

Small-Mammal Community Patterns in Old Fields

Distinguishing Site-Specific from Regional Processes

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I. INTRODUCTION

Community ecologists increasingly recognize that interpretations of local community structure must include processes at local, regional, and biogeographical scales (Wiens *et al.*, 1986; Brown, 1987; Ricklefs, 1987; Roughgarden, 1989). Local processes such as predation and competition often play a strong role in shaping communities over short time scales (Paine, 1966; Connell, 1983; Schoener, 1983; Holt and Lawton, 1994). Yet, local communities typically are embedded in larger landscapes; movements of individuals across space can change the influence of local processes on population dynamics (Huffaker,

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1958; Fahrig and Paloheimo, 1988; Pulliam and Danielson, 1992), and by a variety of mechanisms influence the species richness of local assemblages (Roff, 1974; Vance, 1980; Holt, 1993; McLaughlin and Roughgarden, 1993; Valone and Brown, 1995). Finally, long-term, large-scale processes such as geographical range changes and speciation ultimately determine the pool of possible community members at a given site (Brooks and McLennan, 1993; Ricklefs and Schluter, 1993).

Understanding the interaction of processes at different spatial scales is necessary to understand the effects of habitat fragmentation (Wiens, 1976; Levin, 1992). Fragmentation creates arrays of patches varying in size and distance from one another, arrayed in a matrix of qualitatively different habitats (Wilcox, 1980). The interspersions of different habitats results in spatial heterogeneity, which can alter ecological processes (Saunders *et al.*, 1991). Because species interact with the environment at different spatial scales, species will most likely have different responses to fragmentation (Kareiva, 1986; Gaines *et al.*, 1992a, 1994; Robinson *et al.*, 1992; Diffendorfer *et al.*, 1995a; Margules *et al.*, 1994). For large-bodied species, some patches may be too small for population persistence and such species' disappearances could have indirect effects on community structure, for example, by relaxing competition on smaller bodied species. Because patches become isolated following fragmentation, animal movement patterns will often change, leading to shifts in local population dynamics and in the strength and outcome of interspecific interactions (Holt, 1993). For instance, theoretical and experimental studies have highlighted how dispersal in spatially explicit environments can permit species coexistence that is impossible in closed communities (e.g., of a predator and its prey: Huffaker, 1958; Hassell *et al.*, 1992; or of competitors: McLaughlin and Roughgarden, 1993; Tilman, 1994). Studies of fragmented systems can provide insights into factors influencing community structure in unfragmented habitats and highlight the influence of space on demographic processes (Holt, 1993).

Various investigators at the University of Kansas have been engaged in long-term studies of small mammal populations in the prairie-forest ecotone continually from 1973 to 1996 (with additional though sporadic available data from the 1940s to 1970). These studies have been undertaken mainly by two faculty members—M. Gaines and N. Slade—and their students and associates. Each of the two groups has had a different focus. Gaines and associates initially concentrated on genetics and the biology of dispersal (Gaines and McClenaghan, 1980; Johnson and Gaines, 1987). Since 1984, this group has worked with R. Holt to examine dispersal and population dynamics in the context of an experimental study of habitat fragmentation (Robinson *et al.*, 1992). Slade and associates have worked on a variety of problems with small-mammal ecology, including mass-based demography (Sauer and Slade, 1985, 1986), interference competition (Glass and Slade, 1980), and community structure (Swihart and Slade, 1990).

This chapter and a second paper (Diffendorfer *et al.*, 1995b) represent the first attempts to combine data from the two long-term studies. Here we compare temporal and spatial patterns in old-field small-mammal communities for the period 1984–1992 at study sites separated by just 0.5 km (Fig. 1). One site is a

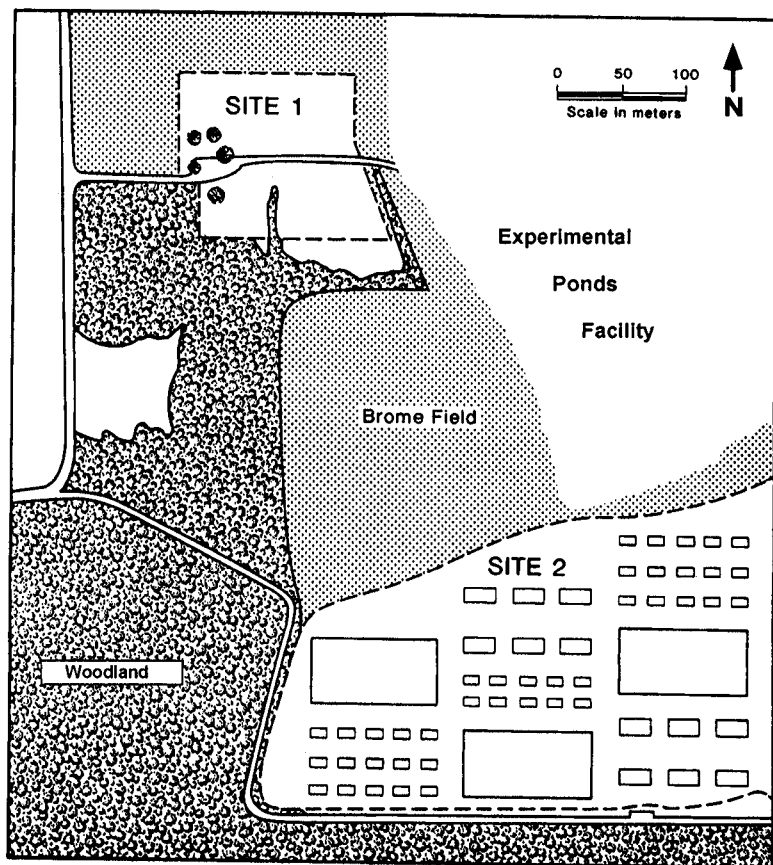


FIGURE 1. Map of part of the Nelson Environmental Study Area (12 km northeast of Lawrence, Kansas) showing the arrangement of the two study sites. Site 1 is a continuous area of approximately 2.25 ha with 1.90 ha of old-field habitat. Site 2, the experimentally fragmented system, has approximately 1.87 ha of successional old-field habitat contained within 6.9 ha of total area. The 40 small patches in Site 2 are each 4×8 m, the 12 medium patches are 12×24 m, and the 3 large patches are 50×100 m. Note that a single large patch is a large block, a cluster of 6 medium patches is a medium block and a cluster of 10 or 15 small patches is a small block. Blocks are separated by 16–20 m and are numbered from west to east, within a block size (e.g., Large 1 is the western most large block, Large 2 the central large block, and Large 3 the eastern most large block).

tract of continuous old-field habitat; the other an experimentally fragmented old-field. Our intent is not to provide rigorous tests of specific *a priori* theoretical predictions, but rather to compare the continuous and fragmented sites in order to search for potential systematic effects of habitat fragmentation on the long-term spatial and temporal dynamics of a community, and to assess the spatial scale relevant to analyses of community organization.

Because these two sites are close in space, they clearly draw species from the same regional species pool and, moreover, are likely to experience parallel fluctuations in climate. Table I lists the small mammal species in our region and the small mammals that compose the communities found on both sites. Some species in the regional fauna might in principle occur on our sites but never have (e.g., plains harvest mice, pine voles, and meadow jumping mice). Some species are likely absent because local habitat in our sites is inappropriate (e.g., eastern chipmunks, southern flying squirrels, and 13-lined ground squirrels). For other species, there may be local or regional barriers to dispersal. At least one species present, the least shrew, is not accurately censused by our standard trapping techniques. The results reported here consider only comparative patterns for the

TABLE I Small Mammal Species Found in Douglas County, Northeastern Kansas, and Captured More Than 20 Times in the Continuous Site and in the Fragmented Site

Species	Location		
	Northeastern Kansas	Continuous	Fragmented
Least shrew (<i>Cryptotis parva</i>)	X	X	X
Prairie vole (<i>Microtus ochrogaster</i>)	X	X	X
Deer mouse (<i>Peromyscus maniculatus</i>)	X	X	X
Western harvest mouse (<i>Reithrodontomys megalotis</i>)	X	X	X
Cotton rat (<i>Sigmodon hispidus</i>)	X	X	X
Short-tailed shrew (<i>Blarina brevicauda</i>)	X	X	
House mouse (<i>Mus musculus</i>)	X	X	
Wood rat (<i>Neotoma floridana</i>)	X	X	
White-footed mouse (<i>Peromyscus leucopus</i>)	X	X	
Bog lemming (<i>Synaptomys cooperi</i>)	X	X	
Meadow jumping mouse (<i>Zapus hudsonicus</i>)	X		
Southern flying squirrel (<i>Glaucomys volans</i>)	X		
Pine vole (<i>Microtus pinetorum</i>)	X		
Plains harvest mouse (<i>Reithrodontomys montanus</i>)	X		
13-Lined ground squirrel (<i>Spermophilis tridecemlineatus</i>)	X		
Eastern chipmunk (<i>Tamias striatus</i>)	X		

species known to be actually present at our sites. Given this focus, we cannot address the question of why some species are missing (though present in the regional pool), even though this is an important dimension of community ecology (Diamond and Case, 1986).

The comparative analyses reported here bear on three distinct issues: (1) the influence of habitat fragmentation on spatial patterns in abundance, (2) the influence of habitat fragmentation on temporal dynamics, and (3) the spatial scale of community processes.

A. The Influence of Habitat Fragmentation on Abundances

We have previously studied the influence of habitat fragmentation on individual movements (Diffendorfer *et al.*, 1995a), population demography (Gaines *et al.*, 1992a,b, 1994; Diffendorfer *et al.*, 1995b), and abundances on different sized patches within the fragmented site (Foster and Gaines, 1991; Robinson *et al.*, 1992). The continuous site studied by N. Slade is in effect a single, very large patch of old-field habitat, four times larger than the largest patch on the fragmented site. This permits us to ask if trends seen in the fragmented site along a gradient of patch size (small to large) extrapolate to a larger patch size.

B. The Influence of Habitat Fragmentation on Temporal Dynamics

Demographic studies of old-field species often show both seasonal and multianual fluctuations in population size (Gaines and Rose, 1976; Johnson and Gaines, 1988; Swihart and Slade, 1990). Variation in numbers can range over 2–2.5 orders of magnitude and include local extinctions (Swihart and Slade, 1990). Although small-mammal ecologists have traditionally emphasized temporal variability in abundance, few studies have rigorously examined long-term temporal changes in the rank-order of abundances among species, or species turnover (*viz.*, colonization/extinction dynamics) in old-field small-mammal communities. Here we examine the influence of fragmentation on these aspects of temporal variability in communities.

C. The Spatial Scale of Community Processes

Spatial coupling in population dynamics requires individuals to move between different populations. Because the two studies combined in this paper use mark-recapture data, we can directly assess the degree of interchange by individuals

between the two sites and the potential for spatial coupling driving local population dynamics over a spatial scale of 0.5 km. Further, because our data come from grids of permanent trap stations, we can examine spatial structuring in the community on a smaller scale within each of our sites. The differences we observe between and within the two long-term studies clarify which aspects of community organization in old-field small-mammal communities might be spatially mediated—effects that would be difficult to gauge otherwise. Finally, the old-field fragments are separated by a road and at least 14 m of mowed turf from nearby woodland. As evident in Fig. 1, the continuous site directly abuts patches of woodland. This difference in surrounding habitat may influence the frequency with which potential community members arrive and use a local site. The results presented in this chapter sharpen our appreciation of the impact of landscape context on local communities, a consideration frequently ignored in comparative community analyses (*viz.* Holt, 1993).

II. MATERIALS AND METHODS

A. Study Sites

The two long-term study sites each encompass comparable areas of old-field habitat. The continuous area (site 1) is 2.25 ha; it contains 1.90 ha of old-field habitat. The fragmented site (site 2) contains 1.87 ha of successional old-field habitat restricted to patches arrayed within 7 ha of mowed grass (Fig. 1). The two study sites are located at the Nelson Environmental Study Area, 14 km northeast of Lawrence, Kansas (Fig. 1), and are approximately 500 m apart. More detailed descriptions of the sites follow.

Slade and associates have trapped monthly at the continuous site since 1973. This site has a narrow dirt road transecting it east–west and a fence row with small trees running north–south in the southern half. A trailer and storage shed are located near the road on the western half of the site. These landscape details seem relevant in permitting some mammal species to occupy the site (see following discussion). The site is maintained as an old field by sporadic mowing to control the invasion of woody plants. The continuous site was mowed to a height of 30–45 cm (invading saplings and shrubs were cut, but large trees along fencerows and sheds were not) in July 1983, and the northern half of the area was plowed in May 1984.

Gaines and his students trapped small mammals on the fragmented site from 1984 to 1992 (this long-term study is currently being continued by W. Schweiger, R. Pierotti, and others). For comparisons, we analyze data from both sites during this time period. The fragmented site was created in August of 1984 by disking an agricultural field and allowing secondary succession to proceed

within rectangular habitat patches. Regular mowing between the habitat patches is used to create these patches of successional habitat, which are organized into clusters of "blocks" (Fig. 1). The interstitial area is closely mowed turf, providing little cover and a substantially distinct plant community from the old field on the patches (Holt *et al.*, 1995). "Large blocks" are single, 50×100 -m patches; "medium blocks" consist of six 12×24 -m patches; and "small blocks" consist of either fifteen or ten 4×8 -m patches. Most blocks span the same amount of total area (5000 m^2), but at differing degrees of fragmentation.

Succession was rapid in the first 3 years of the study on the fragmented site (1984–1987) and following the mowing and plowing on the continuous site in 1983 and 1984, as longer-lived perennials replaced annuals. From 1984 to 1987, both sites had few invading woody species and were dominated by grasses and herbaceous plants. The plant communities reached a quasiequilibrium from 1987 to 1992, associated with dominance by perennial herbs (e.g., *Solidago*). Thus, during the time periods for our comparisons, the vegetation on the two study sites was similar. Within the fragmented site, patch size seems to have had little influence on aggregate measures of plant community structure (Foster and Gaines, 1991) or the rate of succession (Holt *et al.*, 1995), although some plant species did show patch-size effects (Robinson *et al.*, 1992). We therefore believe it is appropriate to compare patterns at our two sites. Since 1992, woody plants have begun to invade the fragmented site, again changing the plant community structure. Our current study suggests this is leading to changes in the small-mammal community and the effect is more pronounced as woody plant species invasion proceeds apace. These recent patterns will be addressed in future papers.

Trapping for the two studies has followed typical small-mammal mark-recapture protocols. However, for historical reasons (slightly different techniques were employed by different research teams), the timing and length of the trapping period differed between studies. In the continuous site, 196 traps at 98 trap stations, spaced 15 m apart, were set for three mornings and two afternoons every month. In the fragmented system, 287 traps at 267 stations were set for two mornings and the intervening afternoon twice a month (for more details on trapping protocol and patch layout, see Swihart and Slade, 1990, and Foster and Gaines, 1991). In both studies, when animals were captured their location was noted, and they were individually marked, checked for mass and reproductive condition, and released.

B. Analyses

The analyses reported here consist of three components. First, we analyze how habitat fragmentation modifies the spatial patterning of abundances. Next, we

examine temporal stability in the small-mammal communities and compare the degree of variability observed in our studies to studies in other biomes. An issue of particular concern is how fragmentation influences the magnitude and patterning of community variation. Finally, we consider the impact of large- and small-scale movements on local abundances. Combined with our between-site comparison, this permits us to attempt to gauge the spatial scale relevant to community dynamics in our particular system.

1. *The Influence of Fragmentation on Abundances*

a. Average densities by site and by degree of fragmentation. We calculated monthly minimum number known alive (MNKA) estimates using Fortran programs kindly provided by Dr. Charles Krebs, and corrected for area to achieve density estimates of MNKA per hectare. To correct for the differences in trapping protocols noted previously, we excluded every other week from data collected on the fragmented site and the third day of trapping from data on the continuous site.

The four most common species on the two sites were cotton rats (*Sigmodon hispidus*), prairie voles (*Microtus ochrogaster*), deer mice (*Peromyscus maniculatus*), and harvest mice (*Reithrodontomys megalotis*). These four species all occurred in sufficient numbers to allow statistical analysis. We previously reported abundance and density data for cotton rats, prairie voles, and deer mice (Gaines *et al.*, 1992a,b, 1994; Diffendorfer *et al.*, 1995b), but not for harvest mice. Because harvest mice were not individually marked on the continuous site until April 1989, we estimated MNKA from the number of captures for the time periods prior to 1989. In order to obtain a regression equation relating captures to MNKA for harvest mice, we regressed MNKA against the number of captures for capture periods since 1989 to the present (this equation was $MNKA = 1.43 + 0.713(CAPTURES)$; $R^2 = 0.845$, $t = 15.81$, $df = 46$).

To test for site differences in harvest mouse densities we used general linear models in which site and year-season were entered as independent variables. Treating each 3-month period as a time unit reduced autocorrelation in the data (e.g., the fall year-season was September through November, winter was December through February, spring was March through May, and summer was June through August).

b. Community composition by site and by degree of fragmentation. We analyzed community composition in three ways. First we studied changes in community composition as a function of varying degrees of fragmentation. We calculated monthly community percentage composition estimates by dividing the MNKA for each species by the total MNKA for all species combined. Because this analysis focused on species' relative abundances, we did not correct the raw

data for trapping protocol differences between sites (as discussed previously). We used MANOVAs (Manly, 1986) to assess changes in community structure by degree of fragmentation and by year-season. The first MANOVA tested for main effects of habitat type (the entire continuous site vs the entire fragmented site) or year-season on community composition. The second MANOVA tested for main effects of block size within the fragmented site (large vs medium vs small blocks) or year-season on community composition. Because proportions calculated from the MNKA estimates sum to 1, the relative abundance estimates for each species are not independent. We therefore transformed the data by dividing a particular species' proportion by the proportion of the rarest species—in our case, harvest mice (when percentage harvest mice = 0, we added 0.002)—and taking the natural log of this ratio. This transformation provides linearly independent measures (for justification of the technique, see Aebischer *et al.*, 1993).

Second, we compared species richness between the two sites. We investigated the effects of patchiness on community structure by comparing species richness on real medium and small blocks to the same measures calculated on "simulated" small and medium blocks, using data drawn in a structured manner from the large blocks. The simulated blocks were created by sorting raw data by trap locations on large blocks to correspond to the spatial arrangement of traps on medium or small blocks. This procedure permits us to compare a small or medium patch with a similarly spatial-structured sample from within a large block. We calculated the species richness for each trapping period for simulated and real blocks. If a species had a positive MNKA at a sample period, it was included in the richness count, even if it was missing in the actual sample. In this analysis, we included the rarer species, wood rats (*Neotoma floridana*), white-footed mice (*Peromyscus leucopus*), and house mice (*Mus musculus*), and compared average species richness on simulated and real blocks with *t* tests.

Third, we compared Shannon–Weiner diversity estimates (*H*) between the two study areas with *t* tests using only MNKA for the four most common species (cotton rats, prairie voles, deer mice, and harvest mice).

2. The Influence of Fragmentation on Temporal Dynamics

Following Rahel (1990), we analyzed temporal trends in community structure at three levels. First, we examined variation in the relative abundances of species over time. Second, at a higher level of organization, we tested for concordance through time of species' ranked abundances. Third, we assessed variability in community membership by examining patterns in local extinctions.

a. Temporal changes in abundances. We calculated the percentage composition for each species in the community as described previously (Sect. II.B.1.b.), and tested for changes in percentage composition over time using a

MANOVA blocked by unique year-seasons. We also compared coefficients of variation in the average Shannon–Weiner diversity index (H) between the continuous and fragmented study areas. In this case, H was calculated for each trapping period, and the time series of resulting indexes used to obtain the CV. Finally, to compare temporal variation to other communities, following Hanski (1990), we determined the average Spearman's rank correlation among all possible pairwise combinations of the four dominant species in each community and the average of the standard deviation in the log MNKA of each species. We then compared those values to the 14 communities presented in Hanski (1990).

b. Concordance in species ranks over time. We calculated Kendall's W (Rahel, 1990) for both sites and the various degrees of fragmentation as a means of assessing concordance in species ranks over time. Kendall's W assumes as a null hypothesis that ranks among members (in this case species) are randomly assigned. Thus, a significant W indicates consistent patterns in the ranks of community members.

c. Extinctions as a function of site and degree of fragmentation. We looked at trapping periods with MNKAs of zero to determine the influence of habitat patchiness on local extinction. What counts as an "extinction" is, of course, a matter of scale. One problem in some island biogeographic analyses is that they do not correct for sample size (area) when comparing islands differing in size (Holt, 1992). Here we assume the frequency of trapping periods with zero MNKA in a given spatial unit provides a reasonable index of local extinction. MNKA is calculated by keeping track of the times of first and last capture for a marked individual, and then counting that individual as present at all intervening time periods (regardless of whether or not the animal is actually captured). Thus, when MNKA is zero, no marked animals were captured both before and after (or during) the trapping period, making it a more conservative estimate of extinction than just raw captures. We compared real medium and small blocks to medium and small blocks simulated from each of the three large blocks. We created three separate simulated sets of blocks from each of the three large blocks. These data files were then analyzed for MNKA estimates as explained previously. We compared the average number of absences that occurred in the 188 trapping periods between simulated and real blocks using t tests (each real block was replicated at least two times; each simulated block was replicated three times).

Finally, we used trapping periods with zero MNKA as an index of local extinctions over the scale of entire study areas. We compared the overall proportion of 188 trapping periods with zero MNKA between the continuous and fragmented sites for all species using χ^2 tests.

3. *The Spatial Scale of Community Processes*

Our study also permits us to examine the potential influence of movement on local demography at various spatial scales. By combining our datasets, we have data on movements at three spatial scales: larger scale movements between the two study sites, smaller scale movements between blocks in the fragmented area, and fine scale space-use patterns within each of the sites.

a. Large-scale movements. We examined known immigrants that moved onto the two study sites to assess the potential for spatial coupling over scales of approximately 500 m. All species captured on the fragmented site were given a unique ear tag with an "s" on the back. On the continuous site, only cotton rats were given unique tags with no letters on the back. Smaller species on the continuous site were toe-clipped. Thus, we monitored the movements of cotton rats between the two sites. Unfortunately, toe clips were not checked on the fragmented site, so movements of prairie voles and deer mice from the continuous to the fragmented site were not recorded. However, movements of these smaller species from the fragmented site to the continuous site were determined.

b. Influence of movements on local MNKA. The patchy nature of the fragmented site provides a unique opportunity to characterize how movements influence local demography at smaller scales. To determine the magnitude of immigration and emigration, we calculated the proportion of the MNKA for a given trapping period consisting of marked animals either moving to or leaving a given block relative to local abundances. Thus, for a given block during a given trapping period, we determined the proportion of the MNKA accounted for by animals that entered the block from another block (immigration), or animals that left the block and were captured some place else (emigration). In the case of immigration, animals were continually counted on a given block as long as they remained there after immigrating. We analyzed the data in two ways. First, we compared the proportion of MNKA made up of either immigrants or emigrants across block sizes using all trapping periods, including those when no movement occurred. This method gives an overall picture of the importance of movement to abundance on a block. We also screened the data using only those trapping periods in which movement occurred; then we compared among blocks. We compared these percentages using ANOVAs blocked by year-seasons.

c. The influence of distance on local movements. In addition to determining the overall proportion of the species' abundance on a block composed of

immigrants or emigrants (dispersers), we studied the influence of distance on the proportion of immigrants to a block. We calculated the proportion of animals on a block that arrived there from another block. Since blocks are not equidistant to each other on the site, we were able to use *t* tests to compare the proportion of animals on a block that came from nearby blocks versus blocks farther away. For a given combination of blocks, we calculated the proportion of individuals on the target block that came from the other blocks. For large blocks, there are four possible combinations of moves (Large 1 to Large 2, Large 2 to Large 1, Large 3 to Large 2, and Large 2 to Large 3; See Fig. 1); these are of similar, but shorter, distances than are two other possible moves (Large 1 to Large 3 and vice versa). We analyzed only movements to and from the same size blocks and combined movements between the large blocks with movements between the small blocks. Since very few animals persisted from one season to the next (Gaines *et al.*, 1994), we calculated these proportions for each season and compared the data using *t* tests.

d. Within-site spatial heterogeneity in abundances. Because our grids involve permanent trap stations, the history of captures at particular stations can provide an assessment of within-grid patterns of habitat use at the spatial scale of our studies. Much of this variation is likely to reflect individual habitat selection and permits us to gauge the scale at which small mammals respond to structural features of vegetation. We mapped space use for each species on each site for the entire time period and for periods of low and high densities. We created maps by calculating the percentage of total captures that occurred at a trap location over the given time period, and using this quantity as the radius of a circle centered at the *x*-*y* coordinates of the trap location. Visual inspection of patterns in these maps quickly reveals spatial patterns in the data, patterns often not evident when the data are examined in other ways.

III. RESULTS

A. The Influence of Fragmentation on Abundances

1. Average Density by Sites and by Degree of Fragmentation

Summary results for cotton rats, prairie voles, and deer mice have been presented elsewhere (Gaines *et al.*, 1992a,b, 1994; Diffendorfer *et al.*, 1995b; see Fig. 2 for a synopsis of these results). In summary, cotton rats (the largest species) achieve highest densities on the large blocks, prairie voles (the medi-

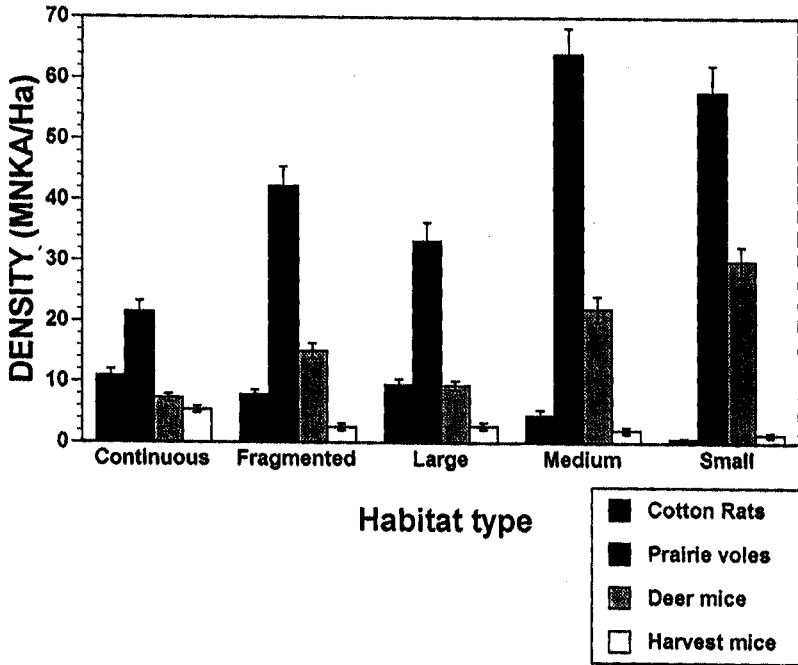


FIGURE 2. Average density (Minimum Number Known to be Alive/ha) with standard error bars by site and by block size for cotton rats, prairie voles, deer mice, and harvest mice. Data come from 7.7 years (August 1984–May 1992) of mark-recapture data.

um-size species) on the medium blocks, and deer mice (the smallest species) on the small blocks. These trends within the fragmented site extrapolate similarly to the continuous site; cotton rats have higher densities on the continuous site, and prairie voles and deer mice have lower densities there.

Harvest mice have higher average densities on the continuous site ($F = 42.21$, $df = 1, 124$, $P < 0.001$, Fig. 2). On average, harvest mice density was higher on large blocks than on small blocks, but not medium blocks ($F = 3.96$, $df = 2, 195$, $P = 0.021$, Fig. 2), consistent with their greater abundance on the continuous site.

2. Community Composition by Site and by Degree of Fragmentation

The continuous site had a number of unique small-mammal species that were captured in low numbers throughout the study. These species were extremely rare or completely absent on the fragmented site. They are house mice

(*Mus musculus*), bog lemmings (*Synaptomys cooperi*), wood rats (*Neotoma floridana*), and meadow jumping mice (*Zapus hudsonicus*). Furthermore, the average H was higher for the continuous site (0.478 ± 0.015) than for the fragmented site (0.369 ± 0.014 , $t = 5.380$, $df = 60$, $P < 0.0001$).

Based on the MANOVAs, the average relative frequencies of cotton rats, prairie voles, deer mice, and harvest mice differed by site and by degree of fragmentation (continuous vs fragmented: Wilk's $\lambda = 0.1620$; $df = 3, 122$; $P < 0.001$; between blocks: Wilk's $\lambda = 0.2155$; $df = 6, 386$; $P < 0.001$; Fig. 3). On average, prairie voles were always the most prevalent species at both sites. However, the community in the continuous habitat had relatively fewer prairie voles, and more cotton rats, than did the community in the fragmented site. With increasing fragmentation, the proportion of deer mice in the community increased, while the proportion of harvest mice decreased. Compared to community structure in blocks with greater degrees of fragmentation, overall community structure in the large blocks was thus most similar to that in the continuous area.

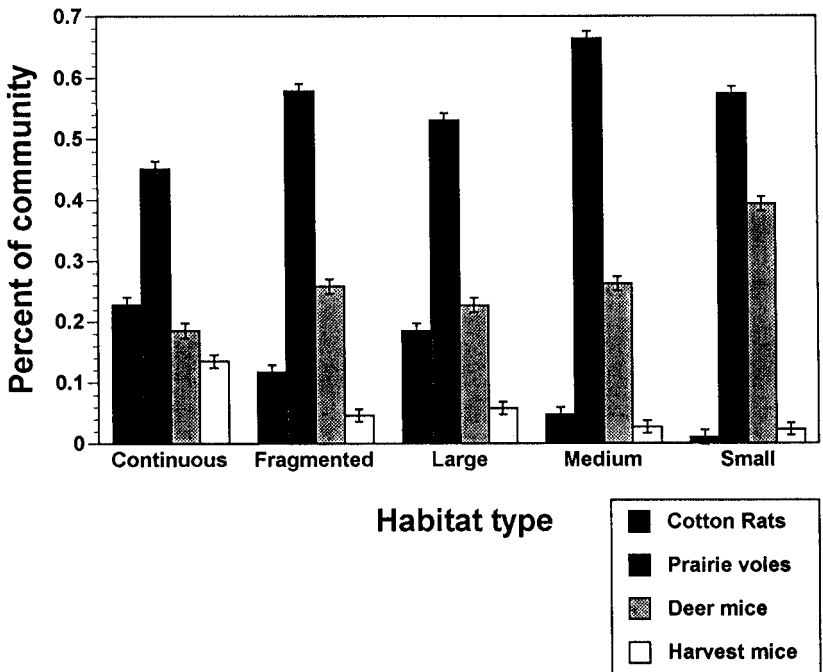


FIGURE 3. Average proportion of the MNKA with standard error bars for cotton rats, prairie voles, deer mice, and harvest mice by site and by block size. Data come from 7.7 years (August 1984–May 1992) of mark–recapture data.

Patchiness significantly influenced species richness; simulated medium and small blocks (i.e., medium and small blocks simulated from a continuous 5000-m² area) had a mean species richness higher than that of real medium and small blocks (mean \pm SE simulated medium = 2.60 ± 0.039 ; real medium = 2.30 ± 0.038 , $t = 5.47$, $df = 371$, $P < 0.0001$; simulated small = 2.64 ± 0.043 ; real small = 2.20 ± 0.034 , $t = 8.05$, $df = 354$, $P < 0.001$). The degree of trap spacing did not influence species richness because there were no differences when comparing simulated medium to simulated small blocks. However, for real blocks, larger blocks (less fragmented) had a greater average species richness (comparing real medium vs real small, $t = 1.88$, $df = 354$, $P = 0.061$).

B. The Influence of Fragmentation on Temporal Dynamics

1. Temporal Changes in Abundances

Species abundances varied through time and in different patterns on each site (Fig. 4). Prairie voles on the fragmented site had a tremendous range in abundance, from nearly zero to ~ 300 per trapping period. However, on the continuous site, prairie vole populations had a lower range, reaching a maximum abundance of about 140 animals. Cotton rats achieved higher numbers in the continuous area; by contrast, deer mice reached highest abundances in the fragmented area. Local extinctions of harvest mice from the fragmented area after 1989 (Gaines *et al.*, 1992a) are expressed in the high frequency of counts in the zero category in Fig. 4.

In all species, temporal variations in abundances were positively correlated across sites (cotton rats: $r = 0.59$, $P < 0.001$; prairie voles: $r = 0.72$, $P = 0.001$; deer mice: $r = 0.36$, $P = 0.024$; harvest mice: $r = 0.79$, $P < 0.001$; in all cases $n = 31$). In general, a given species was common (or rare) simultaneously at both sites. Cotton rat and prairie vole abundances were positively correlated between species within each site (continuous: $r = 0.44$, $n = 31$, $P = 0.006$; fragmented: $r = 0.48$, $n = 31$, $P = 0.003$). On the continuous site, but not on the fragmented site, prairie voles were negatively correlated with deer mice ($r = -0.40$, $n = 31$, $P = 0.013$) and with harvest mice ($r = -0.32$, $n = 31$, $P = 0.041$), and cotton rats were weakly negatively correlated with deer mice ($r = -0.27$, $n = 31$, $P = 0.074$). No other correlations were significant between species pairs on either site. Pairwise trajectories of abundances through time (Fig. 5) revealed substantial differences between sites in the relationship of species to one another.

Following Hanski (1990), plots of the average correlation coefficient across

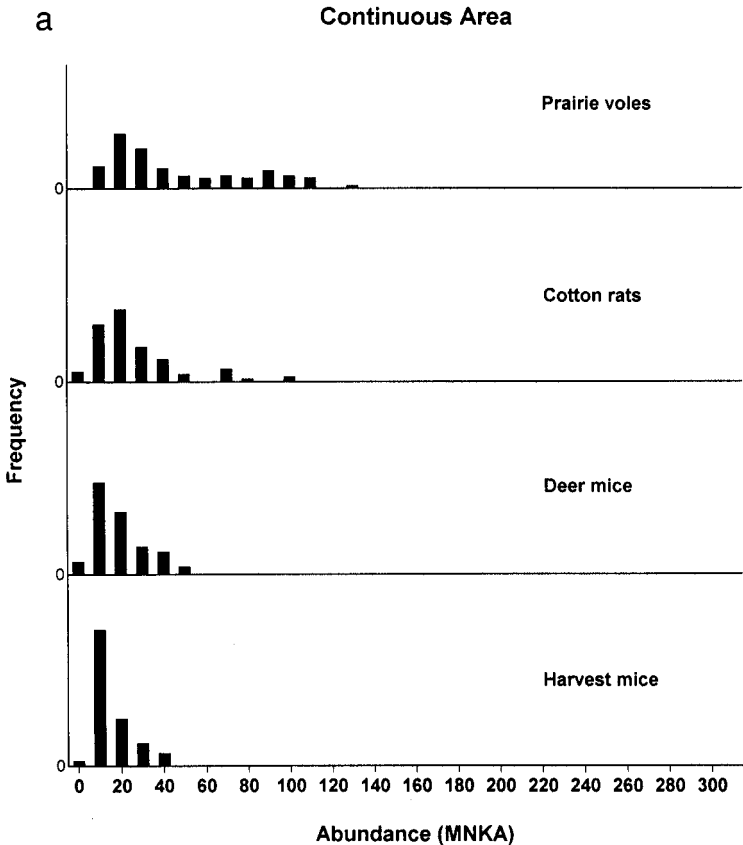


FIGURE 4. Frequency distributions of 92 monthly MNKA estimates for cotton rats, prairie voles, deer mice, and harvest mice on the (a) continuous and (b) fragmented sites.

all pairs of species versus the average standard deviation in MNKA across all species indicates the small-mammal assemblages on each of our sites have both a greater average standard deviation and a lower average correlation than 14 other communities. (Fig. 6).

The relative frequencies of cotton rats, prairie voles, deer mice, and harvest mice changed through time, such that the year-season variable in both MANOVAs was significant (continuous vs fragmented: Wilk's $\lambda = 0.0077$; $df = 90, 366$; $P < 0.001$; between blocks with the fragmented site: Wilk's $\lambda = 0.0426$; $df = 90, 578$; $P < 0.001$; Figs. 7a and 7b). Despite similar trends between sites in the relative abundances of both prairie voles and deer mice, the overall temporal changes in community structure were in different patterns across both sites,

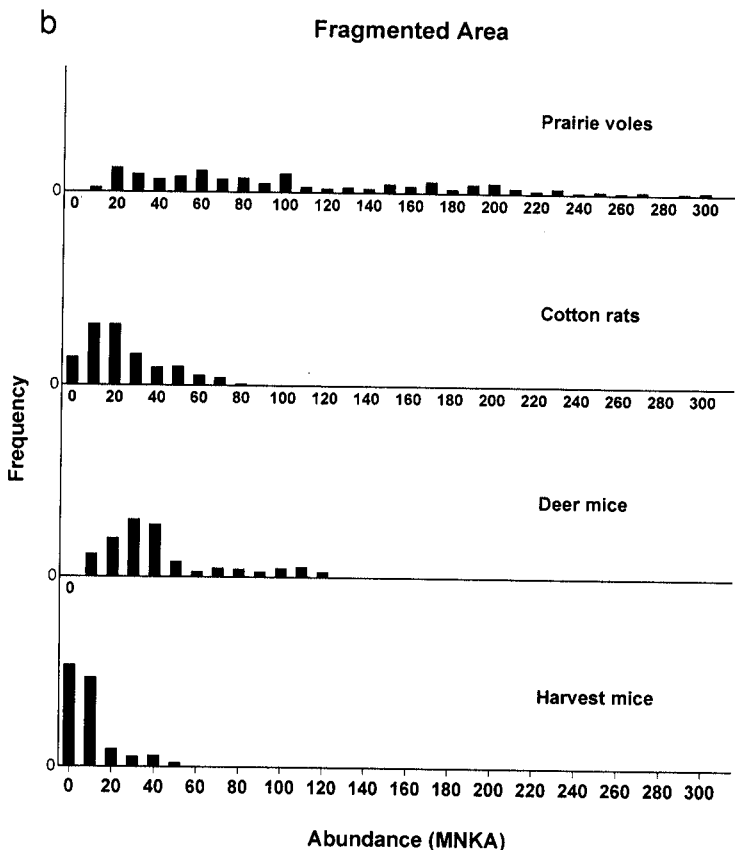


FIGURE 4. (continued)

and across block sizes on the fragmented system, leading to significant interactions in the MANOVAs between year-season and either site (Wilk's $\lambda = 0.0953$; $df = 90, 366$; $P < 0.001$) or block size (Wilk's $\lambda = 0.2126$; $df = 180, 580$; $P < 0.001$). Major shifts in community structure occurred multiannually, mainly caused by crashes in the prairie vole population. Cotton rats tended to become more prevalent in the fall, but declined every winter. Harvest mice nearly disappeared from the fragmented site after the fall of 1989, yet remained present on the continuous site. In general, the fragmented site had a greater magnitude of fluctuations in relative abundances than did the continuous site. Coefficients of variation in H were also higher in the fragmented site (21.22) than in the continuous site (16.90).

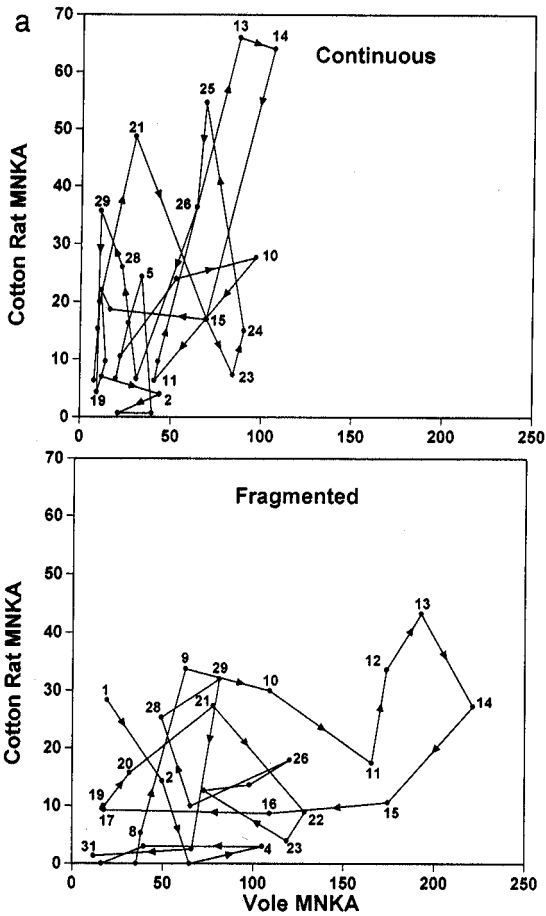


FIGURE 5. Phase plane diagrams of average MNKA for 31 year-seasons for all possible pairwise combinations of the three most common species in the continuous and fragmented communities: (a) prairie voles vs cotton rats, (b) cotton rats vs deer mice, and (c) prairie voles vs deer mice.

2. Concordance in Species Ranks over Time

All five Kendall's W values, for both the continuous and fragmented sites, as well as among the large, medium, and small blocks within the fragmented site, were highly significant, indicating species ranks were positively correlated through time (continuous site: $W = 0.178$, $n = 90$; fragmented site: $W = 0.441$, $n = 96$; large blocks: $W = 0.340$, $n = 96$; medium blocks: $W = 0.515$, $n = 96$; small blocks: $W = 0.597$, $n = 96$; in all cases $P < 0.001$). The value of W calculated for the continuous site was approximately two-fifths that calculated

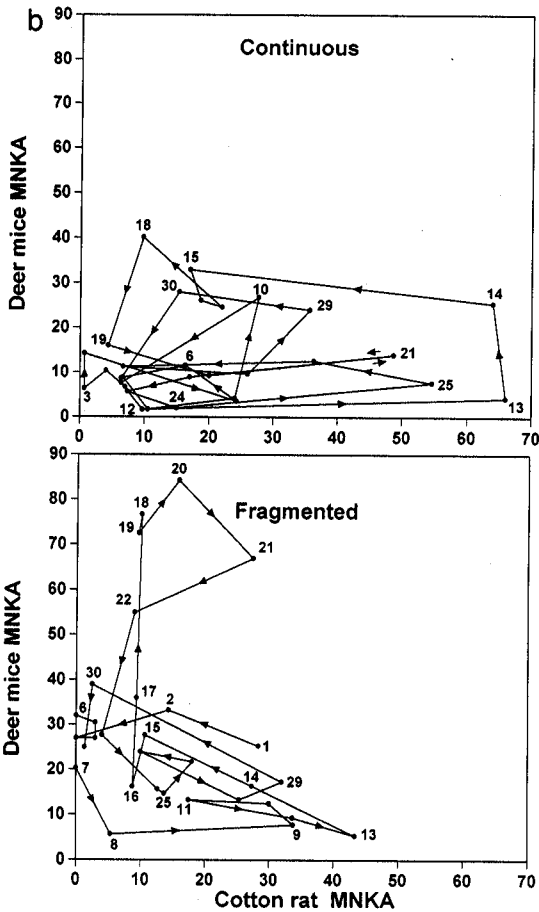


FIGURE 5. (continued)

for the fragmented site; this indicates rank abundances were less correlated (changed more often) through time in the continuous site. Relative to other block sizes, the value of W for the large blocks was most similar to that for the continuous site.

3. Extinctions as a Function of Site and Degree of Fragmentation

For cotton rats, there was no difference between simulated and real medium blocks in the average number of absences. However, real small blocks had

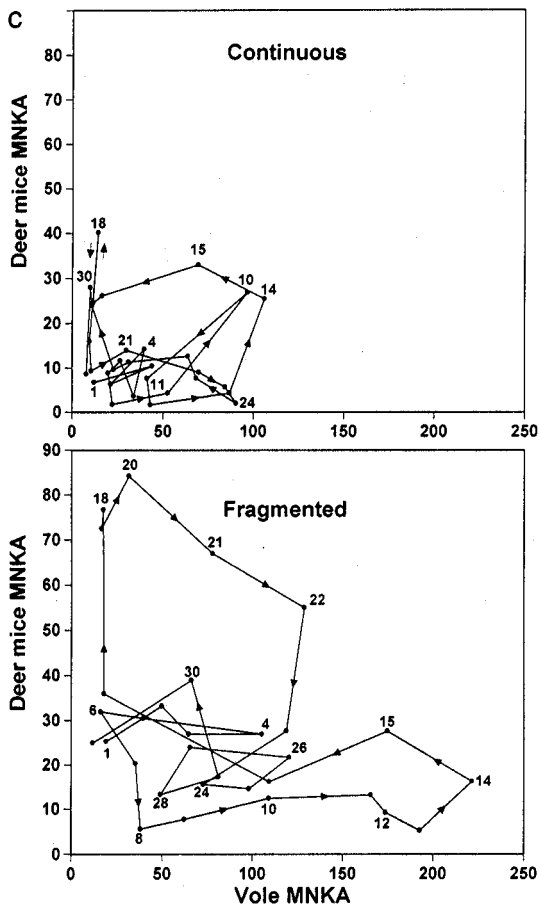


FIGURE 5. (continued)

nearly twice as many cotton rat absences as simulated small blocks (simulated = 91.0 ± 10 ; real = 176.6 ± 1.8 ; $t = 8.13$, one-tailed $P = 0.0075$, $df = 2$). For prairie voles, simulated medium blocks had a higher average number of trapping periods with zero MNKA than did real medium blocks (simulated medium = 27.0 ± 6.1 ; medium = 5.5 ± 5.5 ; $t = 2.63$, one-tailed $P = 0.06$, $df = 2$). Deer mice had a higher number of absences on simulated medium and small blocks than on real blocks (simulated medium = 62.7 ± 16 ; medium = 22.5 ± 6.5 ; $t = 2.28$, one-tailed $P = 0.075$; simulated small = 82.3 ± 22 ; small = 15 ± 8.9 ; $t = 2.87$, $P = 0.05$, $df = 2$ in both cases).

Overall, the two sites had similar and low average numbers of absences

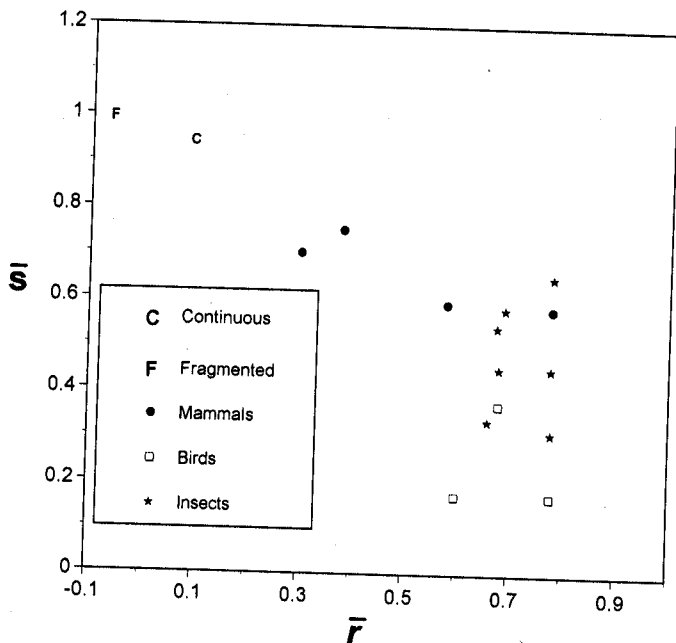


FIGURE 6. The average Spearman's rank correlation (\bar{r}) of all possible pairwise comparisons of species in the community versus the average standard deviation (\bar{s}) in the log of abundances of all species. Fourteen communities of boreal insects (stars), birds (open squares), and small mammals (closed circles) are shown from Hanski (1990). The two communities analyzed here are added to the graph. C, continuous site; F, fragmented site.

across sites for both prairie voles and deer mice. Prairie voles never went extinct in either site. Deer mice never went extinct in the fragmented site and had only one absence in the continuous site. In cotton rats, the fragmented site had a higher proportion (0.112) of extinctions than expected and the continuous site a lower proportion (0.045) of extinctions than expected ($\chi^2 = 3.321$, $df = 1$, $P = 0.0684$).

C. The Spatial Scale of Community Processes

1. Large-Scale Movements

Over nearly 8 years of study, only 10 individual cotton rats and 7 individual prairie voles switched from the fragmented to the continuous site (which are ~ 500 m apart, Fig. 1). During that time a total of 1012 cotton rats and 1702

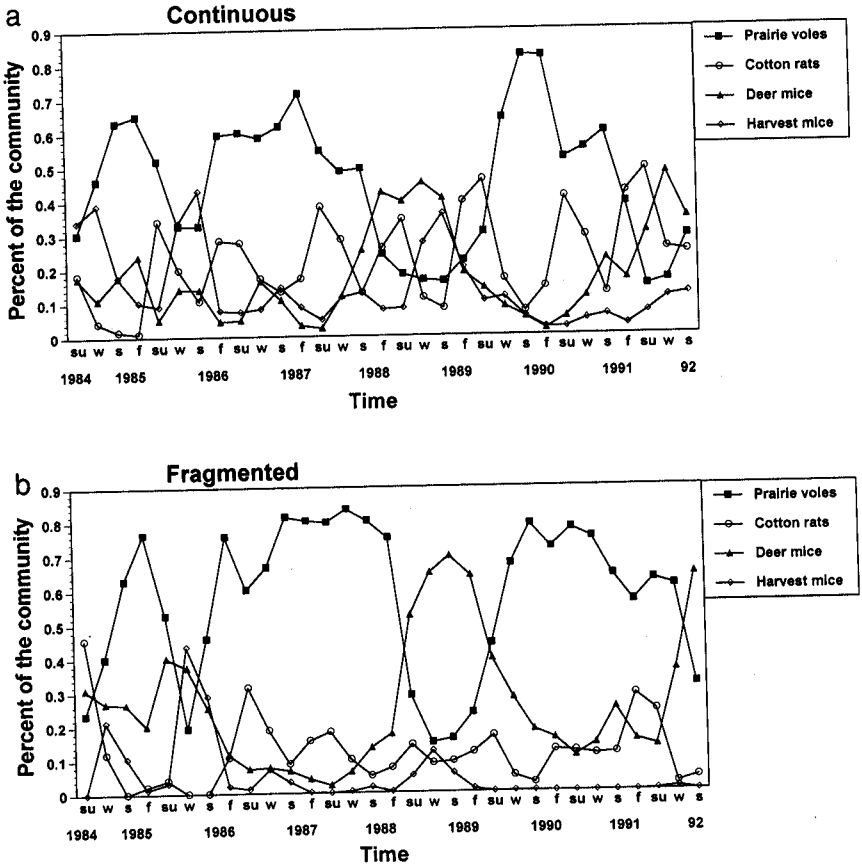


FIGURE 7. Average proportion of the community for 31 year-seasons for cotton rats, prairie voles, deer mice, and harvest mice in (a) the continuous site and (b) the fragmented site.

prairie voles were captured on the continuous site. Since deer mice were not individually marked until April 1989, we have a smaller sample size for this species. From 1989 to 1992, 227 deer mice were captured on the continuous site; during this time 2 deer mice moved from the continuous site to the fragmented site. Thus, for all species combined, fewer than 1% of their total population in the continuous site came from the marked population in the fragmented site.

Similar trends held for cotton rats in the fragmented site. Five cotton rats immigrated from the continuous site to the fragmented site, which contained a total of 1131 marked cotton rats over the study period.

2. The Influence of Movement on Local MNKA

a. *Cotton rats*. Averaging over all trapping periods, including those in which there was no switching among blocks, the proportion of MNKA accounted for by immigrants changed across year-seasons ($F = 3.491$, $df = 27$, 489 , $P < 0.0001$) and in different patterns within each block size, leading to a significant block-size by year-season interaction ($F = 4.876$, $df = 18$, 489 , $P < 0.0001$). Despite this temporal variation, large blocks averaged lower proportions of MNKA accounted for by immigrants than did medium blocks ($F = 16.313$, $df = 1$, 489 , $P < 0.0001$, Fig. 8). The proportion of MNKA accounted for by emigration also differed with time ($F = 6.340$, $df = 27$, 489 , $P < 0.0001$) and in different patterns within blocks across time ($F = 7.814$, $df = 18$, 489 , $P < 0.0001$). As with trends in immigration, large blocks had a lower average proportion of their MNKA accounted for by emigrants than did medium blocks ($F = 70.521$, $df = 1$, 489 , $P < 0.0001$, Fig. 9). (There were too few cotton rats in small blocks to do this analysis.) Using all blocks simultaneously, there was a strong, negative correlation between log (MNKA) and the log of the proportion of MNKA accounted for by both immigrants ($r = -0.915$, $df = 150$, $P < 0.001$) and emigrants ($r = -0.943$, $df = 86$, $P < 0.001$) into, or from, a block.

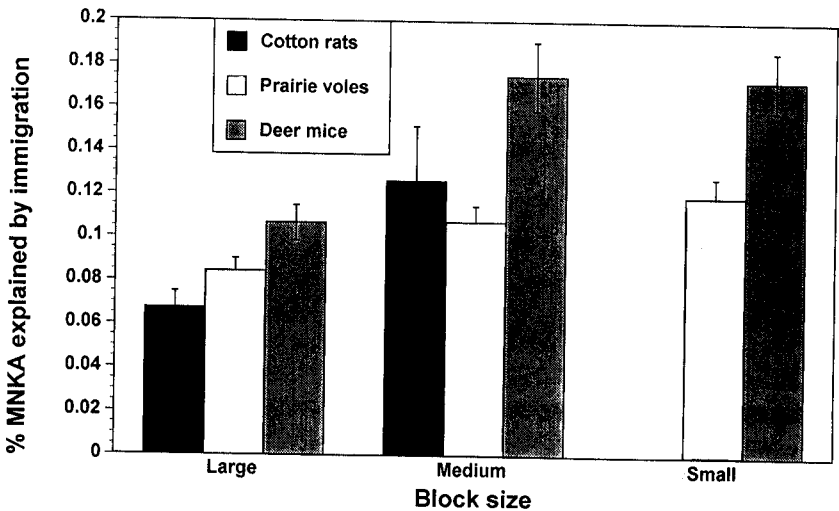


FIGURE 8. The average proportion of the MNKA with standard error bars in large, medium, and small blocks accounted for by marked immigrants from other blocks in the fragmented system for cotton rats, prairie voles, and deer mice.

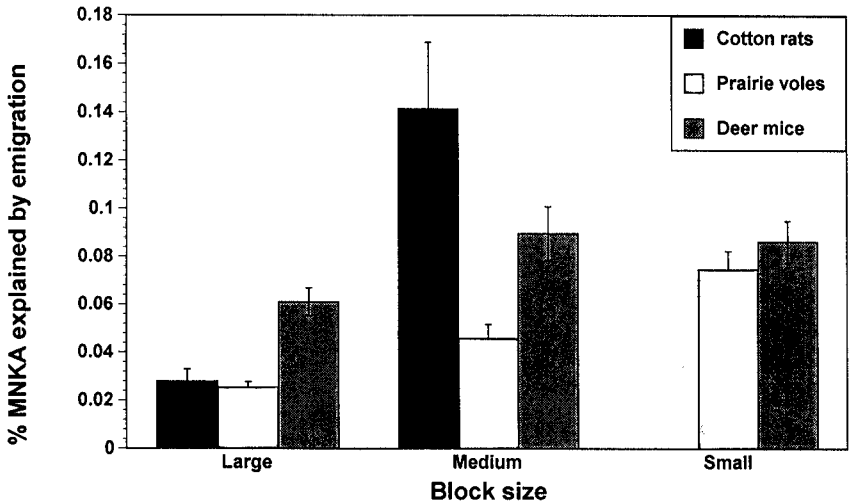


FIGURE 9. The average proportion of the MNKA in large, medium, and small blocks accounted for by marked emigrants that moved to another block in the fragmented system for cotton rats, prairie voles, and deer mice.

b. Prairie voles. Using the entire time series, the proportion of MNKA explained by immigration changed with time ($F = 1.996$, $df = 30, 1305$, $P = 0.029$) and in unique patterns among block sizes ($F = 2.036$, $df = 60, 1305$, $P = 0.049$). However, there were no significant differences among block sizes. The proportion of MNKA lost to emigration changed with time ($F = 2.581$, $df = 30, 1305$, $P < 0.0001$) and in different patterns on each block size ($F = 2.268$, $df = 60, 1305$, $P < 0.0001$). Despite this temporal variation, block size effects on the proportion of MNKA lost to emigration were apparent ($F = 24.483$, $df = 2, 1305$, $P < 0.0001$). Larger block sizes lost a lower proportion of MNKA to emigration than did smaller block sizes (Fig. 9). As with cotton rats, there was a strong and negative correlation between the log of MNKA and both the log of the proportion of MNKA explained by immigration ($r = -0.762$, $df = 760$, $P < 0.001$), and emigration ($r = -0.906$, $df = 444$, $P < 0.001$).

c. Deer mice. Using the entire data set, the proportion of MNKA accounted for by immigrants from other block sizes changed with time ($F = 3.063$, $df = 30, 1276$, $P < 0.001$) and in different patterns on each block size ($F = 1.641$, $df = 60, 1276$, $P < 0.001$). The proportion of MNKA accounted for by immigration was lower on large blocks than on small blocks ($F =$

13.206, $df = 2$, 1276, $P < 0.0001$; Fig. 8). As with immigration, the proportion of MNKA lost to emigration changed with time ($F = 2.234$, $df = 30$, 1276, $P < 0.0001$) and in different patterns within each block size ($F = 1.674$, $df = 92$, 1276, $P < 0.0001$). Despite these temporal changes, large blocks lost a lower proportion of MNKA to emigration than did medium and small blocks ($F = 9.802$, $df = 2$, 1276, $P < 0.0001$; Fig. 9). As with the other species, the log of the proportion of MNKA explained by either immigration ($r = -0.811$, $df = 374$, $P < 0.001$) or emigration ($r = -0.918$, $df = 365$, $P < 0.001$) was negatively correlated with log MNKA.

3. The Influence of Distance on Local Movements

The distance between blocks influenced the proportion of the individuals in that block accounted for by immigration. For both prairie voles and deer mice, short movements accounted for a higher proportion of the individuals in a block, relative to longer movements (prairie voles: $t = 4.29$, $df = 44$, $P < 0.001$, short movements = 0.0263 ± 0.0029 , long movements = 0.0096 ± 0.0025 ; deer mice: $t = 5.29$, $df = 32$, $P < 0.001$, short movements = 0.0687 ± 0.011 , long movements = 0.0075 ± 0.002). In cotton rats, the trend was the same, but the small sample sizes associated with analyzing movements only between the large blocks precluded a statistically significant result ($t = 1.27$, $df = 15$, $P = 0.220$, short movements = 0.0131 ± 0.0057 , long movements = 0.00497 ± 0.0028).

4. Within Site and Spatial Heterogeneity in Abundances

Maps of habitat use (Fig. 10) suggest that at least a few species unique to the continuous site also utilized microhabitats or resources unique to that area, or might be present because the site directly abutted a woodland (Fig. 1). Bog lemmings were captured primarily in areas of brome grass, a forage species which rarely occurs on the fragmented site (Fig. 10a). Wood rats were captured almost exclusively near areas of woody vegetation or young trees in the continuous site (Fig. 10b). Finally, white-footed mice were captured mainly along wooded fencerows or along the southern edge of the plot, immediately adjoining a woodland (Fig. 10c).

A number of species showed nonrandom patterns of space use, including small-scale range expansions with changes in abundances. For instance, cotton rats in the continuous site preferred the northwest corner of the plot (Fig. 11a). In the fragmented site, cotton rats were trapped almost exclusively in the large blocks (Fig. 11b). However, at low abundances (≤ 10 animals), cotton rats in the fragmented site were restricted to the centermost large block (Fig. 11c). At high densities, prairie voles in the continuous site were scarce in the

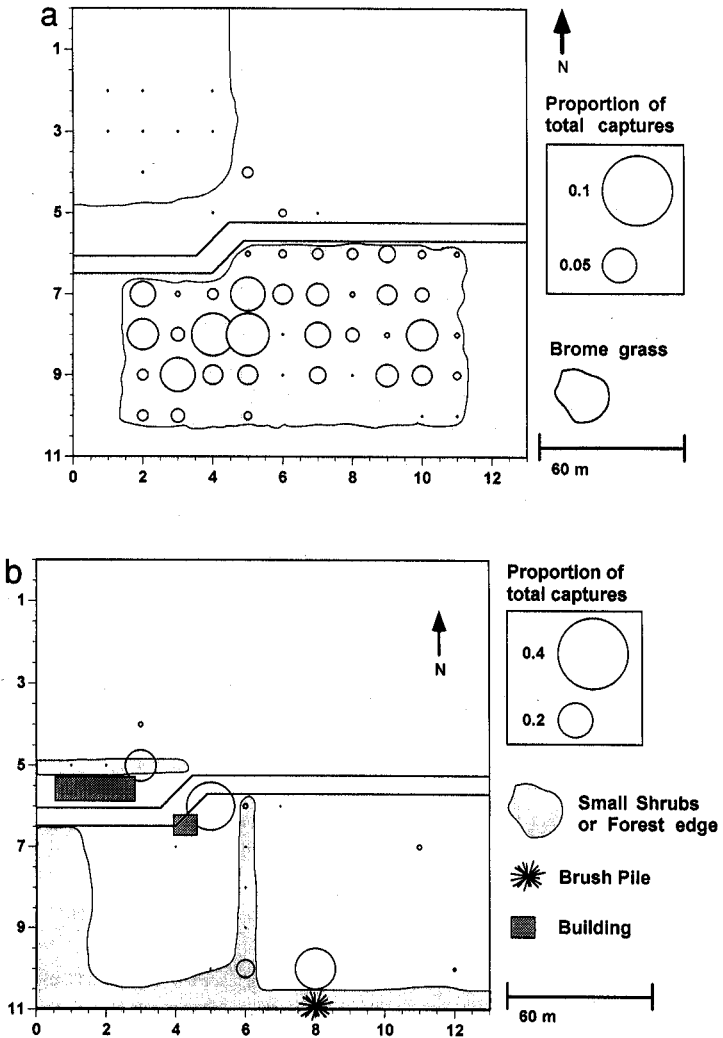
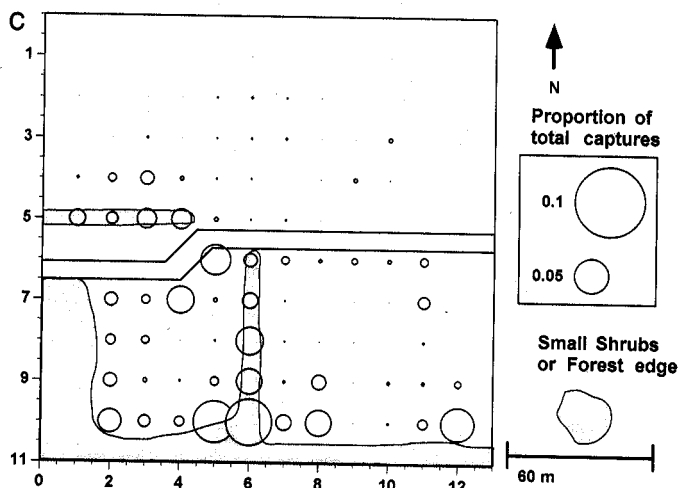


FIGURE 10. Bubble plots of space use for (a) bog lemmings, (b) wood rats, and (c) white-footed mice in the continuous area. The diameter of a bubble is the proportion of the total captures for a given trap location. The x and y axes represent the coordinate system for the trapping grid.

southwestern corner (Fig. 12a), whereas at low abundances (≤ 20 animals), the voles were found almost exclusively in the northeastern portion of the site (Fig. 12b). Deer mice occupied the northern half of the continuous site almost exclusively, regardless of density (Fig. 13a). In the fragmented site, traps in



medium and small blocks captured higher proportions of deer mice than traps in large blocks (Fig. 13b). The relative proportions of deer mice captured in the centermost large block (where cotton rats tended to aggregate at low abundances) were lower than in the other large blocks, particularly when deer mice were at high abundances (≥ 45 animals, Fig. 13b). This pattern is consistent with competitive interactions, though it could also reflect discordant responses to local vegetation. A graduate student (W. Schweiger personal communication) is currently examining our plant data to determine the potential contribution of local heterogeneity in vegetation structure to these spatial patterns.

IV. DISCUSSION

Our comparative analyses have revealed five major patterns: (1) The small-mammal community on the continuous site is more diverse than on the fragmented site. (2) As patch size increases, communities within the fragmented site increasingly resemble communities in the continuous system. Moreover, the species-specific responses to fragmentation extrapolate between sites. (3) Within the fragmented site, patchiness negatively influences species richness. (4) Community structure is highly variable at short time scales and this variability is magnified by fragmentation. (5) Immigration and emigration can have significant impacts on community structure, at a spatial scale of < 150 m;

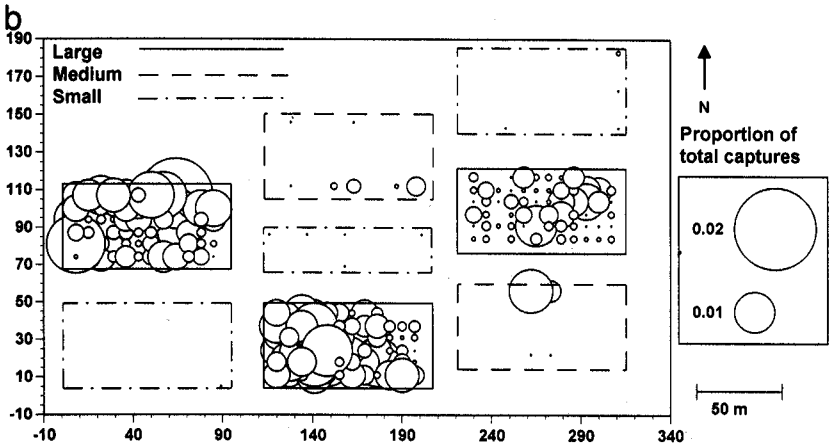
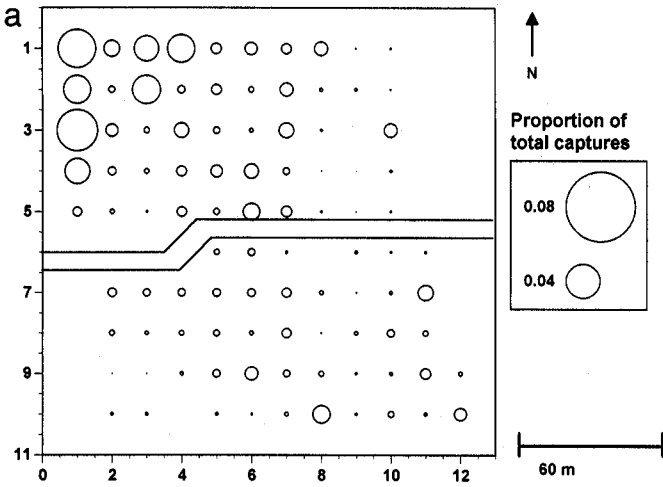


FIGURE 11. Bubble plots of space use for (a) cotton rats in the continuous site, (b) cotton rats at high densities in the fragmented site, and (c) cotton rats at low densities in the fragmented site. The diameter of a bubble is the proportion of the total captures for a given trap location.

however, observed movement rates imply communities may be effectively decoupled at scales >500 m. We discuss each of these patterns in turn and then conclude with some more general observations.

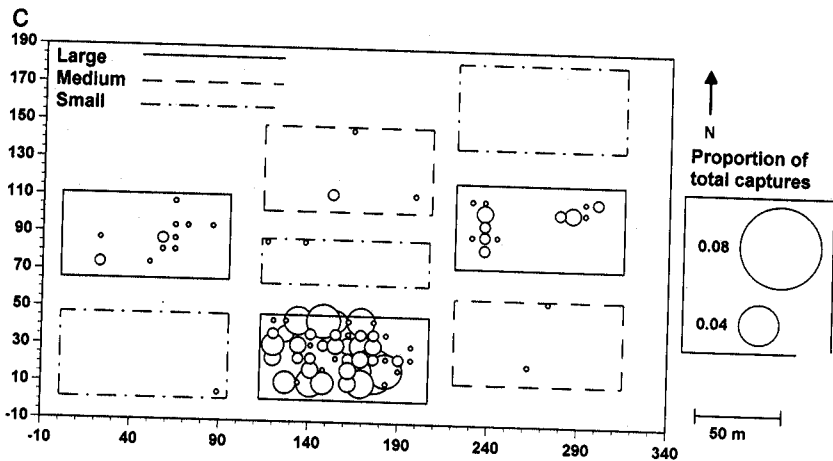


FIGURE 11. (continued)

A. The Effects of Fragmentation on Abundances

1. Higher Species Diversity in the Continuous Site

The total area of old field in our two sites is comparable. Nonetheless, the continuous site had a more diverse small mammal community. For instance, the continuous site had three species never captured in the fragmented site. Furthermore, many of the rare species were captured much more frequently in the continuous site than in the fragmented site. For example, white-footed mice were captured 1471 times out of 15,510 total captures in the continuous site, compared to just 38 times out of 23,227 total captures in the fragmented site. House mice were captured 100 times in the continuous site and only 3 times in the fragmented site. The more frequent captures of these rarer species in the continuous site resulted in a higher average species richness. Furthermore, using just the four species common in both sites, Shannon-Weiner diversity indexes were higher in the continuous system, indicating a more equitable distribution of abundances among species in the continuous site than in the fragmented site.

The higher diversity in the continuous site may reflect both patch size effects and the landscape context in which the two sites are placed. The simplest explanation for the unique species in the continuous site is the increased amount of local habitat heterogeneity found there. Unlike the fragmented site, the continuous site contains brome, patches of shrubs and small

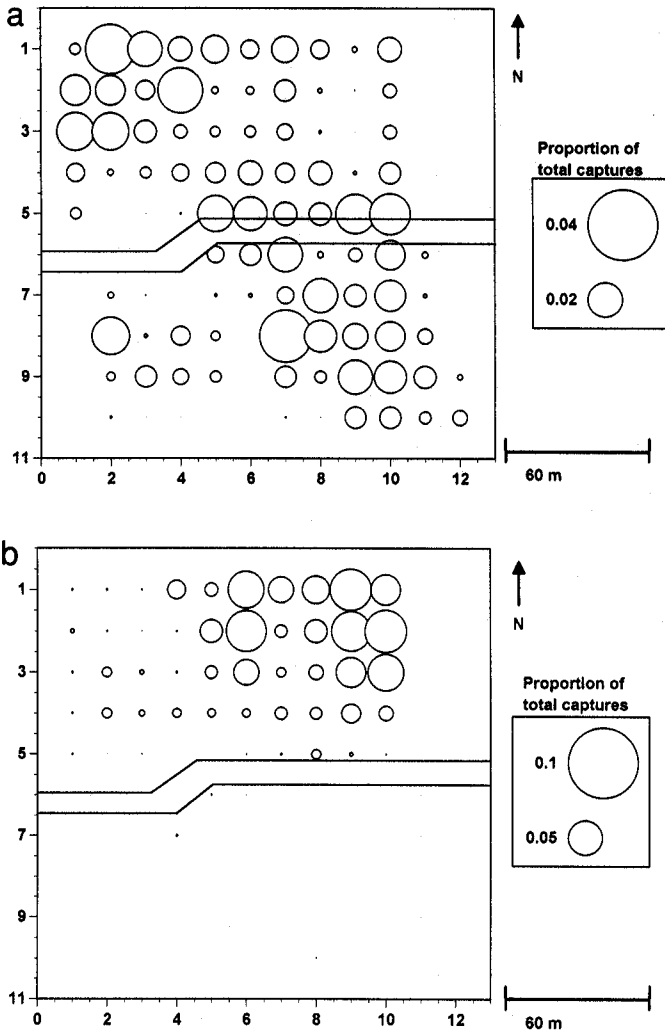


FIGURE 12. Bubble plots of space use for (a) prairie voles at high densities and (b) prairie voles at low densities in the continuous site. The diameter of a bubble is the proportion of the total captures for a given trap location.

trees distributed along fence rows, and small buildings and sheds. The bubble plots indicate that the unique species in the continuous site all preferentially use these habitats. Furthermore, those species (such as white-footed mice) which are rare in the fragmented site but more common in the continuous site also tend to use unique areas of the continuous site.

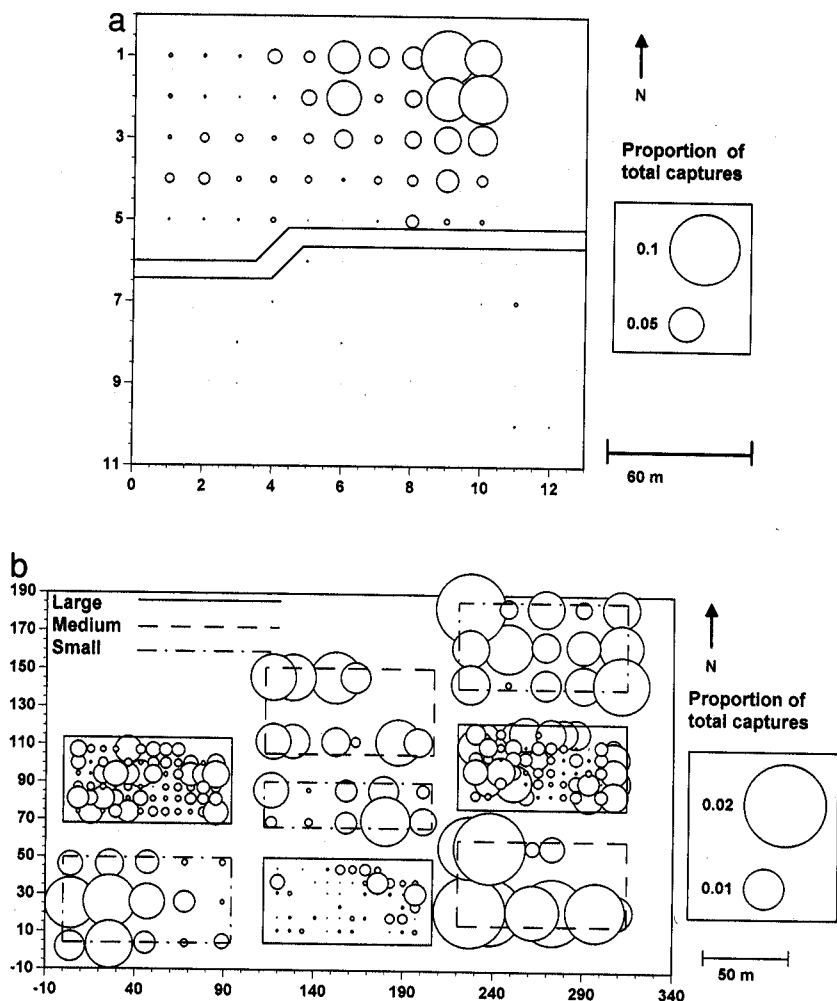


FIGURE 13. Bubble plots of space use for (a) deer mice in the continuous site and (b) deer mice at high densities in the fragmented site. The diameter of a bubble is the proportion of the total captures for a given trap location.

In 1994 the fragmented area was being invaded by woody-stemmed plants and was spotted with many small trees. In that summer wood rats and white-footed mice, species preferring wooded areas, colonized the fragmented site after 10 years of succession (J. E. Diffendorfer and W. Schweiger, unpublished data).

In addition to the unique habitats found in the continuous site, its position in the landscape likely increased the diversity of the small mammal assemblage found there. This is not an effect of fragmentation per se, but rather reflects the fact that the continuous site is juxtaposed to a woodland habitat with a different fauna which can utilize small patches of habitat (i.e., fencerows and small trees) in a way not possible in the fragmented site. There are no obvious barriers to movement from the woodland to the old-field habitat in the continuous site; by contrast, woodland animals must traverse barriers (a road and strips of interstitial habitat) to move into the fragmented site. Thus the landscape context in which a local community is embedded may influence its species richness. Even seemingly minor barriers to dispersal may markedly affect local communities.

2. *Species-Specific Responses to Fragmentation Extrapolate between Sites*

Figure 2 illustrates that large blocks in the fragmented site have communities that, on average, are relatively more similar to the continuous site than they are to smaller blocks. We interpret this as resulting from, in part, a gradient of decreasing competitive influence by dominant species from continuous habitat through large to small blocks. We are not using the observed patterns in abundance to infer competition, but rather drawing on prior, independent evidence of strong asymmetrical competition to interpret the observed spatial patterns. The negative impact of cotton rats on prairie voles was first inferred by noticing declines in prairie vole populations in the presence of cotton rats (Martin, 1956) and the failure of prairie voles to occupy sites when cotton rats were present (Frydenhall, 1969). Later support for the aggressive dominance of cotton rats over prairie voles came from combined laboratory and field studies (Terman, 1974, 1978; Glass and Slade, 1980; Prochaska and Slade, 1981) which documented prairie vole shifts in space use, diel patterns, and reduced population sizes in the presence of cotton rats. It is reasonable to expect this strong competitive interaction to be present in our system as well.

In the fragmented system, the spatial scale is such that medium and small patches are rarely used by cotton rats and are, in effect, competitor-free habitats for prairie voles. This relaxation of competition leads to (1) prairie voles having the highest densities on the blocks of medium patches when comparing among block sizes (e.g., 43% of the prairie vole population is found in the medium blocks, which make up 23% of the habitat in the fragmented site) and (2) higher overall prairie vole abundances in the fragmented site than in the continuous site.

Previous studies have also documented a negative impact of prairie voles on deer mice populations (Abramsky *et al.*, 1979; Grant, 1971, 1972; Redfield *et al.*, 1977; Doonan, 1993). In the past we have interpreted the higher deer mice

densities in the fragmented site as resulting from the ability of deer mice to use resources in the competitor-free interstitial area (Diffendorfer *et al.*, 1995b). This interpretation rests on the assumption that deer mice use the interstitial area, which was initially demonstrated by Foster and Gaines (1991). They showed that for a year (from summer 1986 to summer 1987) more than 50% of the deer mice MNKA in the entire study area came from animals captured in the interstitial area. Early in the fragmentation study, this species apparently viewed the site as a variegated habitat. However, 1994–1995 trapping in the interstitial area captured few deer mice (W. Schweiger, personal communication), indicating deer mice use of the interstitial area had declined. This may reflect a successional shift in the interstitial plant community from annuals to lower productivity perennials (R. D. Holt, unpublished data). Averaged over the years 1984–1992, it seems likely deer mice could utilize the interstitial area as a lower quality habitat, moderating any competitive impact of prairie voles. This could also help explain why deer mice were denser in large blocks than in the continuous site. Animals moving between large blocks and the interstitial area could inflate deer mice densities in patches to levels above those seen in the continuous area, thereby vitiating the effect of resident competitors. The magnitude of this spatial flux should decline with a decreasing perimeter-to-area ratio, leading to the observed decline in density with increasing patch size (small blocks to the continuous site).

Interestingly, prairie voles had higher densities in large blocks than they had in the continuous area. This is somewhat surprising, given our working hypothesis that competition with cotton rats limits their numbers and that cotton rat densities were nearly equal in the continuous area and the large blocks. A significant datum is that a higher percentage of cotton rats in the fragmented site are transients, defined as an animal captured only once (Diffendorfer *et al.*, 1995b). Thus, the actual number of territory-holding cotton rats likely to exhibit strong interference in the fragmented site is almost surely lower. This difference in the social organization of cotton rats could weaken direct competition on prairie voles, and thereby permit prairie voles to reach densities in the large blocks higher than those in the continuous site.

Fragmentation can have at least two possible effects on a community. First, fragmentation could rescale individual species densities among different sized patches, while leaving the dynamical interactions among them unchanged. Second, fragmentation can change the pattern or strength of interspecific processes themselves, which then leads to spatial heterogeneity in abundances. As a metaphor, consider the Lotka–Volterra competition model, which for species i is

$$\frac{dN_i}{dt} = N_i r_i \left[1 - \frac{N_i}{K_i} - \frac{\alpha_{ij} N_j}{K_i} \right],$$

where N_i is the abundance of competitor i where r_i is the intrinsic growth rate, K_i the carrying capacity, and α_{ij} the competition coefficient. Fragmentation could affect r_i and K_i , but leave α_{ij} unchanged. Assuming species 1 is a dominant competitor, such that $\alpha_{12} = 0$, $\alpha_{21} > 0$. In a constant environment, at equilibrium, $N_1 = K_1$, and $N_2 = K_2 - \alpha_{21}K_1$. A given change in the environment could enhance species 2 by either (1) reducing the magnitude of the carrying capacity of the dominant, K_1 , or (2) reducing the strength of competition for individuals, measured by α_{21} .

At our particular spatial scale, it is likely that both mechanisms underlie the effects of fragmentation we have observed. In our system, fragmentation changes the local abundance of competitively dominant species, which may, by itself, result in shifts in the mean abundances of subordinate species and changes in community structure.

Beyond this, a number of patterns suggest changes in interaction strength. For instance, negative correlations in abundance in our time series between prairie voles and both deer mice and harvest mice, and between cotton rats and deer mice occurred only in the continuous site. Community ecologists have often tried to use regression techniques on time series of abundances to estimate competition coefficients between species (e.g., Seifert and Seifert, 1976; Hallett and Pimm, 1979; Rosenzweig *et al.*, 1985). There is a variety of problems with this approach (Carnes and Slade, 1988), stemming in part from the absence of an independent estimate for key parameters other than the coefficients (e.g., r , K), and in part from the influence of unmeasured indirect interactions. A perusal of the phase diagrams (Fig. 5), however, provides suggestive evidence that interspecific interactions were likely modified by fragmentation. It is likely that, were we to calculate competition coefficients for a given pair of species, the estimates would differ between the sites. The basic conceptual point here is that a qualitative modification in species interactions by fragmentation may be a common, indirect effect of habitat fragmentation.

3. Species Richness and Patchiness

Patchiness decreased species richness: real medium and small blocks had lower species richness than did similar-size simulated blocks from large, continuous blocks. Furthermore, simulated medium and simulated small blocks (both simulated from the same large blocks) did not differ in species richness, but real medium and small blocks did. Thus, the amount of patchiness, (i.e., the size, number, and spacing of patches) clearly influences species richness. Our analysis of simulated blocks allows us to reject the hypothesis that this is a sampling artifact.

These trends in species richness seem to reflect the influence of patchiness

on trapping periods with zero MNKA (absences). For cotton rats and deer mice, real small blocks, when compared to small blocks simulated from large blocks, had twice as many trapping periods with zero MNKA. Furthermore, cotton rats had a higher proportion of absences and deer mice a higher average number of absences in real medium blocks compared to simulated blocks. Thus, because species had more absences in more patchy block sizes, species richness declined.

As one would expect, the trends in periods marked as absences were associated with overall density trends across the patch sizes. For example, cotton rats had the highest densities in large blocks and always had fewer absences in simulated blocks than in real medium and small blocks. Prairie voles had highest densities in the medium blocks and had more absences in simulated medium blocks than in real medium blocks. Finally, deer mice had the highest densities, and the fewest absences, in small blocks.

In our two systems, cotton rats were the only species in which the proportion of overall absences (our measure of site-wide extinction) was influenced by fragmentation. The higher proportion of cotton rat absences in the fragmented site reflects the negative effect of fragmentation on this species, which is essentially confined to three small, partially isolated populations in the large blocks (Diffendorfer *et al.*, 1995a; see Fig. 11b). The total population size of cotton rats is smaller in the fragmented site and more prone to periods of low numbers and even local site-wide extinctions there.

B. The Effects of Fragmentation on Temporal Variation in Communities

1. Old-Field Communities Are Highly Dynamic

Temporal variability is the dominant pattern in our community time series data (Figs. 7a and 7b). As is commonly seen in studies of open communities (Williamson, 1981; Holt, 1993), our rare species are sporadic in their occurrence, whereas common species disappear infrequently, despite large fluctuations in their abundance. The pattern of fluctuations in these persistent species ranges from annual cycles to what appears to be multiannual cycles. These qualitative patterns are observed at both sites, but with substantial quantitative differences. For instance, the fragmented system showed higher amounts of variation in Shannon-Weiner diversity (H), reflecting the high variability in prairie vole abundances there relative to the continuous area. It is tempting to speculate that fragmentation, by creating refuges for prairie voles in medium and small patches, effectively reduces the negative competitive influence of cotton rats on prairie voles and allows the rapid growth and occasional high abundances of this species there.

Relative to other communities, our systems showed quite high levels of variation and lower average interspecific correlations in abundances (Fig. 6). We were rather surprised at how different our systems appear to be from other vertebrate communities. The high average variance in small-mammal numbers in old-field communities may result from the cyclic nature inherent to some of the species' demography, compounded by the strong influence of seasonality on animal abundances (Stokes, 1994). The low average correlation coefficients result because some pairs of species in our systems have negative correlations in abundances through time, whereas others have positive correlations, a phenomenon which must not be as common in other assemblages.

The community in the fragmented site had a higher average standard deviation in abundances and a lower average correlation than did the continuous site. In the fragmented site, we believe a reduction in competitive pressure resulted in higher peaks in both prairie voles and deer mice with lows determined by other factors (e.g., weather). This would increase the average standard deviation. The lower correlation in abundances in the fragmented site is more difficult to interpret. We are tempted to speculate that fragmentation weakens the strength of interspecific interactions. Moreover, because interaction strengths may vary among patch sizes, averaging among patch sizes may make it more difficult to discern correlated changes in abundances.

In terms of rank abundances, the Kendall's W test indicates species ranks were positively correlated; hence, by this measure these communities were stable through time. However, based on previously reported values of W (Rahel, 1990), the continuous site has a W lower than 11 of 12 published values, and the fragmented site has a W lower than 10 of 12. Despite being stable in a statistical sense (indicating a degree of order), community structure at both our sites may be unstable relative to other communities. This is particularly so for the continuous site, which has a W almost three times lower than that of the fragmented system.

Note that despite the higher average standard deviations in abundances in the fragmented site, rank abundances were more stable in the continuous site. Why is W so much lower in the continuous site? We feel the best explanation rests on the restriction of cotton rats to the three large blocks, the competitive release of prairie voles, and the extra resources available to deer mice in the fragmented site. These factors result in high numbers of prairie voles and deer mice and consistently lower numbers of cotton rats, leading to relatively stable rank abundances over time. On the continuous site, cotton rats have more available habitat, prairie voles come under competitive pressure, and deer mice have fewer resources available relative to the fragmented site. Thus, species abundances are more similar permitting ranks to change more frequently.

In terms of presence/absence, the core species in the continuous site and the entire community in the fragmented site rarely went extinct. Thus, the

communities in the sense of presence/absence by species were quite stable. There were two clear exceptions. First, harvest mice went extinct in the fragmented site after the first 3 years (Gaines *et al.*, 1992a). Since that initial phase of occupancy they have been sporadic community members, absent in most sampling periods while persistent in the continuous site. Second, the numerous noncore species in the continuous site had frequent extinctions and recolonizations of the area (e.g., possibly reflecting spillover for the adjacent woodland species). Because of the episodic occurrence of these rarer species, one may consider the entire community in the continuous site as somewhat unstable in terms of species presence or absence. The fragmented area did not have the rare species, and the three core species (cotton rats, prairie voles, and deer mice) rarely went extinct.

Our results clearly indicate that different measures of community variability can give quite discordant impressions of stability in comparative analyses of communities at different sites.

C. The Spatial Scale of Community Dynamics

Recent analyses (Diffendorfer *et al.*, 1995a) suggest rates of individual movements may influence spatial patterns in abundances within the fragmented site. We created Markovian matrices of switching probabilities for characterizing movement among blocks, used these to predict the number of animals in a given block, and then compared the predicted abundances to the actual abundances. The matrices contain the probability of an animal switching from one block to another (off-diagonal elements) or remaining in the same block (diagonal elements). Solving the matrices for the dominant eigenvector leads to a predicted steady state of abundances in the various patches, assuming as a null model that observed asymmetries in movement are solely responsible for determining relative abundances (for further details and a sample of the matrices, see Diffendorfer *et al.*, 1995a). We created matrices for prairie voles and deer mice in each season. In all seasons except spring for prairie voles and summer for deer mice, the predicted and observed abundances did not match closely. The results indicated that within the fragmented system (at what we consider a fairly small spatial scale) movements alone cannot account for all the abundance patterns observed over the entire site. However, based on the seasons in which the abundance patterns predicted from the matrices of switching probabilities fit the observed abundances, movements do appear to be capable of influencing the local dynamics in a particular block. In general, these previous findings raised the question of the relative influence of movements on local demography and the spatial scale over which populations are coupled by dispersal.

Our analysis allows us to consider animal movements at three distinct spatial scales. First, we have rough estimates of long-distance dispersal over 0.5 km. Second, we can look at various combinations of movements between blocks in the fragmented site at scales between 15 and 140 m. Third, the bubble plots reflect patterns of space use and are useful in gauging the spatial scale at which small mammals can respond to habitat variation.

1. Large-Scale Movements

For the three dominant community members for which we have data, movements over 0.5 km seem to have little quantitative impact on local populations. If we assume that animals could immigrate to the continuous site from all directions, and that immigrants from the fragmented area account for 60° of the possible 360°, then roughly 5–6% of the total population in the continuous area came from immigrants dispersing from areas outside the site, up to a distance ~0.5 km. This observation is strengthened by considering additional data. In 1984–1985, Foster and Gaines (1991) used 350 traps in brome fields just north of the fragmented site (about 100–200 m away) and used 100 traps in the woodland due south (about 30 m away). They abandoned this additional trapping effort after determining that less than 4% of the total population in the fragmented site over an entire year came from these closely adjacent areas. In addition, our comparisons of the proportion of a given block's population accounted for by short (20–30 m) and long movements (~140 m) within the fragmented site indicate small proportions of local populations (defined as those individuals inhabiting a 50 × 100-m area) are made up of immigrants and further that these proportions decrease with increasing distance between blocks. Thus, even at shorter distances of about 100–200 m, animal movements seem to have little potential to influence local abundances.

2. Small-Scale Movements

Here we discuss the proportion of MNKA that came from or went to any other block on the fragmented site. This procedure measures the cumulative effect of movements on a local population at a scale from 15 to 140 m. For all species, the influence of immigration and emigration on local abundances varies temporally. This temporal variation indicates animal movements may only strongly influence local communities during certain time periods.

Movement of animals explained between 6 to 10% of the MNKA on large blocks across all species. Combining this with our rough estimates of longer scale movements indicates that, in general, 10–20% of a population in a 50 × 100-m block may come from immigrants over the entire disk surrounding the block, up to 0.5 km away. The influence of movements on local abundances

would be even less in larger areas, where the perimeter-to-area ratio is smaller. Our data indicate that for all species, larger blocks, with a low perimeter to area ratio, had a lower proportion of MNKA explained by animal movements than did smaller blocks.

However, the strong negative correlations between the proportion of MNKA explained by immigrants and MNKA for all species indicate that at small population sizes, a different picture emerges regarding the impact of animal movements on local abundances and community structure. When populations are small, movements constitute a much higher proportion of the MNKA, for all species. This relationship may partially explain why populations in smaller block sizes (which have lower abundances of animals) were more influenced by movements than were populations on larger block sizes.

Thus, immigration and emigration can have a strong impact on the abundances of species in old-field small-mammal communities, but only sporadically at times of low abundance, and at relatively small spatial scales (<150 m). Correlations between MNKA and the proportion of MNKA explained by movement are strong and negative. Thus, the impact of movements on local MNKA is greatest when populations are low. The familiar scenario of immigrants saving a local population from extinction may be misleading because the correlations between emigration and MNKA (which might result in local extinction) are just as strong.

3. Fine-Scale Patterns in Habitat Use

The bubble plots (Figs. 10–13) dramatically indicate how small mammals respond to small-scale variation in their habitat. The overall impression from the bubble plots is that small mammals may track preferred habitats that are quite localized, cover small areas, and change through time. We anticipate that the close analysis of spatial patterns will be a useful tool in mammal ecology during the upcoming years, given the traditional reliance on permanent trapping grids and the recent growth of GIS and spatial statistics. For instance, the precise locations of captures during times of population collapse to low numbers may be useful in determining attributes of areas where animals are capable of surviving during harsh conditions, or be used to infer the likelihood of source-sink dynamics (Holt, 1985; Pulliam, 1988; Diffendorfer *et al.*, 1995a).

4. An Overall Assessment of the Role of Spatial Dynamics

We should caution that our conclusions regarding spatial coupling result from observational studies, not from direct experimental manipulation. Because temporal fluctuations in abundances were broadly synchronous between our sites (Diffendorfer *et al.*, 1995b), there may be no particular advantage for

an animal to move more than a few home ranges from where it was born. By contrast, asynchronous fluctuations between our sites might uncover transient phases when immigration/emigration are much more significant. We should note that we have a documented case of a prairie vole moving about 1.5 km on the Nelson Environmental Study Area and a few more cases of long distance movement (J. E. Diffendorfer and N. A. Slade, unpublished data). This anecdotal evidence demonstrates small mammals can at times move long distances over heterogeneous landscapes. These rare, long distance movements may be crucial to colonization after local or regional extinctions. Finally, in the above analysis, we have only counted the immediate demographic effect of immigrants on a population; we have no information on the longer term reproductive output and hence future contribution to a local population an immigrant might make.

Obviously, when a local population is at low numbers, a female immigrant may make a disproportionate contribution to the future population. Theoretical models suggest even small amounts of dispersal can contribute to synchrony in population dynamics, given weak local density dependence (R. D. Holt, unpublished data). Kareiva and Wennergren (1995) point out that in certain predator-prey models, movements can have stabilizing effects on population dynamics even on extremely large scales, reflecting movements of individuals over multiple generations and leading to characteristic spatial scales in ecological patterns much larger than the scale of individual movement. Thus, we may be missing a more diffuse, longer term impact of movements on small-mammal communities because both our temporal and spatial scales are too small.

Despite all these caveats, our results do strongly suggest to us that the spatial scale characterizing small-mammal populations is on the order of 100–200 m. This is probably a much smaller number than what most field workers might casually believe.

V. CONCLUSIONS

To date, most studies of small mammals in old fields have focused on population dynamics rather than community structure. Our results are congruent with previous studies of old-field small mammals in the central United States with respect to aspects of community structure. We, too, have observed pronounced variability in species richness over time (Swihart and Slade, 1990), indications of interspecific competition (Martin, 1956; Frydenhall, 1969; Glass and Slade, 1980; Terman, 1974, 1978), and habitat selection based on vegetation features (Kaufman and Fleharty, 1974; Grant and Birney, 1979; Seitman *et*

al., 1994). Our work indicates that old-field small-mammal communities are among the most variable vertebrate communities reported to date. Our analyses further suggest that in addition to local processes, patch size, the degree of patchiness of the landscape, and the structure of the surrounding habitat (which influences isolation and defines the source pool) can all strongly influence local community structure. Finally, at short time scales (1–10 generations), and spatial scales exceeding 150 m, movements appear to have little impact on community structure. However, movements at smaller scales can influence community structure, particularly at low abundances. We should caution that our studies concerning movements and local abundances were done on a relatively small scale of 5000-m² blocks, separated by only 16 to 20 m. This small scale may inflate our perceived impact of movements on local abundances and community structure by creating spatial blocks of habitat smaller than typically found in nonexperimental landscapes.

Our data indicate movements have the largest impacts at low abundances. Since the two most common and most competitively dominant species in old fields (cotton rats and prairie voles) have either seasonal, annual, or multianual fluctuations, movements may influence populations during low periods and, possibly, at somewhat larger spatial scales than our current study.

Given our general conclusions, it is useful to discuss gaps in our knowledge to guide further research directions. First, we and other ecologists studying old-field small mammals have tended to focus on just the rodents and their interactions. Predators and competing species from other taxa may have profound and, as yet, poorly documented impacts on the community. (Indeed, our working hypothesis regarding the effectiveness of our interstitial area habitat as a barrier to dispersal is that small mammals found there incur a serious risk of predation.)

Second, though the circumstantial evidence for habitat selection in our system is compelling, our bubble plots and previous studies barely scratch the surface of the spatial interplay between small mammal herbivores and their resources. Food supplementation experiments have shown that the distribution of old-field small-mammal populations responds to changes in food resources (Doonan, 1994). Desert small-mammal ecologists have successfully quantified the effects of resource heterogeneity on mechanisms of species coexistence using insights from optimal foraging theory (Kotler and Brown, 1988). Attempting such research on old-field small mammals should be fruitful, given the large amounts of spatial and temporal variation in habitat and the diversity of species. Comparing the results of such studies to desert communities could permit more direct engagement with broader issues in community ecology. We find it intriguing that most work on rodent community ecology has been in desert systems; old-field rodent studies have primarily

focused on single-species questions. This may be because the mechanisms of resource use and predation avoidance are more sharply delineated and obvious in desert habitats (Kotler and Brown, 1988).

Third, further studies aimed at understanding the interplay among animal movements, local abundances, and interspecific interactions are greatly needed. Communities are open systems and determining if the flux of individuals into or out of a community affects local processes such as predation or competition is essential to a clear understanding of local community dynamics. Our data suggest movements can be influential, but only at much smaller scales than we had expected. Analyzing dispersal in conjunction with colonization and extinction dynamics may help us understand variation in species richness through time and the variation seen among communities in different locations.

We opened the paper by emphasizing the need to consider processes operating at different spatial scales when analyzing the structure of local communities. There is, in general, a rough correspondence between the spatial scale of a natural process and the temporal scale required for the full range of variation in that process to be expressed (Steele, 1995). This implies that long-term time series of data are needed to assay with any precision the influence of mesoscale (Holt, 1993) ecological processes in determining local community structure. In the case of our analyses of small mammal communities in old fields, 8 years of data is barely enough to assess patterns in temporal stability, to provide accurate estimates of local extinction rates, or to detect rare but potentially crucial events, such as bouts of long-distance movement. Short-term studies are likely to miss many longer term and larger scale factors influencing local dynamics. Our results also suggest that long-term studies may be of greatest value when carried out in a comparative spatial context, for instance, along a habitat gradient. We believe analyses of the temporal and spatial dynamics of communities provide interdependent, mutually reinforcing intellectual challenges.

VI. SUMMARY

Local communities are influenced by processes operating at multiple spatial and temporal scales. Understanding the interplay of these processes requires long-term studies conducted at distinct but spatially related sites. In this paper, we compare approximately 8 years of detailed mark-recapture data on small mammals from two sites separated by ~ 0.5 km. One site is a continuous old field and the other an experimentally fragmented old field. Within the fragmented site, the degree of fragmentation influences species distribution and abundances of animals; these effects appear to reflect a combination of species-

specific responses to habitat area and an alteration of competitive interactions. Patterns observed along the gradient from small to large patches in the fragmented site extrapolate to the continuous site.

The continuous site has a higher species richness than the fragmented site. This may reflect the presence of unique microhabitats at the continuous site rather than area effects per se, since the site abuts woodland, and the additional species appear to be present because of these differences in landscape context. Temporal variation for both communities in abundances and rank orders of abundance exceeds that reported in many other vertebrate communities, and community variability increases with fragmentation. However, the continuous site has more sporadic community members and overall more apparent extinction/colonization dynamics than does the fragmented site. Analyses of individual movements between sites indicates old-field small-mammal communities may be effectively decoupled at distances of 0.5 km. Analyses of movements within the fragmented site indicate movements can influence demographic trends at spatial scales ≤ 150 m. In general, our comparative study indicates that both landscape structure and processes occurring outside a local community can influence local community dynamics. However, the spatial scale relevant to governing population dynamics in old-field small-mammal communities may be smaller than many ecologists hitherto have believed.

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