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SCALE OF AN IRRUPTING DEER MOUSE POPULATION

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We assessed the spatial and temporal pattern and scale of an irruption by a population of deer mice, *Peromyscus maniculatus* in the summer of 1997 in New Brunswick, Canada. We tested the prediction that spatial scales finer than the extent of the irruption would not reveal domains of population growth. Increases in the abundance of mice were seen across an extensive set of study grids (separated by > 15 linear km): however, growth rates were spatially autocorrelated over short distances (< 300 m). The extensive irruption may have been a result of finer-scale irruptions occurring simultaneously.

Key words: deer mouse, domain, hierarchy, irruption, *Peromyscus maniculatus*, population dynamics, scale, small mammal, spatial autocorrelation, synchrony

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An understanding of the spatial and temporal scale of population dynamics can give us insight into the processes that contribute to the dynamics (Steen et al. 1996). For example, populations can fluctuate in abundance synchronously over large regions, a phenomenon considered to be a response to some region-wide process (e.g., Moran 1953, Myrberget 1973, Ranta et al. 1995). Conversely, some populations exhibit fine-scaled variability in demographic parameters, a phenomenon that suggests the contribution of local, rather than regional, processes (e.g., Bowman et al. 2000, Krohne and Burgin 1990, Montgomery 1989).

Studies that demonstrate either broad synchrony or finer variability in spatial population dynamics often are unable to detect whether populations exhibit levels of organization at other scales (e.g., Steen et al. 1996). This is due, in part, to the infrequent use of cross-scale research designs. Although small-mammal researchers often use single scales of observation to explain spatial population dynamics, multiple levels of spatial dynamics have been suggested (e.g., Goodwin and Fahrig 1998, Holling 1992).

The deer mouse (*Peromyscus maniculatus*) is a non-cyclic species that can occur at very high numbers in some years, likely in response to mast-crop production (Catlett and Brown 1961, Fryxell et al. 1998, Gashwiler 1979, Grant 1976, Herman and Scott 1984, Wolff 1996). One such irruption was observed during a study of small-mammal population ecology in New Brunswick, Canada. The study used a set of nested grids, which gave us the opportunity to assess this irruption across a range of spatial scales. It was known from conducting field work that the irruption was widespread, much like a synchronous regional event. We expected the spatial domain of population growth to coincide with the extent of the irruption. Spatial domain refers to the area over which a process occurs (e.g., Holling 1992). Thus, we predicted that spatial scales finer than the extent of the irruption would not reveal domains of population growth.

METHODS

The study was conducted on the private industrial forest of Fraser Papers Inc., in the Appalachian forest of northwestern New Brunswick (47°N, 67°W). Upland sites were dominated by an overstory of sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*). Lowland sites were dominated by black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*).

We selected a 4900-ha forested landscape that was managed with a low intensity for forest products (e.g., < 15% recent clear cuts or softwood plantations). A set of nested grids was used to sample the 4900-ha landscape for small mammals (Fig. 1). The largest grid had a sampling grain of 1000 m and an extent of 4900 ha (8 x 8; 64 points). Here, grain refers to the minimum distance between sample points, whereas extent refers to the area covered by the samples (e.g., Wiens 1989). Nested within the large grid was a smaller grid with a grain of 250 m and an extent of 310 ha (8 x 8; 64 points) and a 3rd grid with a grain of 125 m and an extent of 31 ha (5 x 6; 30 points). For sampling reasons points were not established within 50 m of roads or water bodies, and the topography of the area was uneven, so some irregularities existed in the shape of the grids. At the top end, our choice of scales was a logistical one; we could not survey more than 4900 ha. The finer scales were chosen for biological reasons with the smallest of these finer than Morris’ (1992) dispersal scale. At a site approximately 15-km north of these nested grids, another 8 x 8 grid (250-m grain, 310 ha extent) also was sampled for small mammals. Other aspects of the study design were described by Bowman et al. (2000).

We trapped the sample points to estimate small-mammal abundance in spring and fall beginning in fall 1996. Five Victor Tin-Cat multiple-capture live traps (Woodstream Corp., Lititz, PA, USA) were used to survey each sample point. One trap was placed at point center, and 4 other traps were placed at each cardinal direction, 35 m from center (Fig. 1 inset). The 5-trap array was designed to survey a 50-m radius around each point. All traps were placed in ‘most likely runway’ positions and prebaited for three days with oats and sunflower hearts. Traps were then set for 4 consecutive nights. Therefore, a single point took 7 days to sample: 3 nights of prebaiting and 4 nights of trapping. The number of sampling points precluded us from trapping all the points simultaneously. Trapping on the largest grid (1000-m grain) spanned 3 of the 7-day periods, whereas the smaller grids were trapped within 1 or 2 periods and we assumed a negligible temporal drift in the samples. Captured animals were weighed, identified to species and sex, checked for reproductive condition, marked with a 1-g monel ear tag (National Band and Tag Co., Newport, KA, USA) and released.

To study the dynamics of the deer mouse irruption, we first calculated capture rates of deer mice across all sites and trapping sessions to evaluate the synchrony of the increase in deer mouse abundance. Next, we determined growth rates of deer mouse populations for each sample point within the nested grids. Growth rates were calculated for the period between each sampling session (i.e, fall trapping, winter growth period, spring trapping, summer growth period). Growth rates were calculated as: $\log_{10}(10 + X_{t+1}) - \log_{10}(10 + X_t)$, where X was the abundance of deer mice at each point (Steen et al. 1996). The 125-m grain grid was not sampled in fall 1996, so raw abundance data from spring 1997 were used as a surrogate for growth rates on this grid during winter 1996--97.

To test our prediction that spatial scales finer than the extent of the irruption would not reveal domains of population growth, it was necessary to determine these spatial domains. Population growth is a contagious process, which should be positively autocorrelated in space (Legendre and Fortin 1989). We assume that the distance of the positive autocorrelation indicates a spatial domain for the process (e.g., Legendre and Fortin 1989, Steen et al. 1996). Positive autocorrelation in population growth rates over distances much shorter than the extent of the deer mouse irruption would suggest that the irruption was an aggregate of finer-scale processes. We assumed deer mouse populations were isotropic in their structure, and so we developed all-directional correlograms (Moran’s I; Legendre and Fortin 1989) to study patterns of spatial autocorrelation for species abundances in each of the three reference-area study grids (125-m, 250-m, and 1000-m grains). Methods for developing the correlograms and testing for significance followed those of Bowman et al. (2000). Briefly, the technique involves assessing the strength of correlations between a variable and its value lagged in space. Thus, the coefficient for Moran’s I is analogous to a Pearson *r*. In a correlogram, coefficients are calculated for each distance class simultaneously, and so tests of significance require the Bonferroni correction (Legendre and Fortin 1989). Bonferroni-corrected significance suggests that the shape of the correlogram can be interpreted as important. Data analysis was conducted using S-Plus 2000 (MathSoft Inc., Seattle, WA, USA).

RESULTS

In 23,820 trapnights carried out during the study, we captured > 7000 small mammals, including > 1800 deer mice. Deer mouse populations underwent a several-fold increase in abundance, and subsequent decline during the study (Fig. 2). The increase took place during summer 1997, and the decline during winter 1998. This irruption event was extensive, occurring synchronously across the entire study area, including an adjacent study site that was approximately 15 km to the north of the nested grids (Fig. 2).

Analysis of structure functions demonstrated that during periods of low population change, growth rates were not autocorrelated at any of the scales that we studied. However, during the deer mouse irruption and during the subsequent summer (1998), population growth rates were positively autocorrelated over relatively short distances (Fig. 3). Only the two finest-scale grids exhibited any autocorrelation in growth rates.

Mean monthly precipitation during the study periods was as follows: summer 1996 (94.3 mm), winter 1996-97 (100.4 mm), summer 1997 (96.7 mm), winter 1997-98 (73.6), summer 1998 (131.7 mm), and winter 1998-99 (83.5 mm).

DISCUSSION

We detected a synchronous increase in deer mouse populations across the entire study area, a spatial extent of > 15 linear km. The large-scale process was likely a climatic event that resulted in widespread production of seeds by mast-crop species. Wolff (1996) has demonstrated that deer mice will exhibit winter breeding only following autumns with bountiful mast-crop production. We saw evidence of winter breeding during 1996--97 (Fig. 2). This period of winter breeding may have contributed to the irruption during summer 1997. We have no direct measure of mast production, but winter breeding in itself is evidence of a good mast year the previous fall (Wolff 1996). Mast-producing species in the study area included American beech (*Fagus grandifolia*) and beaked hazel (*Corylus cornuta*).

Although the irruption was extensive, deer mouse populations exhibited relatively fine-scale growth patterns. That is, population growth rates were autocorrelated over distances of < 300 m. This finding supports the idea that many population processes are local in effect (Krohne and Burgin 1990, Montgomery 1989). The locally distributed sites of population growth may correspond to deer mouse sub-populations. Deer mouse sub-populations in our continuously-forested study area were small in spatial extent (i.e., < 300 m; Bowman et al. 2000).

Some of the fine-scale variation in growth patterns may have resulted from habitat heterogeneity. However, Bowman (2000) demonstrated that deer mice in the study area exhibit spatial population structure that is independent of vegetation patterns, and that occurs over short distances (< 250 m). Thus, these deer mouse populations are not spatially correlated to vegetation patterns at a scale corresponding to the population growth that we measured (i.e., < 300 m).

The irruption of deer mouse populations in our study suggests an interesting dynamic. Deer mice irrupted over an extensive area (> 15 linear km), likely in response to some large-scale event (e.g., mast production). Yet, these mouse populations exhibited a domain of population growth over a relatively small spatial extent (< 300 m). Thus, we envision a process whereby the large-scale population irruption was actually an aggregate of a number of small-scale irruptions occurring simultaneously.

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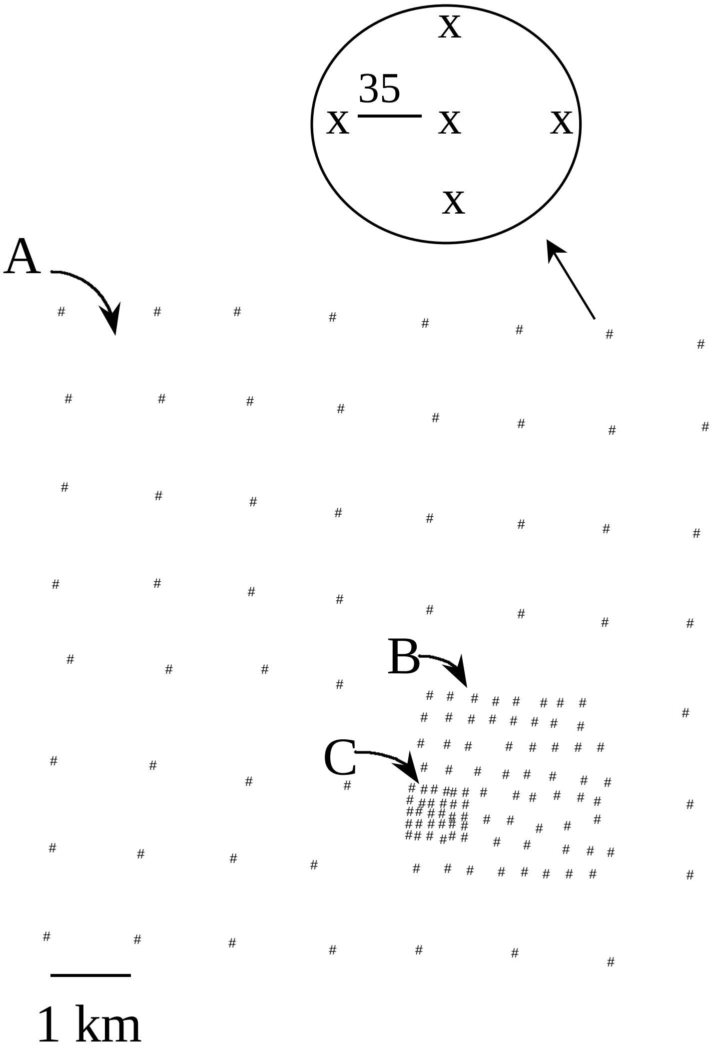

Fig. 1. Layout of 3 study grids on a forest landscape in northwestern New Brunswick, Canada. Three nested scales were surveyed: A = 1000-m grain, 8 x 8 points, 4900 ha extent; B = 250-m grain, 8 x 8 points, 306 ha extent; and C = 125-m grain, 5 x 6 points, 31 ha. Each survey point consisted of an array of 5 traps (inset). Topography of the site contributed to irregularities in the shape of the grids.

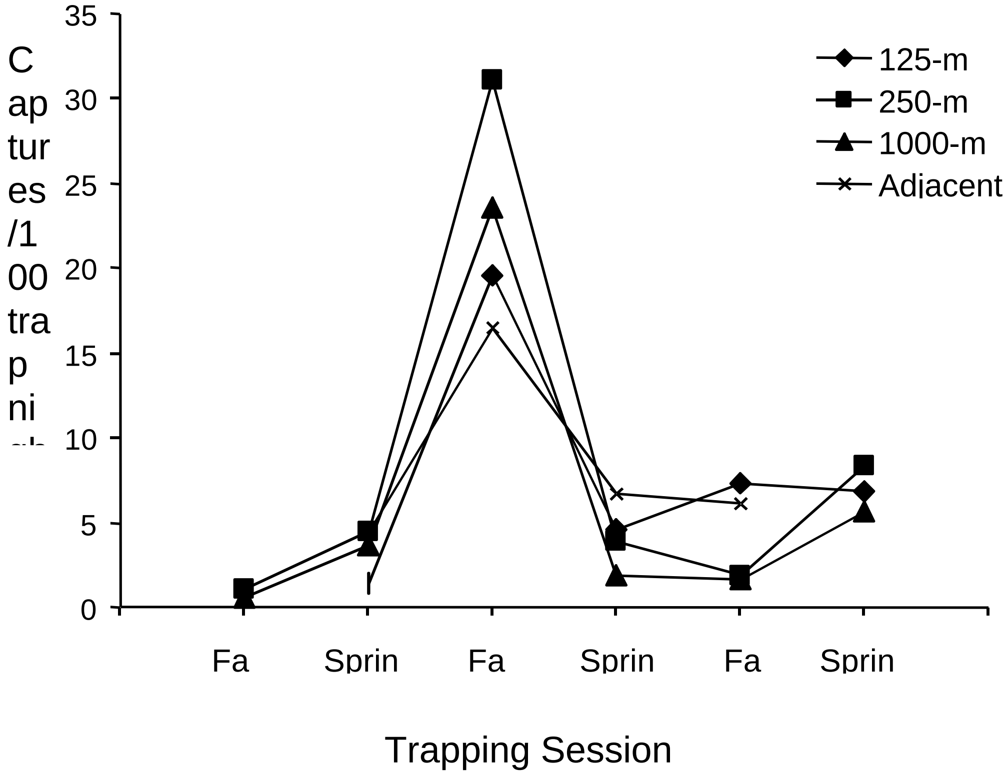

Fig. 2. Relative abundance of deer mice captured on 4 different grids during a study in New Brunswick, Canada. Three nested grids differed in size: 125-m grain, 31-ha extent, 5 x 6 points; 250-m grain, 310-ha extent, 8 x 8 points; 1000-m grain, 4900-ha extent, 8 x 8 points. An adjacent grid was > 15 linear km to the north (250-m grain, 310-ha extent, 8 x 8 points). Trapping began in fall 1996 and continued each spring and fall until spring 1999.

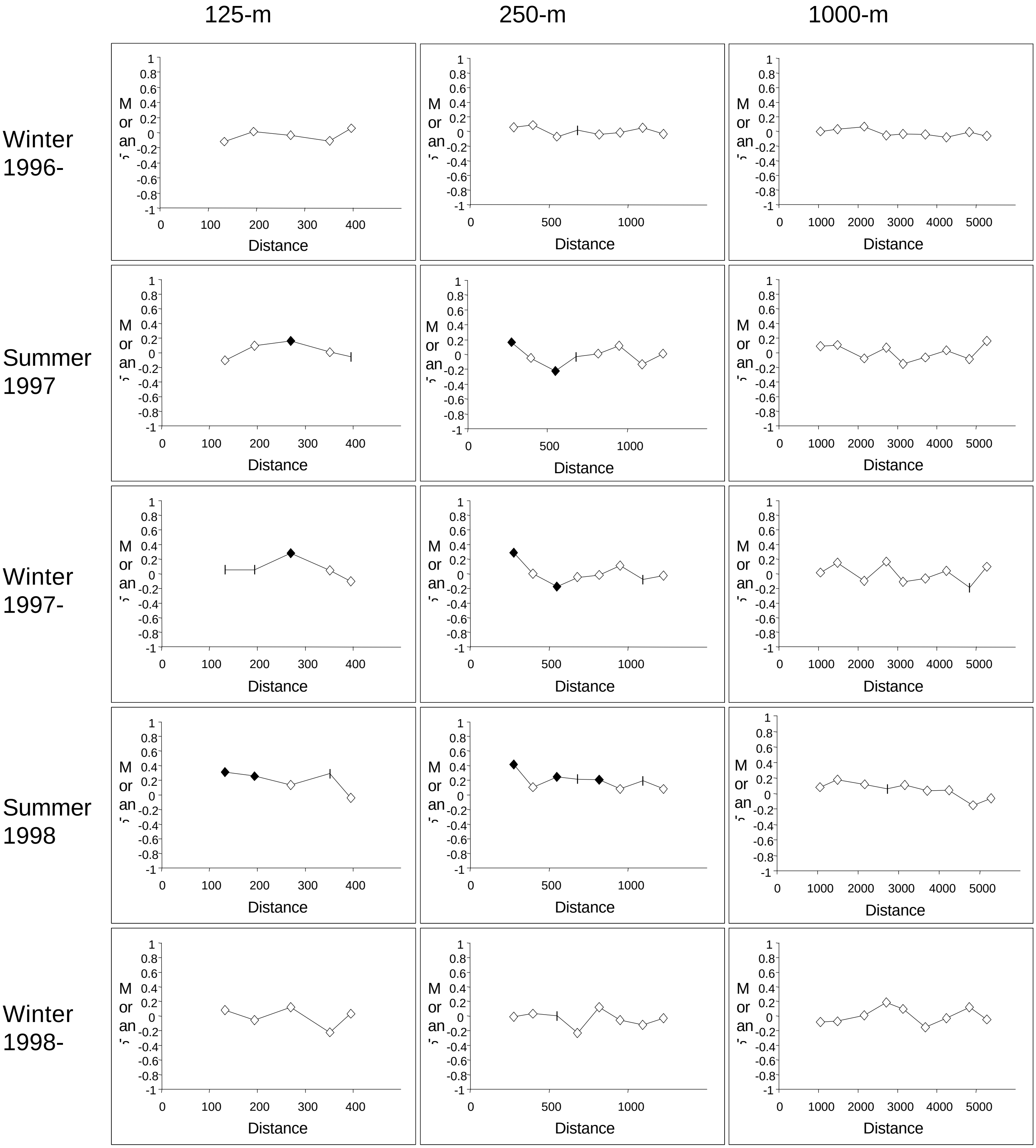

Fig. 3. Correlograms for deer mouse population growth rates on 3 nested grids in a continuously-forested study area in New Brunswick, Canada. Grid dimensions were: 125-m grain, 31-ha extent; 250-m grain, 310-ha extent; and 1000-m grain, and 4900-ha extent. Distances are in meters. Filled symbols indicate global correlogram significance. In these cases, the shape of the entire correlogram is considered significant.