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HABITAT FRAGMENTATION AND MOVEMENTS OF THREE SMALL MAMMALS (*SIGMODON, MICROTUS,* AND *PEROMYSCUS*)[1]

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Abstract. We studied the effects of habitat fragmentation on the movements of cotton rats (*Sigmodon hispidus*), deer mice (*Peromyscus maniculatus*), and prairie voles (*Microtus ochrogaster*) living in a fragmented landscape using 7.7 yr (1984–1992) of mark–recapture data. The study area included three kinds of 0.5-ha blocks: single large patches (5000 m^2), clusters of medium patches (288 m^2), and clusters of small patches (32 m^2). We tested three predictions regarding animal movements. First, animals should move longer distances as fragmentation increases. Second, the proportion of animals moving will decrease as fragmentation increases. Third, species will show more movement from putative sources to putative sinks. In support of our first two predictions, all species (except male cotton rats) moved farther, and lower proportions of animals moved, as fragmentation increased. In testing our third prediction, we found no trends, for all species, between patch size and the net number of animals a block either imported or exported, indicating source–sink dynamics were probably not occurring on our study site. Furthermore, animals of all species (except female deer mice) switched more frequently to blocks of larger patches. For prairie voles in the spring and deer mice in the summer, relative abundances among blocks predicted from a Markov matrix model of switching probabilities showed high congruence with the actual abundances, indicating movement and abundances were related. In both cotton rats and prairie voles but not in deer mice, more juveniles and nonreproductive animals switched between blocks than did adults or reproductive animals. Deer mice switched more frequently than did either cotton rats or prairie voles; the latter species switched in similar frequencies. We discuss the implications of our data for modeling and conservation.

Key words: dispersal; habitat fragmentation; Markov modeling; Microtus ochrogaster; *movement; patchiness;* Peromyscus maniculatus; *scale;* Sigmodon hispidus; *space use; spatial heterogeneity; source–sink dynamics.*

INTRODUCTION

Ecologists are becoming increasingly aware of the role of spatial heterogeneity in population and community dynamics (e.g., Ricklefs 1987, Karieva and Anderson 1988, Karieva 1990, Levin 1992). Movement by individuals determines the scale at which patchiness and spatial heterogeneity affect a species (Fahrig and Paloheimo 1988, Gardner et al. 1991, Harris and Silva-Lopez 1992). Analyses of a species' movement patterns should be essential to interpreting its response to habitat fragmentation, an anthropogenic process that increases heterogeneity across space by degrading once-continuous natural habitats into remnant pieces (Wilcox 1980). If these habitat fragments are not completely isolated, the ensemble of habitat patches in a landscape comprises a metapopulation (Hanski 1988, Hanski and Gilpin 1991). The rate and pattern of movements among subpopulations in a metapopulation can strongly affect spatial and temporal variation in abundance and the probability of persistence for a species (e.g., Roff 1974, Holt 1985, 1993, Lefkovitch and Fahrig 1985, Fahrig and Paloheimo 1988, Burkey 1989, Pulliam et al. 1992, Lamberson et al. 1994). Because species differ in their demographic responses to local environmental factors and in the role of movement in their life histories, a landscape that appears fragmented for one species may be continuous for another.

Here, we report on a study of movement patterns in small-mammal species in an experimentally fragmented landscape in eastern Kansas. The long-term goal of this ongoing project is to analyze how patch size and patch configuration influence the rate and pattern of succession in both plant (Robinson et al. 1992, Holt et al., *in press*) and consumer communities. The three patch sizes are arranged in eight areas (5000 m^2) we call "blocks" (Fig. 1). Given the possibility that small-mammal consumption can significantly affect plant community dynamics (Batzli and Pitelka 1971, Cockburn and Lidicker 1983, Brown and Heske 1990, Huntly 1991, Bowers 1993), and the considerable wealth of local studies on the most common species in our system (Gaines et al. 1979*a*, Johnson and Gaines 1987, Swihart and Slade 1990), a concerted effort has been made to monitor the small mammals present (Foster and Gaines 1991, Gaines et al. 1992*a, b,* Diffendorfer et al. 1995).

The three most common species in the small-mammal community are cotton rats (*Sigmodon hispidus*), prairie voles (*Microtus ochrogaster*), and deer mice (*Peromyscus maniculatus*), which collectively com-

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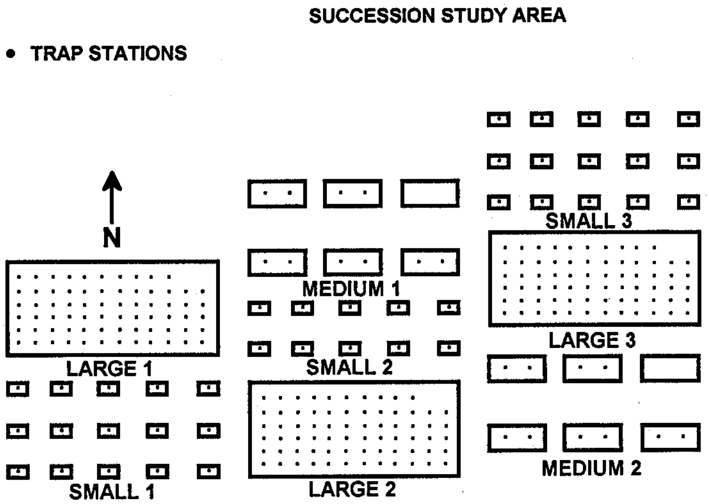

FIG. 1. Diagram of experimental blocks used in eastern Kansas study of small-mammal movements. The 40 small patches are each 4 × 8 m; the 12 medium patches are 12 × 24 m; the three large patches are 50 × 100 m. Note that one large patch is a large block; a cluster of six medium patches is a medium block; and a cluster of 10 or 15 small patches is a small block. Blocks are separated by 16–20 m.

prise nearly 95% of the total trap records from the site (J. E. Diffendorfer, *unpublished data*). We have reported on many aspects of population biology of the three species (Foster and Gaines 1991, Gaines et al. 1992*a, b,* Diffendorfer et al. 1995). Fragmentation influences a wide range of demographic variables, from abundances, to age structure, to survivorships. Given these population level effects, we felt that the scale of fragmentation should also influence movement patterns in predictable ways.

Our specific aim was to assess three hypotheses about movement patterns:

1) Distances moved. An animal should move farther distances as fragmentation increases, because the distance between suitable areas with mates, sources of food, and cover also increases with fragmentation.
2) Propensity to move. Animals should stay longer on more isolated patches. Thus, the proportion of animals moving should decrease as fragmentation increases. A standard prediction of optimal patch use models is that increasing distance between patches often leads to an increase in the amount of time spent in a patch because of the higher travel costs associated with greater isolation.
3) Assessing source–sink dynamics. We developed a source–sink hypothesis (see Pulliam 1988, Pulliam and Danielson 1992) to explain an interesting pattern of species distribution among the block sizes (Gaines et al. 1992*a*). The three species sort out according to body size, such that the largest bodied species (cotton rat, average adult mass = 145 g) has the highest densities on large blocks; the medium sized species (prairie vole, average adult mass = 44 g) has the highest densities on blocks of medium sized patches; and the smallest bodied species (deer mouse, average adult mass = 22 g) is densest on blocks of small patches (Table 1). We hypothesized (Gaines et al. 1992*a*) that large blocks are sources for cotton rats because of their large body size, whereas small and medium blocks are sinks. Medium blocks are sources for prairie voles, while large and small blocks are sinks because of negative competive interactions with cotton rats on large blocks and lack of resources on small blocks. Finally, small blocks would be sources for deer mice if they were outcompeted on medium and large blocks (sinks) by the larger species. Based on our source–sink hypothesis, we predicted that species will show more movement from putative sources to putative sinks than vice versa.

TABLE 1. Mean density (Minimum Number Known Alive per hectare) ± 1 SE by block size for cotton rats, prairie voles, and deer mice estimated from 171 live-trap censuses (1984–1991) in eastern Kansas.

	MNKA/ha by block size		
Species	Large	Medium	Small
Cotton rats	12.2 ± 0.9	4.4 ± 0.6	NA
Prairie voles	41.2 ± 2.7	77.3 ± 3.88	69.4 ± 4.1
Deer mice	13.0 ± 0.73	29.7 ± 2.1	40.0 ± 2.4

NA, not applicable.

In addition to testing these three predictions, we examined the relationship between asymmetry in movements and spatial variation in abundances, the identity of switchers, and species differences in the propensity to switch.

MATERIALS AND METHODS

Study site

The study site is located in the Nelson Environmental Study Area, 12 km northeast of Lawrence, Kansas. The 12-ha site was created in 1984 by mowing and discing a farm field, then allowing succession to proceed (Foster and Gaines 1991, Robinson et al. 1992). By continued mowing of the interstitial areas separating patches, we created habitat patches of three different sizes: large patches of 5000 m^2 (50 × 100 m), medium patches of 288 m^2 (12 × 24 m), and small patches of 32 m^2 (4 × 8 m) (Fig. 1). The different sized patches were arranged in 5000-m^2 blocks such that blocks of medium and small patches represented increasing levels of habitat fragmentation relative to the continuous large blocks. Thus, a "large block" consisted of one 5000-m^2 patch. A "medium block" consisted of six medium (288-m^2) patches, and a "small block" consisted of 15 small (32-m^2) patches. The spatial design of our system was guided by prior information on the spatial requirements and dispersal behavior of locally common small-mammal species. Blocks were ≈16–20 m apart. (See Foster and Gaines 1991 for more details on spatial design.)

Rodents were trapped on the western half (6 ha, shown in Fig. 1) of the 12-ha site nearly twice a mo from August 1984 to May 1992, (≈7.7 yr) using Sherman live traps. (See Foster and Gaines 1991 for details.) During a trapping session, traps were checked during two consecutive mornings and the intervening afternoon. Upon capture, animals were identified by ear tags (or given an ear tag if newly captured), sexed, weighed, checked for reproductive condition, and their location was noted. The data set consisted of 23 185 captures, from which we constructed individual histories of movement for animals captured more than once.

Statistical analysis

Prediction 1: distances moved will increase as fragmentation increases.—We calculated the mean squared distance (MSD) (Slade and Swihart 1983) as an estimate of animal movement, where

$$\mathrm{MSD} = \frac{\sum_{i=1}^{n} (x_i - \bar{x})^2 + \sum_{i=1}^{n} (y_i - \bar{y})^2}{n - 1};$$

x_i and y_i are individual trap location coordinates, $\bar{x}$ and $\bar{y}$ are the mean of the x and y coordinates, and n is the number of captures for an individual. MSD is a two-dimensional variance estimate in the locations in which an animal is captured, and has units (square metres). We chose MSD over other estimates of movement because we captured most animals only a few times, making other home range estimates unreliable. Also, MSD is more highly correlated with other measures of home range size than is linear distance moved between trap captures (N. A. Slade, *personal communication*).

We used three-way ANOVAs with GT2-method multiple comparisons of means (Sokal and Rohlf 1969) to test for block size (i.e., degree of fragmentation), sex, and year–season effects on average MSD moved. Using unique year–seasons as temporal units focused the analysis on the degree of fragmentation and sex differences in MSD, while taking into account temporal variation in the population. When a given year–season had no data for a unique sex and block size, that year–season was excluded from the analysis. We log-transformed the data to meet ANOVA assumptions. Because the log of zero is undefined, ANOVAs tested for movement only when movement in fact occurred.

Prediction 2: the proportion of animals moving will decrease as fragmentation increases.—We tested this prediction with two analyses. First, we used chi-square tests to compare the proportion of animals moving between patches by the degree of fragmentation. We defined "interpatch movement" as movement between patches within a 5000-m^2 block. We also compared the proportion of interpatch movements in small and medium blocks to that in simulated small and simulated medium blocks within single large patches, to avoid the problem of different trap spacing on various block sizes. The simulated blocks were created by sorting the data using trap locations. We divided the large, continuous patches into superimposed "virtual" blocks of trap locations similar to blocks of medium and small patches. The absence of cotton rats from small blocks precluded analysis there. We did not use contingency tests or log-linear models to test for proportional differences in interpatch movements because our data did not follow the Poisson distribution assumed by these tests (Kramer and Schmidhammer 1992). Instead, we calculated weekly estimates of the proportion of animals that moved between patches within a block by dividing the number of individuals moving by the total number of animals that could have moved. Animals that could have moved in week t were defined as all animals captured in both weeks t and $t + 1$ (i.e., animals captured twice in two consecutive trapping periods). The data were arcsine transformed and analyzed with paired comparisons t tests to take into account temporal variation in interpatch movements. Weeks with no data for one or more of the block types were excluded.

Prediction 3: species will show more movement from putative sources to putative sinks than vice versa.—A salient feature of source–sink population structures is that sink habitats should import more animals than they export, whereas source habitats should export more animals than they import. We can use movement data to test this prediction. We first looked for general trends in the direction of switching. Here, "switching" was defined as movement from one block (i.e., a single large patch, a block of medium patches, or a block of small patches) to another. We estimated the proportion of switches in different directions by dividing the number of individuals switching by the total number of potential switchers. Potential switchers for week t were defined as all animals captured in both weeks t and $t + 1$ (i.e., animals captured twice in two consecutive trapping periods). Data were categorized by switching direction (to larger blocks; to smaller blocks; and to blocks of the same size), sex, and year–season, and were then analyzed using three-way ANOVAs on arcsine-transformed data. The data were weighted by sample size in the analyses.

In addition to analyzing the direction of switching, we calculated the net number of individuals a block either imported or exported. We subtracted the number of animals leaving a block that were later captured elsewhere from the number that entered after having been previously captured elsewhere. For each species and block, we calculated the net number of switchers for each season over the entire data set. Chi-square tests were used to determine whether or not the number of animals leaving or entering a block deviated from an expected 1:1 ratio.

Relationship between movements and abundances.—We examined the relationship between individual movement patterns and spatial variation in abundance by creating 8 × 8 Markov transition matrices summarizing the movement data. Using these matrices to predict an expected spatial distribution, we then compared this expectation to the observed abundances. Matrix elements are probabilities of an animal switching from one specific block to another. Matrix columns contain probabilities of an animal switching from one block to any of the other seven (off-diagonal elements of the matrix), or staying in its current block (diagonal elements). The column elements sum to one. If we assume these probabilities are temporally invariant and that birth and death rates are negligible over the time scales associated with movement, the stable patch distribution (i.e., the eigenvector associated with the dominant eigenvalue, which for a Markov matrix is unity) gives the expected relative distribution of animals among the eight blocks. The stable patch distribution for a spatial dispersal matrix is analogous to the stable age distribution of a Leslie matrix. The basic approach is to generate a null model where the only factor influencing abundance is movement. We created Markovian switching matrices for each season for both prairie voles and deer mice. Because so few cotton rats switched to or from small blocks, their matrices were not further analyzed.

The expected distribution of animals based on the switching matrices was then compared to seasonal Minimum Number Known Alive (MNKA) estimates for each block. The stable patch distribution and the estimates of MNKA were normalized by dividing all elements of each vector by the sum of the elements in the vector. We compared the expected and observed abundances using correlations and chi-square tests.

Species differences in switching propensity.—We tested for species differences in the propensity to switch between blocks by taking weekly estimates of the total proportion of animals in each species switching between blocks in all directions and comparing among species with a one-way ANOVA.

Identity of switchers.—Within each species, we compared the proportion of animals switching between blocks by age and reproductive condition. We analyzed the sexes separately and sorted the data either by reproductive condition (males: testes scrotal or not scrotal; females: nipples medium or larger) or by mass. Cotton rats with mass >112 g were considered adults, as were prairie voles >33 g and deer mice >18 g (Gaines et al. 1992*b*). We used t tests weighted by sample size to analyze estimates of the percent (arcsine transformed) of animals switching between blocks.

RESULTS

Prediction 1: distances moved will increase as fragmentation increases

Cotton rats.—We did not analyze movements on small blocks because few cotton rats were found there. Furthermore, the low sample sizes of animals on medium blocks precluded testing for interactions among sex, year–season and degree of fragmentation. Instead, we analyzed only the main effects. Average MSD moved changed through time but there were no apparent patterns ($F = 2.530$; df = 26, 604; $P < 0.001$). Both sexes moved similar distances, as did animals living in different degrees of fragmentation (Table 2).

Prairie voles.—As with cotton rats, prairie vole MSD moved changed with time but no patterns were obvious ($F = 3.006$; df = 20, 2137; $P < 0.001$). Furthermore, different patterns on each block size resulted in a significant block by year–season interaction ($F = 1.661$; df = 40, 2137; $P = 0.006$). Despite this variation, voles on average moved farther on more fragmented, small blocks than on medium blocks, and farther on medium than on large, continuous blocks ($F = 79.141$; df = 2, 2137; $P < 0.001$; Table 2). Male prairie voles moved farther, on average, than did females ($F = 37.667$; df = 1, 2137; $P < 0.001$; Table 2).

Deer mice.—In deer mice, average MSD moved changed over time ($F = 2.981$; df = 17, 538; $P < 0.001$). Deer mice moved farther on small than on medium, and farther on medium than on large blocks ($F = 27.269$; df = 2, 538; $P < 0.001$; Table 2). The sexes moved similar MSD.

In summary, prairie vole and deer mouse movements supported prediction 1 but cotton rats movements did not.

Prediction 2: the proportion of animals moving will decrease as fragmentation increases

For all three species, the proportion of interpatch movements (movements between patches within a

TABLE 2. Mean squared distance (MSD) moved by cotton rats, prairie voles, and deer mice, analyzed by block size and by sex. *N* represents the number of individuals whose MSDs were included in the calculations. For prairie voles and deer mice, means among all block sizes were significantly different ($P < 0.001$). Prairie vole males moved significantly farther than females ($P < 0.001$). No other differences among means were statistically significant.

	MSD in m^2 (mean ± 1 SE) by block size					
Sex	Large	*N*	Medium	*N*	Small	*N*
			COTTON RATS			
Males	201.8 ± 13.8	289	172.8 ± 50.3	15	NA	
Females	166.3 ± 10.5	304	228.8 ± 83.2	25	NA	
Total	183.8 ± 8.6	593	207.8 ± 55.0	40	NA	
			PRAIRIE VOLES			
Males	139.6 ± 6.6	796	202.3 ± 21.3	203	283.5 ± 22.7	176
Females	96.8 ± 5.6	952	118.8 ± 13.7	305	217.1 ± 18.4	179
Total	116.3 ± 4.3	1748	152.1 ± 12.0	508	250.0 ± 14.7	355
			DEER MICE			
Males	162.2 ± 14.1	259	259.7 ± 34.4	70	311.8 ± 40.4	67
Females	114.3 ± 11.0	215	216.5 ± 33.7	98	279.4 ± 31.9	95
Total	140.5 ± 9.2	474	234.5 ± 24.3	168	292.8 ± 25.0	162

NA, not applicable.

block) decreased as fragmentation increased from continuous large to fragmented small blocks (cotton rats: $\chi^2 = 52.69$, df = 1; prairie voles: $\chi^2 = 531.33$, df = 2; deer mice: $\chi^2 = 102.33$, df = 2; $P < 0.001$ in all cases; Table 3). Since this analysis did not take into account differences in trap spacing across blocks, we simulated the arrangement of trap locations found on medium and small blocks within large blocks.

Simulated blocks represent continuous habitat with trap locations separated by distances nearly equal to those on the smaller blocks. Real blocks are the actual, fragmented, 5000-m^2 areas. We expected lower proportions of interpatch movements on real blocks than on simulated blocks. For cotton rats, we could not compare the proportion of interpatch movements on simulated vs. real small blocks because no animals were captured more than once on the small blocks. However, a lower proportion of interpatch movements occurred on real than on simulated medium blocks ($t = 2.36$, df = 13, one-tailed, $P = 0.017$; Table 4). Prairie voles had a lower proportion of interpatch movements on real than on simulated blocks for both small and medium block sizes (small blocks: $t = 1.42$, df = 137, one-tailed, $P = 0.079$; medium blocks: $t = 2.05$, df = 145, one-tailed, $P = 0.021$; Table 4). Deer mice showed no influence of habitat fragmentation on the proportion of interpatch movements. For both medium and small blocks, the proportions of interpatch movements did not differ between real and simulated blocks.

In summary, all three species had lower frequencies of interpatch movements as fragmentation increased in comparisons across block sizes. However, an analysis based on simulated fragmentation within contiguous habitat indicated that for cotton rats and prairie voles, but not for deer mice, the proportion of interpatch movements decreased as fragmentation increased.

Prediction 3: species will show more movement from putative sources to putative sinks than vice versa

Cotton rats.—As with the MSD analysis, low numbers of cotton rats in the spring and on medium blocks resulted in empty cells and precluded tests for higher order interactions. Therefore, the ANOVA tested for the unique effects of time (year–seasons), direction, and sex on the proportion of cotton rats switching between blocks. The proportion of animals switching between blocks did not change with time. A higher pro-

TABLE 3. Proportion (mean ± 1 SE) of interpatch movements within a block for cotton rats, prairie voles, and deer mice, analyzed by block size. Parentheses indicate number of individuals sampled.

	Block size		
Species	Large	Medium	Small
Cotton rats	0.968 ± 0.008 (557)	0.864 ± 0.029 (140)	NA
Prairie voles	0.913 ± 0.007 (1788)	0.698 ± 0.012 (1443)	0.598 ± 0.018 (719)
Deer mice	0.895 ± 0.013 (514)	0.761 ± 0.019 (523)	0.651 ± 0.027 (304)

NA, not applicable.

TABLE 4. Proportion (mean ± 1 SE) of interpatch movements on small, medium, simulated small, and simulated medium blocks for cotton rats, prairie voles, and deer mice. Sample sizes (in parentheses) are the number of weeks in which the percent of animals switching was compared.

	Block type			
Species	Medium	Simulated medium	Small	Simulated small
Cotton rats	0.196 ± 0.001 (14)	0.642 ± 0.002 (14)	NA	0.826 ± 0.088 (67)
Prairie voles	0.156 ± 0.002 (145)	0.227 ± 0.002 (145)	0.510 ± 0.034 (138)	0.570 ± 0.043 (138)
Deer mice	0.468 ± 0.081 (46)	0.417 ± 0.059 (46)	0.746 ± 0.063 (67)	0.690 ± 0.083 (67)

NA, not applicable.

portion of cotton rats switched toward larger blocks (*F* = 142.0; df = 2, 1854; $P < 0.001$; Table 5). Males switched in higher average proportions than did females (*F* = 7.82; df = 1, 1854; *P* = 0.005; Table 5). The net number of animals a block imported or exported never deviated from an expected 1:1 ratio. Blocks in the summer and fall lost or gained a greater number of animals than in other seasons (Fig. 2A).

Prairie voles.—Despite a statistically significant three-way interaction between year–season, direction, and sex (*F* = 10.214; df = 60, 14 430; $P < 0.001$), voles showed obvious trends in switching. The proportions of voles switching changed with time (*F* = 10.14; df = 30, 14 433; $P < 0.001$), yet higher proportions of both sexes switched toward larger than toward smaller blocks (*F* = 260.553; df = 2, 14 433; $P < 0.001$; Table 5). Males switched in greater average proportions than did females (*F* = 53.676; df = 1, 14 433; $P < 0.001$; Table 5). The net number of animals a block imported or exported never deviated from an expected 1:1 ratio. Blocks lost or gained more animals in the fall than in other seasons (Fig. 2B).

Deer mice.—As in voles, the interaction between year–season, direction, and sex significantly influenced the proportion of deer mice switching (*F* = 3.181; df = 52, 3507; $P < 0.001$). Despite the interactions, higher average proportions of animals switched toward larger blocks (*F* = 166.592; df = 2, 3507; $P < 0.001$; Table 5). Males switched in higher proportions than did females (*F* = 16.885; df = 1, 3507; $P < 0.001$; Table 5). However, females did not show a bias in the direction of switching. As with the other species, the net number of individuals a block imported or exported never deviated from an expected 1:1 ratio. In the spring, blocks imported or exported more animals than in other seasons (Fig. 2C).

In summary, a greater proportion of animals in all species switched from smaller to larger blocks, with males switching in greater proportions than females. For all species, the net numbers of animals a block imported or exported did not deviate from a 1:1 ratio. Species showed different seasonal trends in the number of animals imported and exported.

The relationship between movements and abundances

For prairie voles, the predicted stable patch distributions of block abundances generated from the Markovian switching matrices were positively correlated with observed abundances in all seasons except sum-

TABLE 5. Proportion (mean ± 1 SE) of animals switching between patches, analyzed by direction and sex. *N* represents sample size and includes the weighting factor used in the ANOVAs. Statistically higher percentages of all species switched to larger blocks ($P < 0.001$), and higher percentages of males switched than females ($P < 0.005$).

	Switching direction					
Sex	To larger	*N*	To smaller	*N*	To same size	*N*
			COTTON RATS			
Males	0.374 ± 0.075	32	0.028 ± 0.004	427	0.037 ± 0.006	402
Females	0.188 ± 0.057	48	0.018 ± 0.003	510	0.026 ± 0.005	466
Total	0.264 ± 0.046	80	0.023 ± 0.003	937	0.031 ± 0.004	868
			PRAIRIE VOLES			
Males	0.072 ± 0.005	1088	0.031 ± 0.002	2237	0.008 ± 0.000	2727
Females	0.048 ± 0.003	1656	0.020 ± 0.001	3119	0.006 ± 0.000	3792
Total	0.057 ± 0.002	2744	0.025 ± 0.001	5356	0.007 ± 0.000	6519
			DEER MICE			
Males	0.171 ± 0.015	310	0.117 ± 0.001	573	0.018 ± 0.002	735
Females	0.108 ± 0.010	483	0.096 ± 0.008	618	0.010 ± 0.001	869
Total	0.132 ± 0.008	793	0.106 ± 0.006	1191	0.014 ± 0.002	1604

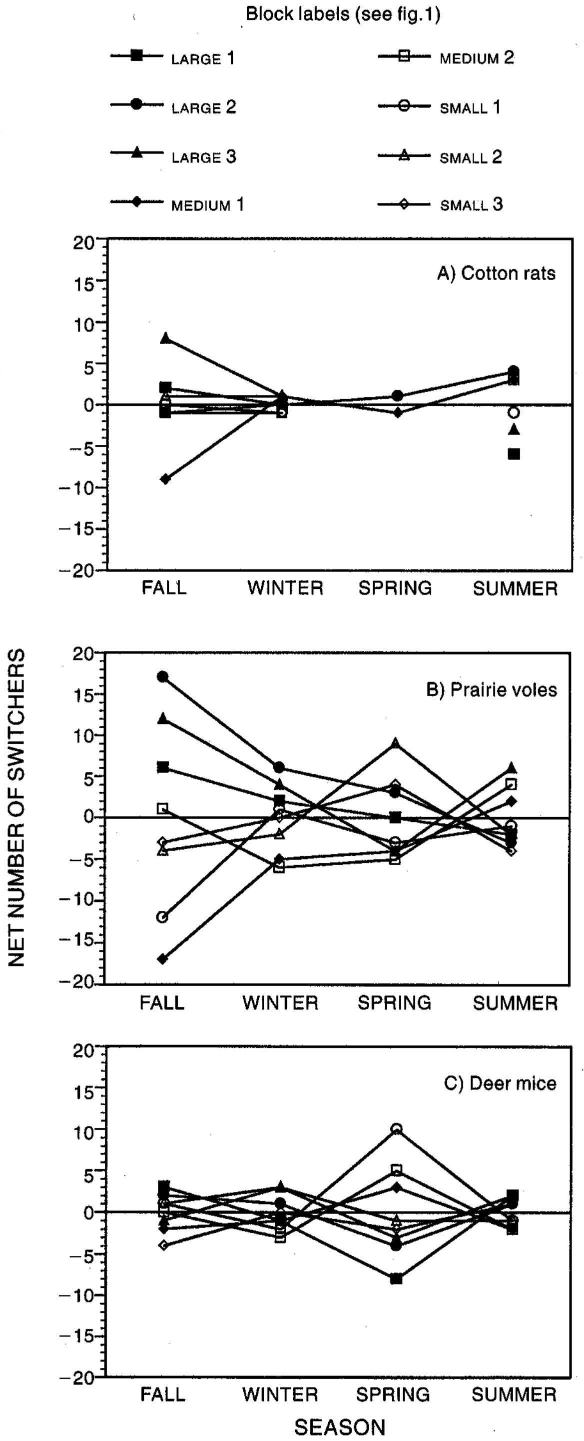

FIG. 2. The net number of (A) cotton rats, (B) prairie voles, and (C) deer mice switching into or out of the eight blocks in the study area. Positive values mean the block is gaining individuals; negative values mean the block is exporting individuals. The numbering system labels blocks of a given size from west to east. Thus, "Small 1" refers to the westernmost small block and "Small 3" the easternmost. "Small 2" is in between (see Fig. 1).

TABLE 6. Correlations and chi-squares between observed abundances and abundances predicted from matrices of per capita switching for prairie voles and deer mice. Eight comparisons were made, so correlation coefficients have 6 df and chi-squares have 7 df.

Season	Statistics for observed vs. expected small mammal abundances: Correlation	Chi-square
	PRAIRIE VOLES	
Fall	.803*	26.11***
Winter	.906*	17.44*
Spring	.899*	7.47
Summer	.674	17.13*
	DEER MICE	
Fall	.658	10.20
Winter	.300	51.20***
Spring	.292	13.29
Summer	.954*	2.46

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

mer (Table 6). The goodness-of-fit tests indicated significant differences among predicted and observed numbers of voles on the blocks in all seasons except spring. Predicted abundances of deer mice were positively correlated with observed abundances in the summer. Goodness-of-fit tests were significant only for winter but not for the other seasons. (See Fig. 3 for a representative matrix and associated vectors. All eight matrices and vectors of abundances are available on request from the ESA Supplementary Publication Service.[2]) In summary, the high correlation and low chi-square for prairie voles in the spring and deer mice in the summer indicate a close fit between observed abundances and those expected based solely on movement.

Species differences in per capita switching

Deer mice switched blocks in higher proportions (17.66 ± 0.24% [mean ± 1 SE], weighted $n = 2530$) than did either cotton rats (8.86 ± 0.28%, weighted $n = 1348$) or prairie voles (6.94 ± 0.05%, weighted $n = 8810$). Cotton rats switched in higher proportions than did prairie voles (ANOVA weighted by weekly sample size: $F = 1774.71$; df = 2, 12 685; $P < 0.001$). Deer mice also had a higher percentage of animals making reciprocal switches, defined as multiple switches to and from the same blocks (cotton rats: 22.83 ± 4.38%, $n = 92$; prairie voles: 26.86 ± 2.10%, $n = 443$; deer mice: 38.49 ± 2.99%, $n = 265$; $\chi^2 = 13.342$, df = 2, $P = 0.001$).

Characteristics of switchers

Cotton rats.—Adult males (as defined by body mass) switched in greater average proportions than did ju-

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[2] See ESA Supplementary Publication Service Document Number 9501. For a copy of this document, contact the senior author or order from the Ecological Society of America, 328 East State Street, Ithaca, New York 14850 USA. There is a small fee for this service.

Matrix
Prairie voles, spring

Abundances

$$
\begin{array}{c}
 \\ S1 \\ L1 \\ L2 \\ S2 \\ M1 \\ M2 \\ L3 \\ S3
\end{array}
\begin{array}{cccccccc}
S1 & L1 & L2 & S2 & M1 & M2 & L3 & S3
\end{array}
\qquad
\begin{array}{cc}
\text{Predicted} & \text{Observed}
\end{array}
$$

$$
\begin{array}{c|cccccccc}
 & S1 & L1 & L2 & S2 & M1 & M2 & L3 & S3 \\
\hline
S1 & .750 & .022 & .005 & 0 & 0 & .008 & 0 & 0 \\
L1 & .150 & .927 & .011 & .016 & .023 & .008 & .0174 & 0 \\
L2 & .05 & .017 & .926 & .081 & 0 & .025 & .013 & 0 \\
S2 & .025 & .009 & .021 & .726 & .092 & .025 & .013 & .012 \\
M1 & 0 & .009 & .005 & .129 & .840 & 0 & .009 & .048 \\
M2 & .025 & .004 & .016 & 0 & .008 & .875 & .017 & 0 \\
L3 & 0 & .013 & .016 & .016 & .031 & .050 & .896 & .036 \\
S3 & 0 & 0 & 0 & .032 & .008 & .008 & .035 & .905
\end{array}
\qquad
\begin{array}{c}
\text{Predicted} \\ \hline
.188 \\ .209 \\ .180 \\ .131 \\ .070 \\ .023 \\ .088 \\ .112
\end{array}
\qquad
\begin{array}{c}
\text{Observed} \\ \hline
.288 \\ .201 \\ .202 \\ .105 \\ .112 \\ .033 \\ .043 \\ .078
\end{array}
$$

FIG. 3. Matrix of per capita switching rates from one block (columns) to another (rows), predicted abundances calculated from the matrix, and a normalized vector of the observed abundances on each block for prairie voles in the fall. See Fig. 1 for block assignments (L, large; M, medium; S, small) and Table 6 for results.

venile males (t = 8.00, df = 581, $P < 0.001$; Table 7). Reproductive males switched in greater average proportions than nonreproductive males (t = 7.97, df = 542, $P < 0.001$). In females, juveniles switched in greater average proportions than adults (t = 3.78, df = 651, $P < 0.001$), and nonreproductive females tended to switch more frequently, on average, than reproductive females (t = 2.66, df = 634, P = 0.008).

Prairie voles.—The average proportion of juvenile males switching was greater than the average proportion of adult males switching (t = 5.45, df = 3452, $P < 0.001$; Table 7). Nonreproductive males switched in greater average proportions than reproductive males (t = 4.65, df = 3294, $P < 0.001$). Juvenile females switched in greater average proportions than adult females (t = 8.26, df = 4587, $P < 0.001$). Finally, nonreproductive females switched in greater average proportions than reproductive females (t = 3.97, df = 4353, $P < 0.001$).

Deer mice.—In both males and females, neither age (i.e., body mass) nor reproductive condition had statistically significant effects on the average proportions of animals switching.

In summary, a greater proportion of nonreproductive juveniles switched between blocks in both sexes of voles and in female cotton rats. In male cotton rats, adults and reproductive animals switched in greater proportions. In deer mice, age and reproductive condition did not influence the proportion of animals switching. Finally, in our earlier analysis of the direction of switching (see prediction 3), males switched in greater proportions than females in all species.

DISCUSSION

Taken as a whole, our data indicate an interesting dichotomy in species' responses to fragmentation. At a within-blocks spatial scale (i.e., with 5000-m^2 patches), the three small-mammal species responded similarly to fragmentation. However, at the larger scale of switching between blocks over the entire 6-ha site, each species showed a different response to fragmentation.

Predictions 1 and 2

The predictions that (1) animals will move farther as fragmentation increases, and (2) the proportion of animals switching will decrease as fragmentation in-

TABLE 7. Sex, age, and reproductive status differences in switching behavior in cotton rats, prairie voles, and deer mice. Data are expressed as proportion (mean ± 1 SE) of animals switching between blocks. N is the sum of the number of individuals used to calculate proportions in each trapping period.

Age class or condition	Proportion switching between blocks			
	Males	N	Females	N
	COTTON RATS			
Juvenile	0.060 ± 0.005	487	0.072 ± 0.005	489
Adult	0.209 ± 0.031	86	0.031 ± 0.007	164
Not reproductive	0.053 ± 0.006	432	0.059 ± 0.005	506
Reproductive	0.214 ± 0.027	112	0.031 ± 0.008	130
	PRAIRIE VOLES			
Juvenile	0.077 ± 0.008	509	0.059 ± 0.004	783
Adult	0.057 ± 0.001	2945	0.037 ± 0.001	3806
Not reproductive	0.079 ± 0.006	776	0.048 ± 0.002	2085
Reproductive	0.062 ± 0.000	2520	0.039 ± 0.001	2270
	DEER MICE			
Juvenile	0.163 ± 0.009	502	0.114 ± 0.008	500
Adult	0.175 ± 0.008	572	0.140 ± 0.006	659
Not reproductive	0.188 ± 0.009	484	0.131 ± 0.007	628
Reproductive	0.169 ± 0.008	568	0.131 ± 0.001	514

creases, represent movements at a small spatial scale within 5000-m^2 blocks. At this scale, movements probably reflect daily foraging and other short-term decisions. In fragmented habitats, the three species either moved farther distances or moved less often than they did in continuous habitats. In general, these findings support our first two predictions. Although the distance cotton rats moved and the proportion of deer mouse interpatch movements were not influenced by fragmentation, in no instance did animals move either smaller distances or more often as fragmentation increased.

Unlike voles and deer mice, cotton rats did not increase movements as fragmentation increased. Possibly, at this scale, fragmentation did not affect movement distances for this species. However, small sample sizes and large variances for MSDs on blocks of medium patches made distinguishing among block size effects statistically difficult.

Although the proportion of interpatch movements by deer mice decreased with fragmentation across block sizes, this trend did not hold when comparing simulated to real blocks. Given this inconsistency, we believe the comparisons between simulated and real blocks are more reliable because they are not confounded with trap spacing effects. We are uncertain why the proportion of deer mice moving between patches on simulated blocks did not differ from the proportion switching on real blocks. One explanation is that deer mice use the mowed, interstitial area between patches (Foster and Gaines 1991) and may not view the patches as the only usable habitat type within a block. Therefore, our experimental method of imposed fragmentation may not inhibit their propensity to switch patches. Radiotelemetry studies would help to answer this question.

Interestingly, the proportion of interpatch movements for all species was smaller on medium and simulated medium than on small and simulated small blocks (Table 4). This seems counterintuitive because the small blocks are more fragmented than the medium blocks. However, based on trap locations, the medium blocks, though having more available habitat, actually have a higher degree of insularity (i.e., greater distances between trapping stations) than do small blocks. Therefore, we might expect the actual percentage of animals moving between patches within a block to be higher on blocks of small patches (simulated or real) than on blocks of medium patches. As a consequence of trap spacing, trap locations within medium blocks are more isolated than those within small blocks, despite less fragmentation.

At the small scale of 5000 m^2, our data support the hypotheses that most animals faced with living in a fragmented habitat are (1) forced to move farther distances when they do move, presumably to find food and mates, and (2) do not move as often, presumably because of costs associated with the longer distances traveled. We found exceptions, but in no cases did increasing fragmentation decrease the distances moved or increase the proportion of animals switching.

Prediction 3. Species will show more movement from putative sources to putative sinks than vice versa

Taken together, the consistent pattern of all species moving from smaller to larger blocks and the lack, for all species, of any block size trends in net number of switchers are evidence against our hypothesis (Gaines et al. 1992*a*) implying source–sink dynamics on the study site. Furthermore, all three species have highest persistence rates on large blocks (Gaines et al. 1994), which also argues against the source–sink hypothesis.

There are two basic ways a sink population can be maintained in a spatially heterogeneous environment (Holt 1993). First, random or passive dispersal can produce sinks in low-quality habitat. Second, interference competition in high-quality habitat can force subordinate individuals into inferior habitats. If animals can discern habitat quality accurately and are not prevented from settling by interference, one expects spatial patterns of abundance to match the ideal free distribution (IDF, Fretwell 1972). An IDF does not contain sink populations. The fact that our data, to date, do not support source–sink dynamics may suggest two things. First, the spatial separation of the patches in our system may be small enough that animals can accurately compare and choose among habitats. Second, interference among individuals may not be sufficiently strong to force emigration into inferior habitats.

The apparent absence of source–sink dynamics among blocks may be related to the relatively small scale of our study site. Our system is open and may, as a whole, act as a source or sink in the larger landscape. We are currently attempting to synthesize 20 yr of records of tagged animals switching between a number of locations in the landscape near our study site (M. S. Gaines and N. A. Slade, *unpublished data*). From these data, we will attempt to estimate emigration and immigration rates for long-range dispersal. Combining these rates with detailed demographic analysis may enable us to determine if our manipulation has resulted in a large, sink habitat or if the populations existing on our fragmented site maintain themselves without emigration.

We find it intriguing that, in all species, a greater proportion of switching occurs from smaller to larger blocks. This may reflect the species' evolutionarily-shaped dispersal strategies in a heterogeneous environment. A theoretical model developed by McPeek and Holt (1992) predicted that a conditional dispersal strategy, with the rate of local emigration inversely dependent upon local patch carrying capacity (K), should be the evolutionarily stable dispersal strategy in spatially- and temporally-variable environments. If so, near-equal numbers of individuals should switch between patches with different carrying capacities, and a greater proportion of animals should leave patches with a low, rather than high, carrying capacity.

Our results are consistent with this theoretical expectation. Nearly equal numbers of animals of all three species switched in opposite directions, despite differences in densities between blocks, which implies an inverse correlation between local dispersal rate and local abundances. For example, exactly 111 deer mice switched both from large to small, and from small to large blocks. Sixty-five prairie voles switched from medium to small, and 62 from small to medium blocks. Although all species showed differences in the net number of switchers between any two block sizes, these were not statistically significant based on chi-square tests. Similarly, the proportion of animals switching from smaller (presumably lower K) blocks was greater than the proportion of individuals switching from larger (presumably higher K) blocks. However, these data should not be considered a conclusive test of the McPeek–Holt hypothesis because we have no independent measure of carrying capacity for the blocks.

Regardless of the mechanisms involved, we currently do not have enough data, even after nearly 8 yr, to fully understand the general prevalence of the observed bias in percentage movement from smaller to larger blocks. We are currently developing spatially-explicit simulation models that can be used to help assess various hypotheses. Intensive radio-telemetry studies of different sexes or mass classes, done at various seasons or densities, coupled with an analysis of block-specific birth and death rates may be needed to illuminate the mechanisms responsible for this pattern.

The relationship between movements and local abundances

Processes other than immigration and emigration (such as reproduction and death) obviously affect local population sizes. Thus, we did not initially expect a close match between the relative abundances estimated from the matrices of per capita switching and the observed abundances on individual blocks. However, for prairie voles in the spring and deer mice in the summer, predicted abundances were positively correlated and chi-square values nonsignificant. Overall, real and predicted abundances were positively correlated in three of four and one of four seasons for prairie voles and deer mice, respectively. Chi-square tests indicated a significant lack of fit between observed and expected abundances for three of four seasons in prairie voles and for deer mice in the winter. Thus movement behavior may influence, but does not entirely determine, local relative abundance.

For deer mice, it was not surprising that predicted abundances did not correlate well with observed abundances in most seasons. Deer mice utilize the interstitial area and, therefore, abundances on the blocks may be influenced by movements of animals into and out of the untrapped, mowed areas, as opposed to movement from other blocks. It was surprising that the chi-square tests indicated no statistical difference between observed and expected abundances in all seasons except winter. For deer mice, though the deviations between observed and expected values were not large, they were in different directions across blocks, resulting in low correlation coefficients.

For prairie voles, the large deviations between observed and expected abundances resulted in significant chi-square values but the pattern of deviations across blocks was such that correlation coefficients were high. The matrices of switching tended to overestimate abundances on the large blocks, which always had the highest observed abundances, and to underestimate abundances on the smaller blocks, which had lower observed abundances. Thus, correlations between observed and expected abundances remained high despite discrepancies in the actual numbers between the two vectors.

For deer mice and for prairie voles, our data indicate that, to a degree, movement biases and spatial variation in abundance may be linked in some causal fashion. Our data suggest the existence of conditional dispersal strategies (McPeek and Holt 1992), in that the rate of switching (which may function as an index of dispersal) varies with the habitat type (i.e., large to small patches). With heterogeneous dispersal rates, the Markov transition model predicts a particular spatial pattern in relative abundances, given that demographic parameters are spatially constant. The correspondence between observed and predicted distributions suggests that asymmetric mobility affects spatial variation in abundances.

We caution, however, that dispersal interacts with fecundity and mortality to affect abundance. In an experiment designed to test the selective basis of dispersal, Johnson and Gaines (1987) found that dispersing prairie voles had higher relative fitnesses than did residents. If switchers in our study are dispersing individuals, then they may influence abundances in their new block by reproducing or by interfering with other individuals. However, to determine the influence of switchers on block abundances, we would need detailed information on the permanence and reproductive success of switchers in blocks. Such information, if it exists, is difficult to tease out of mark–recapture data. Moreover, dispersal tends to evolve such that fitnesses are equilibrated across space (Holt 1985, McPeek and Holt 1992). In our system, we do not yet know whether movement is responsible for the distribution of animals, or whether the distribution of animals (with resultant effects on fitnesses due to local density dependence) causes the switching patterns leading to the correspondence seen in Table 6.

Species differences in between-block switching

Unlike the general movement trends expressed by all species at the small scale of 5000 m^2 within blocks, at the larger scale of the entire study site, different species reacted in varying degrees to habitat fragmentation. The most obvious differences were in overall proportions of animals switching. Surprisingly, the smallest bodied species (deer mice) switched twice as often as the other two species and nearly 40% of deer mice made reciprocal switches (switching to and from the same blocks). Although cotton rats and prairie voles switched in similar proportions (8% and 6%, respectively), only 20% of the cotton rats made reciprocal switches whereas nearly one-third of the voles did. Furthermore, the species did not show similar temporal trends in proportion of animals switching (Fig. 2A–C).

What is surprising is the low level of switching by cotton rats and prairie voles. Despite distances of only 16–20 m separating blocks, >90% of the individuals of both species never switched. Given these low switcher numbers, population dynamics within blocks may be driven mainly by processes intrinsic to the block itself. If so, the overall cotton rat and prairie vole populations on the area may actually be metapopulations, with several distinct local populations linked by dispersal.

Deer mice, unlike the other two species, utilize the interstitial area and their response to fragmentation is not as dramatic. We suggest that, in fragmented landscapes, it is crucial to discriminate between species that can use disturbed habitats separating the fragments (even to a small degree) and those that cannot. For the former, individuals may perceive the landscape as a mosaic of habitats varying in quality. For the latter, the landscape may represent isolated patches.

Identity of switchers

The proportion of individuals switching between blocks varied by age class and reproductive condition among species. The only consistent trend among species was a greater proportion of males switching between blocks. This result has been observed in many small-mammal species (Gaines and McClenaghan 1980). In cotton rats, juvenile females switched more often than adult females, indicating that young females may have been dispersing from their natal site. Our finding of a prevalence of juvenile female dispersers differs from previous studies of cotton rat dispersal, which indicated that dispersers did not differ in sex or age from source populations (Joule and Cameron 1975, Stafford and Stout 1983). However, our findings corroborate those of T. Doonan (*unpublished data*), who has found lower than expected proportions of reproductive female transients on study sites 0.6 km north of our study site. Trends in prairie vole switching indicated that juveniles of both sexes switched in higher proportions than adults, a result consistent with earlier studies of vole dispersal (Krebs et al. 1976, Gaines et al. 1979*a, b*). Thus, the majority of vole switching was most likely to be dispersal. Unlike the other species, adult and juvenile deer mice switched in similar proportions, indicating that in our system, switching may not be true dispersal for this species. Most studies indicate that greater proportions of juvenile deer mice disperse (Wolff 1989). The fact that deer mice switching is not dispersal is sensible, given that deer mice use the mowed turf between the patches.

Implications for modeling

Our data have implications for theoretical studies of habitat fragmentation. Three small mammal species had different responses to the same imposed pattern of habitat fragmentation. In addition to species-specific responses, there was intraspecific heterogeneity in movement patterns. Male and female deer mice responded differently to fragmentation, and for all species, both switching and movement patterns changed drastically with time. Analytical models predicting the effects of dispersal should examine a broad parameter space to insure pertinence to species with varied dispersal propensities. In applications, we should recognize that spatially-explicit models are necessarily species-specific and ideally would be based on highly accurate estimates of dispersal and movement of the modeled species. Moreover, temporal variation in movement patterns may influence model accuracy; researchers should try to estimate movements over at least an annual time period. Attempts to generalize models across species or sample periods should thus be done with caution. In our system, a model developed around the movement patterns of deer mice would not generalize to either cotton rats or prairie voles. Neither would a model based on only one season or possibly even 1 yr of movement data for any of the species. Indeed, the weak link in spatially-explicit models may be lability in dispersal behavior of the organism being modeled.

Recently, Fahrig and Merriam (1994) stressed the importance of landscape structure and spatial arrangement of habitat patches to population survival. They pointed out that some models assume "all local populations (in the patches) are equally accessible by dispersers" and argued that such models will most likely be inaccurate when used for applied, conservation oriented problems. The low proportions of animals switching to same-sized blocks on our study area support their argument. The spatial configuration of the study area is such that blocks of similar sizes are never adjacent (Fig. 1). Thus, switching to same-sized blocks requires moving a much greater distance than switching to blocks of different sizes. In all species, the proportion of animals switching between same-sized blocks was nearly nine times less than those switching to larger blocks, and 3.5 to 7 times less than switching to smaller blocks for voles and deer mice. Furthermore, the matrices of switching probabilities clearly indicate that animals are more likely to switch to closer blocks.

Conclusions

Species differences in the propensity to switch between blocks highlight the need to understand the scale at which fragmentation affects a species. Generalizing the effects of habitat fragmentation across species may be possible only if we understand how species differ in the scale at which they utilize the landscape (Wiens 1989). Otherwise, such generalizations may lead ecologists and conservation biologists astray. Furthermore, the dichotomy we have observed in species' responses to fragmentation at different scales highlights the complexities ecologists face. Empirical studies such as ours are rare and difficult to replicate properly at the large scales needed to fully understand phenomena such as regional extinction. Information gleaned from smaller scale empirical studies can be used to construct models potentially applicable to larger scales. The interface between empirical studies and theory development should provide a powerful and promising tool for gaining insights into the complex consequences of habitat fragmentation at larger landscape scales. The results presented here may help to strengthen this interface.

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