

SPATIAL AND TEMPORAL DYNAMICS OF SMALL MAMMALS AT A REGIONAL SCALE IN CANADIAN BOREAL FOREST

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Spatial synchrony is a common feature of mammalian population dynamics that appears to be caused by different processes in different systems. We sampled 60 sites across >900 km in northern and central Ontario, Canada, from 2001 to 2004 to assess spatial and temporal trends in abundance and population growth of small mammals. We tested alternative predictions for 3 causes of synchrony: dispersal, predation, and correlated environmental perturbations (the Moran effect). During 25,680 trap nights, *Myodes gapperi*, *Tamias striatus*, and *Peromyscus maniculatus* were the most commonly captured species. Populations of all 3 species fluctuated markedly during the 4 years of sampling, but fluctuations appeared to occur over a relatively small spatial extent (<200 km for all species). No pairwise combination of species exhibited positive interspecific synchrony, suggesting that nomadic predation was not synchronizing declines among species. Our data were most consistent with the dispersal hypothesis or a Moran effect caused through synchronous food crops.

Key words: acorns, chipmunk, *Clethrionomys*, deer mouse, dispersal, Moran effect, predation, red-backed vole, seedfall, synchrony

Spatial synchrony is a common feature of mammalian population dynamics, for which 3 main explanations have been posited. First, nomadic predators may synchronize declines (Norrdahl and Korpimäki 1996; Ydenberg 1987). Alternatively, spatially correlated environmental perturbations can synchronize populations. This has been termed the Moran effect (Ranta et al. 1997; Royama 1992). Finally, dispersal from areas of high population density to those of low population density can synchronize regional dynamics (Ranta et al. 1995; Swanson and Johnson 1999).

These different explanations for synchrony produce different spatial and temporal patterns in animal population dynamics, and therefore the patterns can be used to infer the cause of synchrony in different systems (Steen et al. 1996). For example, if

a nomadic predator was causing synchrony in population dynamics of small mammals, there should be interspecific synchrony in declines of species of small mammals of similar size and habitat use (e.g., Korpimäki et al. 2005; Lambin et al. 2006). Moreover, the scale of synchrony caused by a predator would be related to the movement distance of the predator. Where synchrony is caused by dispersal, there is an assumed negative relationship between distance and the level of synchrony at a scale that corresponds to dispersal distance (Swanson and Johnson 1999). The Moran effect should produce synchrony at a scale corresponding to the environmental perturbation, and may or may not have a distance-decay structure similar to dispersal. This would depend on the spatial structure of the perturbation.

A number of studies have tested for the presence and inferred causality of spatial synchrony in mammalian systems (e.g., Krebs et al. 2002; Predavec et al. 2001; Ranta et al. 1995, 1997; Steen et al. 1996; Swanson and Johnson 1999). General conclusions are difficult to draw from this research, because different studies have supported either dispersal, the Moran

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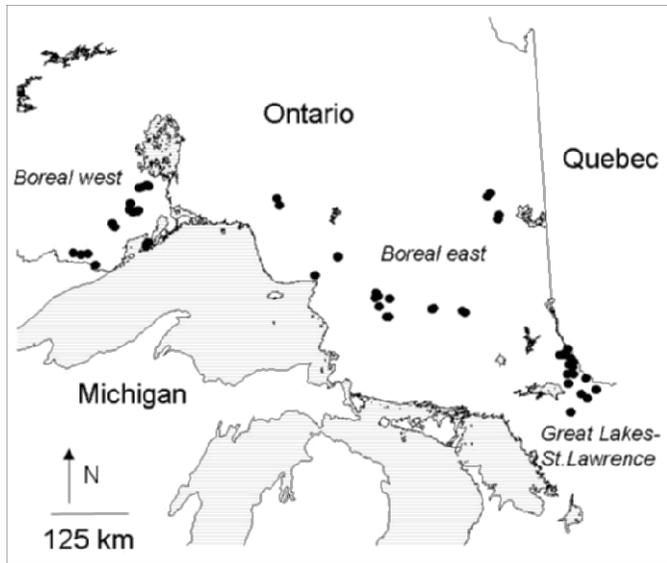


FIG. 1.—Map of the study area in Ontario, Canada, showing plots (black points) where small-mammal trapping was undertaken during 2001–2004.

effect, predation, or a combination of these (Hanski et al. 1991; Huitu et al. 2005; Korpimäki et al. 2005; Krebs et al. 2002; Swanson and Johnson 1999). An obvious generality appears to be that causes of synchrony are system- and situation-specific, and possibly also multifactorial (Lidicker 1988). Given the importance of synchrony to an understanding of the dynamics of any particular system, further investigations into the magnitude and causes of synchrony in additional ecological settings are needed.

We studied the spatial synchrony of species in the small-mammal community of the boreal forest in Ontario, Canada. To our knowledge, there are no studies of spatial synchrony in small mammals from Canadian boreal forest. It is generally thought that these populations are not cyclic, but fluctuate interannually (Falls et al. 2007; Fryxell et al. 1998; Grant 1976), and it is unknown whether these fluctuations are synchronous. We assessed the inter- and intraspecific patterns of fluctuations and tested them against patterns predicted by different causes of spatial synchrony.

MATERIALS AND METHODS

Study area and field methods.—We established 60 permanent plots for small mammal sampling within the managed forest area of Ontario, including 20 plots within each of 3 regions (Great Lakes–St. Lawrence ecotone, boreal east, and boreal west; Fig. 1). The permanent plot network within each region was stratified by type of primary forest cover with plot locations selected from random points generated in forest stands > 100 and $< 1,000$ m from road access. Five plots each of young, mature conifer, mature mixed-wood, and mature deciduous forest types were selected in each region. The maximum distance between the sites in the boreal west and those in the Great Lakes–St. Lawrence ecotone was > 900 km (Fig. 1).

At each plot, 20 Sherman live traps ($7.6 \times 9.8 \times 22.9$ cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were set at 10-m intervals along a 90-m transect. At each station, 2 traps were set within 1–3 m of one another and adjacent to natural cover or runways such as fallen logs or stumps. Traps were supplied with 2 tablespoons of rolled oats, a cube of potato, and natural cotton batting. An aluminum cover was placed over each trap to reduce thermal extremes and provide shelter from precipitation. Trapping occurred from mid-July through August from 2001 to 2004 (inclusive). Trapping consisted of 2 sessions each year, spaced a minimum of 2 weeks apart and a maximum 3 weeks apart. During each session, traps were set for 3 consecutive nights and checked daily. As such, we carried out 120 nights of trapping per plot per year.

We determined age and sex of all captured animals, and identified them to species using a key developed for the area (Holborn et al. 2003). Beginning in 2002, animals were marked with 1.0-g Monel ear tags (National Band and Tag Co., Newport, Kansas). Animals captured with tags were noted as recaptures if previously captured that year according to the tag number. Empty traps with closed doors (misfires), missing or destroyed traps, or traps with missing bait also were recorded. All animal handling procedures were approved by the Ontario Ministry of Natural Resources Animal Care committee and were consistent with the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Data analysis.—Our analysis was restricted to the 3 most abundant species, deer mice (*Peromyscus maniculatus*), red-backed voles (*Myodes gapperi*), and eastern chipmunks (*Tamias striatus*). Data on captures were available for all 60 of the plots for 2002–2004, and for 34 of the 60 plots in 2001; no trapping was carried out during 2001 in the 20 boreal west plots, in 3 boreal east plots, or in 3 Great Lakes–St. Lawrence ecotone plots.

We estimated abundance of each species as number of captures per 100 trap nights. Trapping effort was determined by subtracting missing traps plus one-half the misfired and missing bait traps from the total trap nights (Beauvais and Buskirk 1999). Although animals were marked with ear tags beginning in 2002, to compare with data from 2001 where possible, we used total captures per 100 trap nights as an estimate of population size. To assess the validity of this index we correlated it with the number of uniquely marked individuals captured for each year and species. With 3 species and 3 years of marked animals (2002–2004), there were 9 correlations. All of these were highly explanatory ($r \geq 0.93$, $n = 60$ plots).

We assessed the spatial structure in abundance trends for each species using correlograms (Legendre and Fortin 1989). Spatial patterns in temporal variability were assessed by estimating the s -index for each species at each plot. The s -index, calculated as the standard deviation of \log_{10} -transformed abundances, is an index of variation in densities (Henttonen et al. 1985). Where available, we included data for 2001 in s -index calculations. We were interested in characterizing the amount of interannual variability in abundance at each plot. We assessed spatial structure in this variability for each species using correlograms of the s -index.

We then carried out a spatial analysis of intraspecific trends in population growth, using methods adapted from Steen et al. (1996). For each plot, we estimated the rate of population growth $r = \ln(n_t/n_{t-1})$ for the 2 intervals 2002–2003 and 2003–2004. A constant of 1 was added to all population estimates to avoid division by 0. For each sample plot, we then calculated the position of each species in 2-dimensional (Euclidian) population growth space, where x- and y-axes were $r_{2002-2003}$ and $r_{2003-2004}$, respectively. For geographical distance, the 2-dimensional axes represented x- and y-coordinates (in a Lambert conformal conic projection), and the location of a plot in this geographic space was compared to the location of a species in population growth space using a Mantel correlogram (Steen et al. 1996).

Our Mantel test procedure (above) was followed to assess interspecific spatial structure in population growth (synchrony). Instead of comparing population growth space of a species to geographic distance however, we made comparisons of population growth between each pair of species. For all sample plots, we calculated the position of each species in 2-dimensional (Euclidian) population growth space, where each measured growth interval was a dimensional axis. A Mantel test of correlation between each species of interest at different distance classes was then undertaken, to test for interspecific spatial correlations.

All Mantel and Moran's *I* statistics were considered significant where Bonferroni-corrected $P < 0.1$ (Steen et al. 1996). Statistical analyses were conducted with S-Plus 6.0 (Insightful Corp., Seattle, Washington).

RESULTS

During 2001–2004, we captured individuals of 19 different species 6,084 times during 24,477 trap nights (25,680 trap nights were attempted, including misfires). Our analyses of synchrony were limited to the 3 species that were abundant in each region of the study area, the deer mouse, the red-backed vole, and the eastern chipmunk.

When data on captures were summarized by region, the patterns appeared differentiated. In the Great Lakes–St. Lawrence ecotone, populations of mice and chipmunks showed similar trends, declining during 2001–2002 and again during 2003–2004, and increasing during 2002–2003. Red-backed voles declined throughout the 4 years. All 3 species showed declining trends during the 4 years in the boreal east, except for small increases in 2003 by mice and chipmunks. In the boreal west, voles showed a very large peak in abundance in 2002, declined in 2003, and then all 3 species increased from 2003 to 2004 (Fig. 2). The mean (SE) *s*-indices for voles, mice, and chipmunks were 0.57 (0.07), 0.82 (0.09), and 0.77 (0.08), respectively.

The correlogram of abundance for red-backed voles demonstrated a nearly monotonic decrease, suggesting a gradient (Fig. 3A; Fortin et al. 1989). Abundances were positively autocorrelated at distances < 300 km, and negatively autocorrelated at distances of 600 km. This gradient was consistent with the apparent greater abundance of voles in the northwest, compared to farther east and south (Fig. 2). Similarly, the

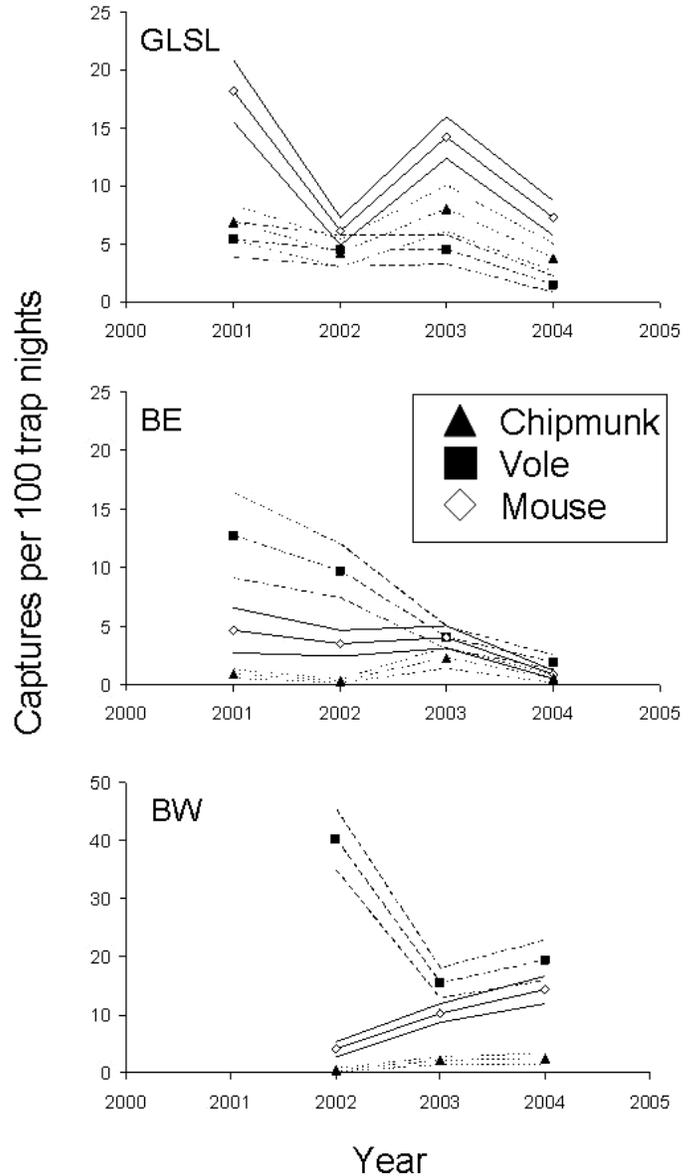


FIG. 2.—Trends in abundance in all regions of a study area in Ontario, Canada, where small mammals were censused during 2001–2004. Mean (bounded by ± 1 SE) captures per 100 trap nights are depicted for eastern chipmunks (*Tamias striatus*), red-backed voles (*Myodes gapperi*), and deer mice (*Peromyscus maniculatus*). Captures are summarized over 3 regions, the Great Lakes–St. Lawrence ecotone (GLSL), the boreal east (BE), and the boreal west (BW). Note that the y axis differs for the BW graph because of elevated abundance of voles.

s-index showed a pattern of decrease, and there was negative autocorrelation in *s* at a distance of about 600 km (Fig. 3B). There was no positive spatial synchrony in population growth at the shortest distances, but there was at a distance of 200 km (Fig 3C). Negative synchrony occurred at 400 km.

Chipmunks exhibited a trimodal pattern of abundance, with peaks of positive autocorrelation at <50 km, 400 km, and >800 km (Fig. 4A). Rather than a gradient, this suggests a patchy population structure, with 3 nodes of abundance

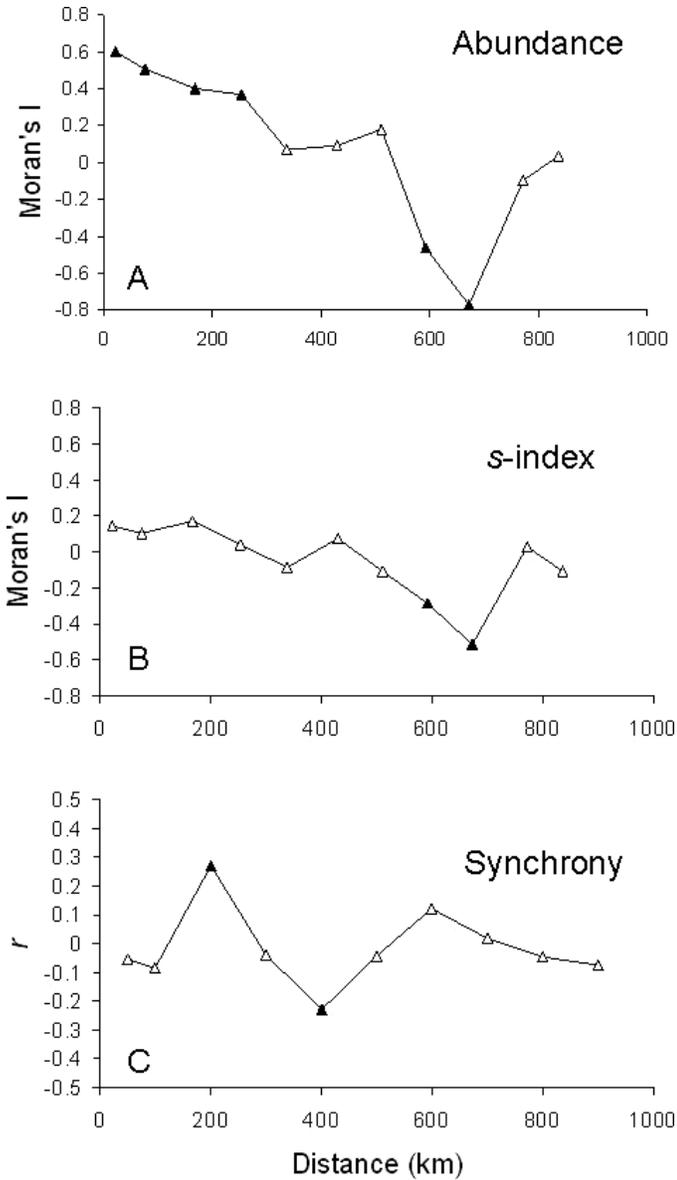


FIG. 3.—Spatial patterns in A) abundance, B) *s*-index, and C) intraspecific synchrony in population growth for red-backed voles (*Myodes gapperi*) in Ontario, Canada, from 2001 to 2004. Synchrony was estimated using a Mantel correlogram of geographic distance (x and y coordinate) and rates of increase during 2002–2003 and 2003–2004. Closed symbols represent significance where Bonferroni-corrected $P < 0.1$.

separated by about 400 km. There was no spatial structure in the *s*-index for chipmunks (Fig. 4B). However, there was a positive correlation between population growth for chipmunks and distance at distances of < 50 km, and also at a distance of 700–800 km. There was some negative correlation at 200 and 600 km (Fig. 4C).

Deer mice exhibited negative autocorrelation in abundance at 400–600 km, and 2 nonsignificant peaks of positive autocorrelation separated by about 800 km (Fig. 5A). This suggested 2 clusters of abundance, 1 at each end of the study area (1 each in the west and southeast of the study area). There was

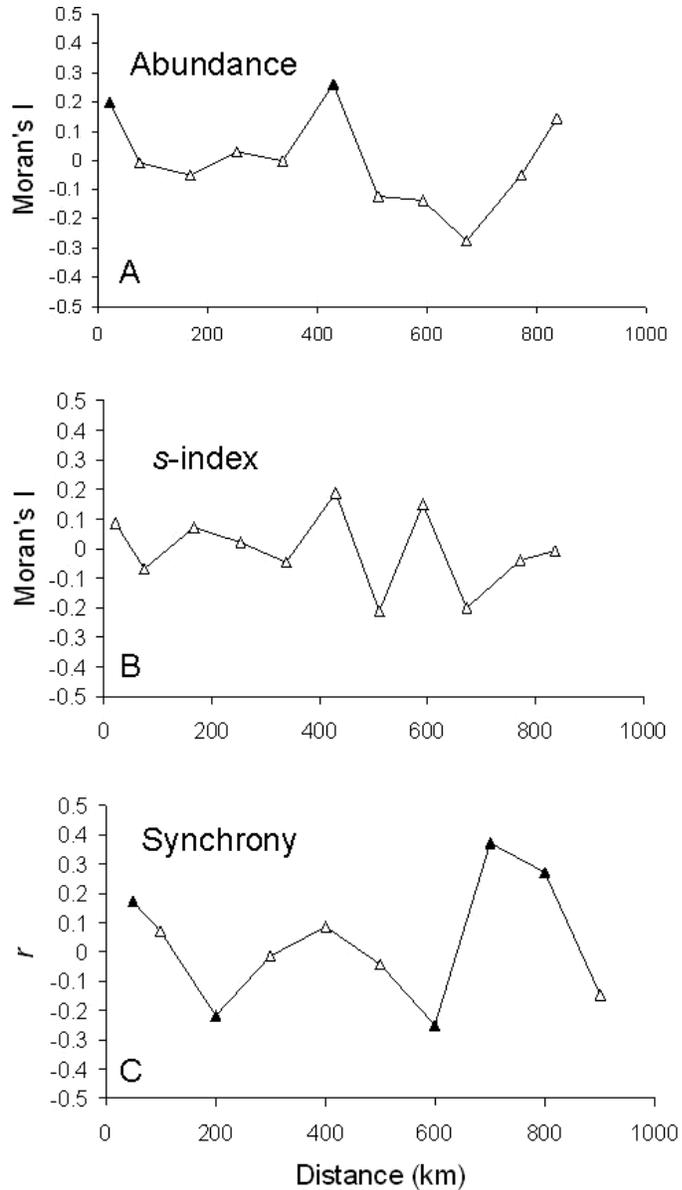


FIG. 4.—Spatial patterns in A) abundance, B) *s*-index, and C) intraspecific synchrony in population growth for eastern chipmunks (*Tamias striatus*) sampled in Ontario, Canada, from 2001 to 2004. Synchrony was estimated using a Mantel correlogram of geographic distance (x and y coordinate) and rates of increase during 2002–2003 and 2003–2004. Closed symbols represent significance where Bonferroni-corrected $P < 0.1$.

no spatial structure in the *s*-index (Fig. 5B), but there was positive synchrony at distances < 50 km (Fig. 5C).

There was no positive spatial correlation in population growth between any pairwise combination of the 3 species (Fig. 6). There was some negative correlation between voles and both chipmunks and mice.

DISCUSSION

We detected no positive spatial correlations in interspecific comparisons of population growth, suggesting that over the

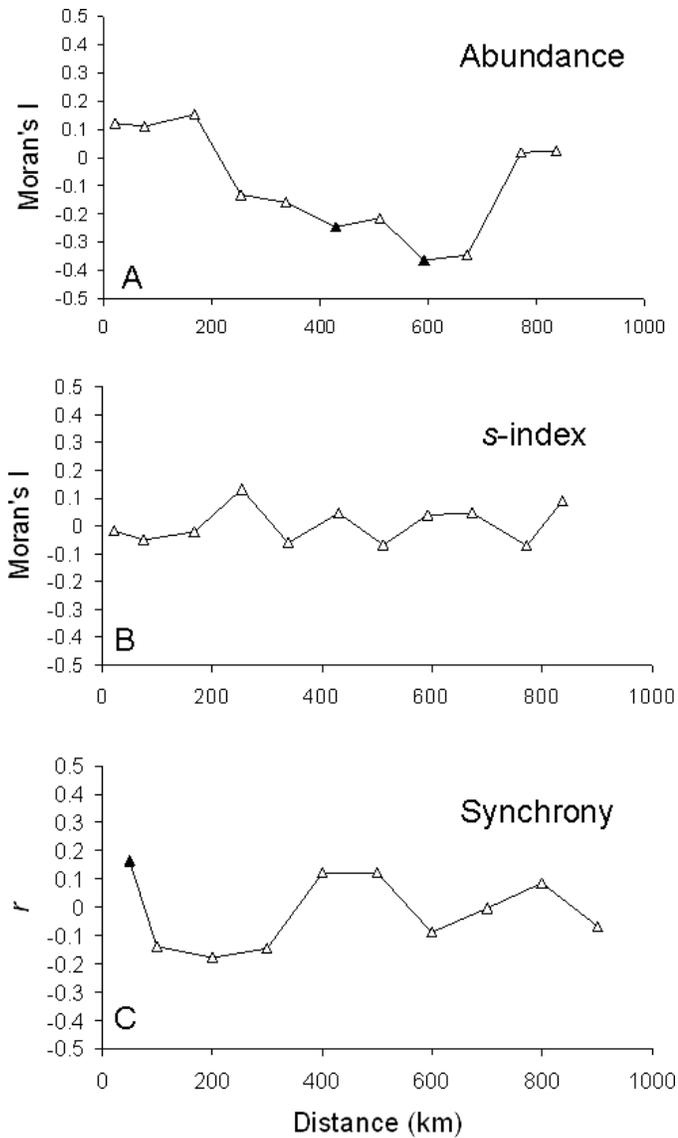


FIG. 5.—Spatial patterns in A) abundance, B) *s*-index, and C) intraspecific synchrony in population growth for deer mice (*Peromyscus maniculatus*) sampled in Ontario, Canada, from 2001 to 2004. Synchrony was estimated using a Mantel correlogram of geographic distance (*x* and *y* coordinate) and rates of increase during 2002–2003 and 2003–2004. Closed symbols represent significance where Bonferroni-corrected $P < 0.1$.

temporal and spatial scales we observed, predators were not synchronizing population dynamics of these species. The major predators of small mammals in the study area were marten (*Martes americana*), ermine (*Mustela erminea*), and numerous raptors. Studies in Fennoscandia have supported the predation hypothesis (Korpimäki et al. 2004), including an extension called the alternative prey hypothesis, which suggests that predators will switch between alternative prey species such that there is an interspecific synchronous low (Korpimäki et al. 2005).

Instead of interspecific synchrony, each species in our study had different spatial patterns of fluctuation. However, each

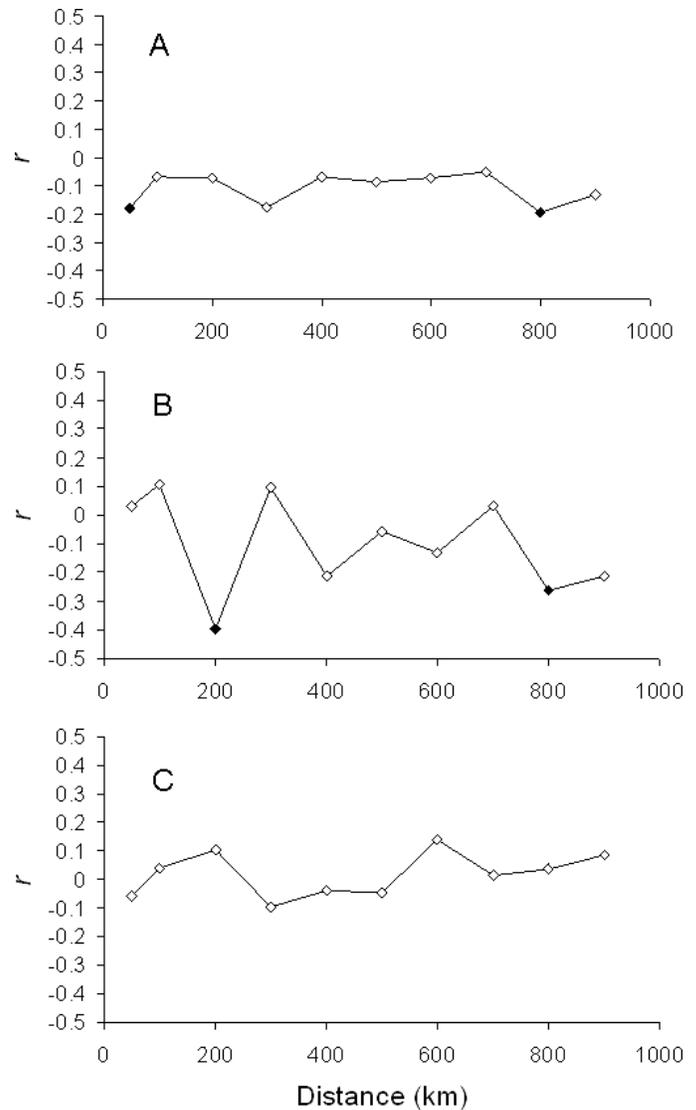


FIG. 6.—Interspecific synchrony between pairs of species sampled in a study area in Ontario, Canada, from 2002 to 2004. Synchrony was estimated using Mantel correlograms of rates of increase during 2002–2003 and 2003–2004 for each species. Pairwise comparisons are for A) red-backed vole (*Myodes gapperi*) and deer mouse (*Peromyscus maniculatus*), B) red-backed vole and eastern chipmunk (*Tamias striatus*), and C) deer mouse and eastern chipmunk. Closed symbols represent significance where Bonferroni-corrected $P < 0.1$.

species exhibited some amount of local synchrony in population growth. Such local synchrony (<50 km for mice and chipmunks and <200 km for voles) might be explained either by dispersal or the Moran effect. Mantel tests generally showed a positive correlation at short distances, decaying to a negative correlation at slightly longer distances (although these negative correlations were not always significant). This type of small-scale distance-decay structure is more indicative of a dispersal process generating synchrony than a Moran effect, which need not have a distance-decay structure (Bowman et al. 2000; Swanson and Johnson 1999). Moran effects also might be expected to occur over a larger area than 50–200 km, given the

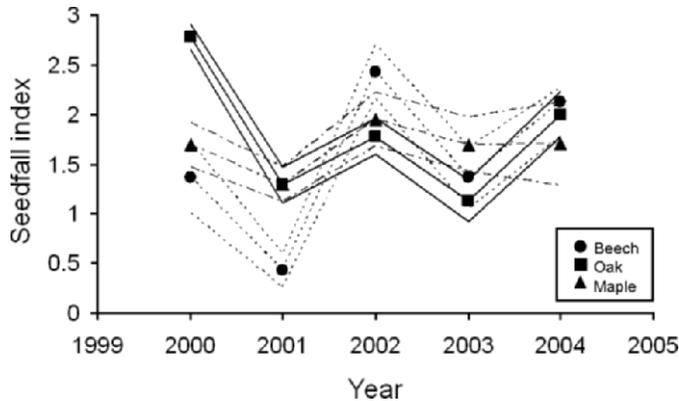


FIG. 7.—Indices of seedfall in central Ontario, Canada, based on annual surveys undertaken by the Ontario Ministry of Natural Resources. Mean (bounded by ± 1 SE) indices for beech (*Fagus grandifolia*), oak (*Quercus*), and maple (*Acer*) are shown.

regional nature of weather, which often is posited as the cause of Moran effects (Ranta et al. 1997). Several recent studies have concluded that synchrony is consistent with either the Moran effect (Krebs et al. 2002; Ranta et al. 1997), dispersal (Steen et al. 1996), or both (Swanson and Johnson 1999).

Part of our study area, in particular the Great Lakes–St. Lawrence ecotone region and the southern part of the boreal east region, was characterized by an ecotonal mixture of trees that included temperate hardwoods such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and red oak (*Quercus rubra*). These species periodically produce seedfall that appears to increase the overwinter survival and reproduction of deer mice and chipmunks such that they exhibit a lagged numerical response during the summer after a mast year (Falls et al. 2007; Wolff 1996). All 3 of these crops masted in the southern part of our study area during 2002 (Fig. 7; Bowman et al. 2005), which would explain the increase in mice and chipmunks in the summer of 2003, particularly in the south, but also possibly in the northwest (e.g., see the relationship between seedfall in Wisconsin and central Ontario in Falls et al. [2007]). A similar synchronous masting event occurred in 2000, which would explain the relatively large populations of mice and chipmunks in 2001. These patterns suggest a modification of the Moran-effect hypothesis as follows. It may be that the Moran effect occurs in this system through weather synchronizing seedfall, which in turn synchronizes growth of populations of mice and chipmunks by increasing overwinter survival and reproduction following masting years. Koenig and Knops (2000) have shown that synchrony in masting by trees may be due to the Moran effect. They found that oak masting was synchronous over distances as great as 500 km. Both chipmunks and deer mice showed patchy distributions and patchy population growth according to our spatial analyses. It is conceivable that centers of synchronous population growth for these species could correspond to locally synchronous seedfall.

A similar Moran effect could be posited for red-backed voles. Voles showed dramatic temporal and spatial variation

across the study area, but only local synchrony in population growth (<200 km). Northern red-backed voles (*Myodes rutilus*) appear to be limited by overwinter survival, which is a function of berry crops in autumn (Boonstra and Krebs 2006). Similarly, Elias et al. (2006) showed that temporal abundance of voles is related to seedfall by white pine (*Pinus strobus*). These studies suggest that a Moran effect could synchronize food crops, which subsequently synchronize growth of populations of voles through increased overwinter survival. We have no data to suggest which food (or foods) might be most important in Ontario.

To summarize, for all 3 species we conclude that either the dispersal hypothesis or a modified Moran-effect hypothesis, where weather synchronizes food crops, provide the best explanations for our data. We caution that the strength of inference from our data is limited by the short duration of sampling (3–4 years), although ours is among the most extensive field samples collected to assess synchrony in North American small mammals.

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