam and Lynch 1993, Ranta et al. 1995*a*, Sutcliffe et al. 1996) and may be caused by a variety of factors (Ims and Steen 1990, Royama 1992, Ranta et al. 1995*b*). Extensive (global) dispersal may serve

to synchronize the dynamics across an entire region. The restricted dispersal capacity and the positive correlation in the dynamics of the two rodent species indicate that an external source of synchronization may also be involved. Synchrony in Scandinavian rodents has been linked to the action of nomadic avian predators (Ydenberg 1987, Ims and Steen 1990). Such predators are, however, scarce in Hokkaido (Henttonen et al. 1992). Large-scale climatic variation affecting the demography directly (Royama 1992, Sinclair et al. 1993, Ranta et al. 1995*a*, *b*) or indirectly through synchronization of vegetation and resources (Selås 1997) are likely sources of this synchrony.

Spatial covariance above the region-wide synchrony may arise in a homogenous environment as a consequence of ecological processes that has a finite spatial extent (de Roos et al. 1991, Holmes et al. 1994, Neubert et al. 1995). Limited dispersal of individuals, their resource, or their enemies are important factors inducing spatial pattern. The scale of the pattern will be determined by the movement ability of the interacting organisms. The *x*-intercept of the spline correlogram is an estimate of the L_0 correlation length, and measures the spatial distance for which the covariance between populations is above the region-wide average synchrony. It may, hence, be seen as an estimate of the scale of the spatial pattern (see, for example, Sokal and Wartenberg 1983, Epperson 1993, Bjørnstad and Falck 1997). It should be noted that for systems with long correlation lengths, there will be a negative bias in the estimate (sometimes called the ''volume effect,'' Bayly et al. 1993). However, as long as the spatial design is the same, biases will be similar so that comparative studies should be robust.

The local scale of regulation may be defined as the area across which covariance is induced through diffusion of individuals (e.g., Kawata 1997). The scale of regulation, is likely to be smaller than the L_0 correlation length due to the diffusive nature of ecological interactions. The ecological theory pertaining to the relation between spatial covariance and spatial processes is not well developed (compared to, for instance, the analogous theory for temporal covariance and dynamic processes). The following arguments should therefore, at best, be seen as a rough approximation to bridge the gap between the scale of the pattern and the scale of the processes. Considering individual movement or dispersal (of predators, prey, diseases or seeds) as the most important spatial process, it is natural to use some simple diffusive models as a yardstick (e.g., Bartlett 1975, Okubo 1980, Turchin and Thoeny 1993, Holmes et al. 1994). Such models lead to a spatial covariance that decreases approximately exponentially with distance (see Bartlett 1975: chapter 3, Okubo 1980: chapter 5, Lande 1991, Slatkin and Arter 1991, Myers et al. 1995, 1997), although specific processes may lead to the spatial correlation falling somewhat faster or slower than exponentially. The decay is determined by the average movement distance. We will, therefore, use the exponential decay model as a heuristic tool to make a link between the statistical scale of the pattern and the scale of the underlying processes.

We apply the heuristic model to our results on the two rodent species by generating multivariate normal random numbers with exponentially decaying covariance. The actual geographic locations of the sampling stations are used in the simulations. In this way, the synthetic data has the same spatial design and experiences the same spatial constraints as the rodent data. Calculating the distances between the locations and thereafter evaluating each distance in the exponential covariance function generates a target covariance matrix for the random variable. A vector of random variables with the prespecified spatial dependence may subsequently be generated by the Choleski method (Ripley 1987). A mean of two and a variance of one are assumed for all random variables (corresponding to the mean and variance of the log-abundance data of the vole). Synthetic data sets are generated with either one observation or 30 observations per station (corresponding to the one univariate and the two multivariate descriptors of the dynamics). The 30 observations are, for simplicity, assumed to be independent of one another. We simulate 1000 data sets for each of nine exponential parameters. The range of decay parameters are chosen to span the range of the biological processes reviewed in *Materials and methods: The species.* The smallest scale is that of rodent dispersal with movement distances ~1 km, to the largest due to predator movement that may be as extensive as 25 km. The nonparametric covariance function is applied to each data set. The sequence of simulation and analysis took ~2 wk on an SGI Power Challenge L with four R10.000 processors.

The estimated L_0 correlation lengths for these synthetic data sets are summarized in Table 2. Increasing the exponential parameter invariably increases the correlation length of the pattern: as the scaling of the ''process'' (the exponential parameter) is increased from 1 to 30 km, the estimated correlation length increases from 10 to 50 km. From this we draw two tentative conclusions: (1) The scales of processes relevant for the Japanese rodents as determined by dispersal and dispersion of the ecological interactants (described in *Materials and methods: The species*) give rise to scales of pattern spanning those observed in the biological data sets (under the assumption of exponential decay). (2) A correlation length similar to that for the grey-sided vole (50–55 km) is obtained if an exponential decay process with parameter 20 km or more is simulated on the map of the sampling sites. The corresponding parameter giving rise to the correlation length of the Japanese wood mouse (20–30 km) is ~5 km. There is a good fit between the empirical spatial covariance function and that expected under exponential models with parameters 7 and 20 km (Fig. 7).

TABLE 2. The estimated correlation length (in kilometers) with 95% range (in parentheses) when applied to data with exponential covariance of different parameters.

No. obs.	φ (km)					
	1	3	5	7	10	15
1	13.6 (6.4, 40.1)	16.2 (7.8, 45.4)	20.6 (9.6, 54.3)	25.6 (11.4, 60.8)	31.1 (14.0, 62.8)	37.8 (17.3, 75.3)
30	10.7 (9.4, 12.5)	12.7 (11.1, 15.3)	19.2 (14.5, 33.0)	25.7 (18.9, 39.0)	32.5 (24.8, 44.5)	39.3 (32.1, 48.6)

Notes: The data are generated on an identical spatial grid to that of the rodents (Fig. 1) according to the Choleski method (Ripley 1987). The spatial covariance in the data was fitted using a spline correlogram with 25 degrees of freedom. Average estimates and 95% ranges are calculated on the basis of 1000 simulations for each of the nine parameters. ''No. obs.'' refers to the number of observations per site (see *Discussion*).

We may compare the results from the simulation with those from the review of the ecological community of the rodents; the movement distances required to generate more-than-average similarity of populations 50 km apart are clearly much larger than the capabilities for movement by the grey-sided vole. The movement distances required to generate more-than-average similarity of populations 20–30 km apart are slightly greater than the typical movement of the Japanese wood mouse. On the basis of the spatial pattern and the review of the ecology of the two species (presented under
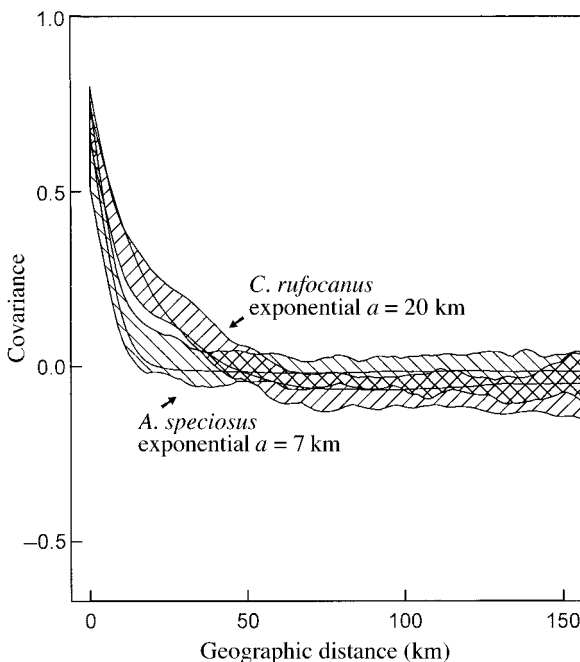

FIG. 7. Spatial covariance functions in annual rates of change of the grey-sided vole and the Japanese wood mouse. The 99% confidence interval for the spatial covariance functions as estimated by the spline correlogram is shown as in right hatching (grey-sided vole) or left hatching (Japanese wood mouse) shading. The mean estimated covariance functions across 1000 data sets with exponential covariance (with decay parameter 20 and 7 km) are superimposed. The covariance functions intersect at $y < 1$ because of sampling error (the synthetic data has been contaminated by 25% sampling error).

Materials and methods: The species) we postulate the following hypotheses for future testing:

1) The regulation of the populations of Japanese wood mouse appears to take place at a scale slightly larger than the current information on individual movement would predict. Population regulation due to spacing, dispersal, and interactions among individuals is predicted to give rise to a correlation length ~10 km (Table 2). A candidate hypothesis to explain the observed pattern is that the population is regulated at the local scale (with current dispersal distances being underestimates) or at the scale of seed masting.

2) The scaling of the dynamics of the grey-sided vole is much larger than that expected from the spatial extent of individual movement. A candidate hypothesis to explain regulation at this larger scale, is the predators of the grey-sided vole (although other processes are conceivable).

3) The difference in scaling of the two species may, tentatively, be seen as due to their differential vulnerability to predation and possibly due to differences in the diet of the rodents.

Testing these hypotheses may be tricky. However, if regulation takes place at the scale of rodent movement and dispersal, the genetic spatial covariance function may be similar to the covariance function for the dynamic (Stacy et al. 1997). This is because the spatial genetic covariance is also induced by the movement rates of individuals (e.g., Epperson and Li 1997). However, if regulation is mainly due to trophic interactions, the genetic and population dynamic covariance may be very different (Stacy et al. 1997). Our prediction for future testing is that the relative discrepancy between the genetic and the dynamic profile should be greatest in the grey-sided vole.

The relatively large scaling of the population dynamics of the rodents may provide an explanation why field experiments manipulating food supply, predator abundance, and various other factors, have given inconclusive results (e.g., Stenseth and Ims 1993). Rodent dispersal alone may give rise to spatial correlation across 10 km as a result of pure diffusion (Table 2). Experimental plots of 100 × 100 m (which would be considered large for most rodents), are small relative

Table 2. Extended.

	ϕ (km)	
20	25	30
42.7	46.4	46.9
(19.8, 76.4)	(21.4, 80.6)	(22.8, 83.0)
43.9	47.3	49.4
(37.2, 52.5)	(40.5, 55.0)	(43.1, 56.2)

to such natural correlation lengths. A large scale of regulation of population dynamics may also underlie the apparent resilience to manipulation of other fluctuating populations (e.g., Krebs et al. 1995, Myers and Rothman 1995). Population fluctuations may arise for a large number of reasons, but those arising from predator–prey (or parasitoid–host) interactions may be expected to show a scale of regulation that is larger than the scale of prey movement because natural enemies typically have greater mobility than their resource.

The log-transformed time series (LN), the annual growth rate (R), and the S-index of population variability show consistent spatial covariance functions for each species. These descriptors are clearly not independent measures. They nevertheless emphasize different aspects of the population fluctuations. There is, for instance, evidence of statistical dissimilarity at far distances (<150 km) in the covariance for S in the grey-sided vole (Fig. 5). Distant dissimilarity is not seen in the other descriptors. Such significant dissimilarity in connection with significant similarity at short distances indicates clinal variation (Sokal 1979, Legendre and Fortin 1989). In such a situation the spatial variation is continuous, and the issue of scaling is blurred. This is because any change in the extent of the study area will alter the estimated average region-wide similarity. The gradient in variability of grey-sided vole populations has previously, and more directly, been documented by Stenseth et al. (1996). Large-scale gradients in variability appear to be a relatively common phenomenon for many microtine rodent species (e.g., Hansson and Henttonen 1985, Makin-Rogalska and Nabaglo 1990, Hanski et al. 1994).

The distinct spatial scale inherent in a variety of demographic descriptors for any one of the species suggests that the population dynamics of these two rodents possess a dominant scale of regulation. The spline correlogram appears to be a statistical tool that has the required power and statistical rigor to estimate spatial scaling, and to provide the confidence regions necessary for testing and inference (Bjørnstad and Falck 1997). In addition to the previous lack of dedicated statistical tools, there is also the problem that conclusions regarding population dynamics are strongly affected by the spatial scaling of the study design (most importantly the ''grain'' and the ''extent''; e.g., Wiens 1989). It is therefore not always clear what is biological

reality and what is a methodological artifact. In our study, the two species of rodents showed evidence of distinct scaling (the Japanese wood mouse being more local than the grey-sided vole) despite being subjected to identical spatial constraints; the data for the two were collected at the same locations and using the same methodology. Analyses of synthetic data with known spatial covariance and an identical spatial design to the rodent data further suggest that the results are likely to be of biological, rather than of methodological, origin (Table 2).

Although more than one dominant process of regulation is possible, we do not see the scale of population regulation as an entirely arbitrary and continuous function of study design as advocated in hierarchy theory. On the contrary we feel that the comparative analysis we have undertaken by investigating data on two different rodent species, lends support to the idea that there are dominant scales of regulation of the dynamics of these species. The scale of regulation is relatively wide compared to the spatial requirements of individual rodents.

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