

Patterns and Impacts of Movements at Different Scales in Small Mammals

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Introduction

Understanding how patterns of movement are affected by the spatial structure of an environment is a key question for landscape ecologists (Wiens 1995). All organisms exist in spatially heterogeneous environments and movement through these mosaics clearly has impacts on individual fitness (Fretwell and Lucas 1970, Morris 1992), population demography (Pulliam 1988, Hanski and Gilpin 1991, Pulliam and Danielson 1991) and community structure (Connell 1961, Danielson 1991, 1992, Holt 1993, McLaughlin and Roughgarden 1993, Abramsky et al. 1994, Brown 1996). Ostfeld et al. (1996) consider heterogeneity to be a unifying hypothetical foundation in ecology and conservation.

Despite recognizing heterogeneity, we do not fully understand how movements interact with spatial mosaics to influence population-level processes (Wiens 1995). Theoretical studies have shown that movements over heterogeneous landscapes, even as simple as two distinct habitat types, can generate a multitude of dispersal patterns and population dynamics (Holt 1985, Pulliam 1988, Pulliam and Danielson 1991, McPeck and Holt 1992, Dias 1996). Movement is a common denominator in the understanding of how spatial heterogeneity influences ecological processes. Thus, landscape ecologists need to focus on how spatial heterogeneity influences movement patterns and how movements, in turn, influence spatial patterns of abundance across space. A number of authors have delineated conceptual frameworks for studying the interaction between spatial heterogeneity and movement patterns (Senft et al. 1987, Gautestad and Myrsetrud 1993, Ims 1995, Morris 1995), with all emphasizing that movements are influenced by factors at different spatial scales. We should expect that as scales change, different processes cause movements and impact population demography in a variety of ways.

In fragmented or patchy landscapes, movement may reflect the size and spacing of habitat patches. We suggest studying movement at three spatial

scales: (1) When patches are smaller than home ranges and individuals must move between patches to satisfy daily foraging needs; (2) When patches are larger than home ranges but movement is within the patch. Here, patch characteristics (e.g., perimeter-to-area ratio) may influence the size and shape of home ranges, within patch movements, and potential dispersal rates; and (3) When patches are larger than home ranges but movements are between patches. These interpatch movements may either be short-term, long-distance forays into unknown areas or dispersal events.

The underlying processes causing movement differ at three different scales. If scale is not explicitly considered, then similar patterns in movements can be incorrectly ascribed to similar processes. For example, we may study voles in enclosures and birds in forest fragments and conclude that both species increase their distance moved in response to habitat fragmentation. Voles, however, may increase distances moved because they have enlarged their home range to encompass more than one patch, whereas birds may disperse farther because patches are more isolated. Generalizing these two responses may incorrectly imply a common cause.

Movements at all three of these scales may influence population structure. For example, if home ranges are split between small patches, the energetic demands of moving or increased predation in the interstitial areas may lower abundances. When patches are larger than home ranges, space use may expand if individuals do not need to guard the sides of their home range along patch edges. This expansion of home range may decrease overall population density in fragments relative to continuous areas (Bowers et al. 1996). Finally, the size, shape, and distance between patches, as well as the connectivity of the interstitial habitat, may modify dispersal rates between patches.

In this chapter, we analyze mark-recapture data from two long-term studies to address key points about small mammal movements at different scales in spatially heterogeneous landscapes. We will first present analyses of movements when patches are smaller than home ranges. Given the nature of our studies, we cannot analyze movements within patches when patches are larger than home ranges. Most of the paper will focus on movements between patches, where patches are larger than home ranges. Finally, we present data on the impacts of these movements on local demography and extinction/colonization dynamics.

Data were collected from an ongoing study of habitat fragmentation begun in 1984 at the Nelson Environmental Studies Area, northeast of Lawrence, Kansas. The study area consists of 55 patches of successional old-field scattered throughout 6.9 ha of area (Fig. 4.1). The patches are organized into 5,000 m² units called blocks. Large blocks are continuous, 50 × 100-m patches. Medium blocks consist of six, 12 × 24-m patches; small blocks consist of 10 or 15, 4 × 8-m patches. We maintained the fragmentation pattern by mowing the interstitial area around the blocks. Animals were trapped every 2 weeks from 1984 to 1992. Animals were marked with ear tags or toe clips, weighed, and checked for reproductive activity and location. Three species (*Sigmodon*

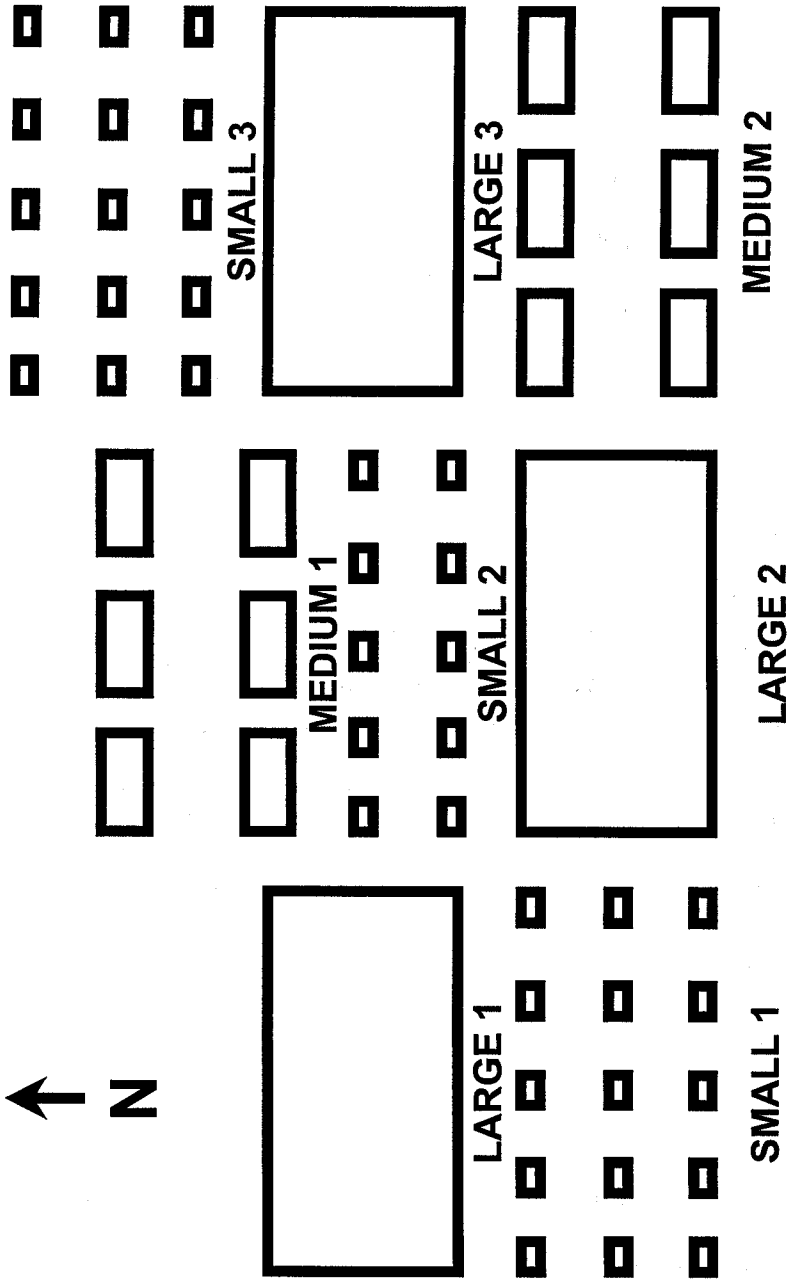


FIGURE 4.1. Diagram showing the experimentally fragmented system. The study area has approximately 1.87 ha of successional old-field habitat contained within 6.9 ha of total area. The three large patches are 50×100 m, the 12 medium patches are 12×24 m, and the 40 small patches are 4×8 m. Note that a single 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 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).

hispidus, *Microtus ochrogaster*, and *Peromyscus maniculatus*) account for approximately 90% of the captures. We will present data for these species.

Movements at Different Scales

Patches Smaller Than Home Ranges

At this smallest scale, heterogeneity in the landscape is smaller than a home range. Movements at this scale are frequent and determined by resource or other needs that occur at short-time scales (hours or days). Movement patterns under these conditions have been studied intensively by behavioral ecologists. Landscape ecologists can use optimal search and foraging theory to predict species responses to spatial heterogeneity at small scales (Ims 1995). In general, the quality, size, and distance between patches should all influence the amount of time an individual remains on a patch and the frequency of movement between patches. In our system, home ranges of the three species are larger than the small (32 m²) and possibly the medium (244 m²) patches. Thus, movements among patches within blocks are movements within a home range. We predicted that within blocks on the fragmented site, animals should move less frequently, as the degree of fragmentation increased.

We tested this prediction by comparing the proportion of animals moving between patches on small and medium blocks relative to the proportion moving on patches of similar size within large blocks (i.e., simulated small and medium blocks; Diffendorfer et al. 1995a). We used the average proportion of animals moving between sequential trapping periods to measure movement. We created simulated blocks by selecting data from trap stations on large blocks that corresponded to the spacing patterns of patches and traps on small and medium blocks. For cotton rats and prairie voles, but not deer mice, individuals moved between patches less frequently in the truly fragmented blocks, than between similarly spaced traps on the simulated small and medium blocks (Table 4.1). One possible explanation is that predation rates are higher in the mowed area, which inhibits movement among the patches. Observations from a viewing platform indicated that predation rates are higher on real small blocks compared with the larger block sizes (P. Wilson, pers. comm.). The lack of difference in the proportion of deer mice moving among patches on the real versus simulated blocks suggests that deer mice perceive the interstitial area differently than cotton rats and prairie voles. Thus, a species' assessment of habitat quality in a mosaic may alter movement patterns.

Results of La Polla and Barrett (1993) and Wolff et al. (1997) support our conclusions. La Polla and Barrett (1993) studied meadow voles (*Microtus pennsylvanicus*) in oldfields with paired patches. Some patches were connected by corridors and in other cases they were not. Most males maintained home ranges between two patches and moved less between patches without corridors compared with those with corridors. These data indirectly support

TABLE 4.1. Percentage (\pm S.E.) of interpatch movements on small, medium, simulated small and simulated medium blocks for cotton rats, prairie voles and deer mice.

| Species | Block type | | | |
|---------------|-------------------------|-------------------------|-------------------------|-------------------------|
| | Medium medium | Simulated medium | Small small | Simulated small |
| Cotton rats | 19.6 \pm 0.1 (14) | 64.2 \pm 0.2 (14) | N/A | 82.6 \pm 8.8 (67) |
| Prairie voles | 15.6 \pm 0.2 (145) | 22.7 \pm 0.2 (145) | 51.0 \pm 3.4 (138) | 57.0 \pm 4.3 (138) |
| Deer mice | 46.8 \pm 8.1 (46) | 41.7 \pm 5.9 (46) | 74.6 \pm 6.3 (67) | 69.0 \pm 8.3 (67) |

Sample sizes (in parentheses) are the number of weeks in which the percentage of animals switching were compared.

the prediction that fragmentation reduces movement by demonstrating that more isolated patches without corridors were used less often. Wolff et al. (1997) found a significant decrease in the proportion of individuals moving between 5×5 m² patches separated by 4 m of bare ground compared with the same area before the fragmentation treatment (prefragmentation = 60% of both sexes moved, postfragmentation = 15% of males and 6% of females moved). These results are encouraging because they indicate a possible general response to fragmentation; namely, that when average home range size is larger than patch size in the landscape, fragmentation reduces movement between patches.

Movements Between Patches

The largest scale of movement, other than migration, occurs when patches are larger than a home range, so that movement between patches represents dispersal at a landscape scale. We note that movement between patches at this scale is not necessarily dispersal—an individual could maintain areas of space use on the edges of two large adjacent patches; however, we will limit our discussion here to dispersal between the patches. At this scale, movement is a fundamentally different process from the local space use patterns and movement within patches described previously. We will focus on movements of small mammals between areas separated by 20–500 m. Because there is a dearth of knowledge about vertebrate movements across landscapes (Ims 1995), we will first describe patterns of movements and how they differ between species. We will then discuss factors that appear to influence dispersal between patches.

Patterns of Movements Between Species

Given the nearly 23,000 captures on the fragmented site, we were able to investigate movement between the blocks in some detail. See Diffendorfer et

al. (1995a) for additional details of block to block movements. Figure 4.2 a–c, gives a visual summary of all the movements for each species. The figures were generated from a computer program that traces the trap history of individuals across a map of the study area. Cotton rats were primarily found on the three large blocks, and most of the movements were between these three areas. They occasionally moved to and from medium and small blocks. Both prairie voles and deer mice were found on all three block sizes and their movement patterns reflected these trends. In both species, patterns of movement were much more cosmopolitan than they were in cotton rats.

Figure 4.2 a–c seems to indicate a large amount of movement among the blocks; however, the probability that an individual moved from the block where it was first captured was low and varied among species (Diffendorfer et al. 1995a). Indeed, 91% of cotton rats, 93% of prairie voles, and 82% of deer mice (captured more than once) were captured on only one block and never moved. Of those animals that did move, 77% of the cotton rats, 74% of the prairie voles, and 62% of the deer mice moved only once, suggesting that most movements between blocks (particularly for cotton rats and prairie voles) were true dispersal events.

In addition to the differences in the general spatial patterns and propensities for movement, there were species-specific effects of season, sex, age, and reproductive condition (Diffendorfer et al. 1995a). For instance, most movements in cotton rats occurred in the fall, and males moved more than females. Prairie voles moved between blocks primarily in the fall and juveniles moved more than adults. Deer mice moved between blocks most often in the spring, and males moved more than females, but neither age nor reproductive condition affected movement. One important task for future work will be to interpret such effects in terms of basic life histories, resource requirements, and social structure.

Factors Influencing Movements Between Patches

Here we investigate three factors that influence dispersal between patches: (1) distance between patches; (2) patch size and geometry; and (3) local population density. Harrison and Fahrig (1995) discuss some of these factors when reviewing simulation studies at the landscape scale. They emphasize, however, how these factors affect regional population survival, not patterns of movement.

We studied the impact of distance on movement in two ways. First, we compared the proportion of animals moving between the fragmented site and another study conducted concurrently by Dr. N. Slade (the “continuous site”). His site is approximately 500 m away from our area. We compared the percentage of animals moving between the two study sites with the percentage of animals moving between blocks within the fragmented site (distances from 20 to 160 m). The effects of distance were dramatic (Diffendorfer et al. 1996). Approximately 9% of cotton rats moved between blocks within the fragmented site; however, only 5 of 1131 individuals (0.44%) moved from the fragmented site to the continuous site, and 10 of 1013 (1%) from the continu-

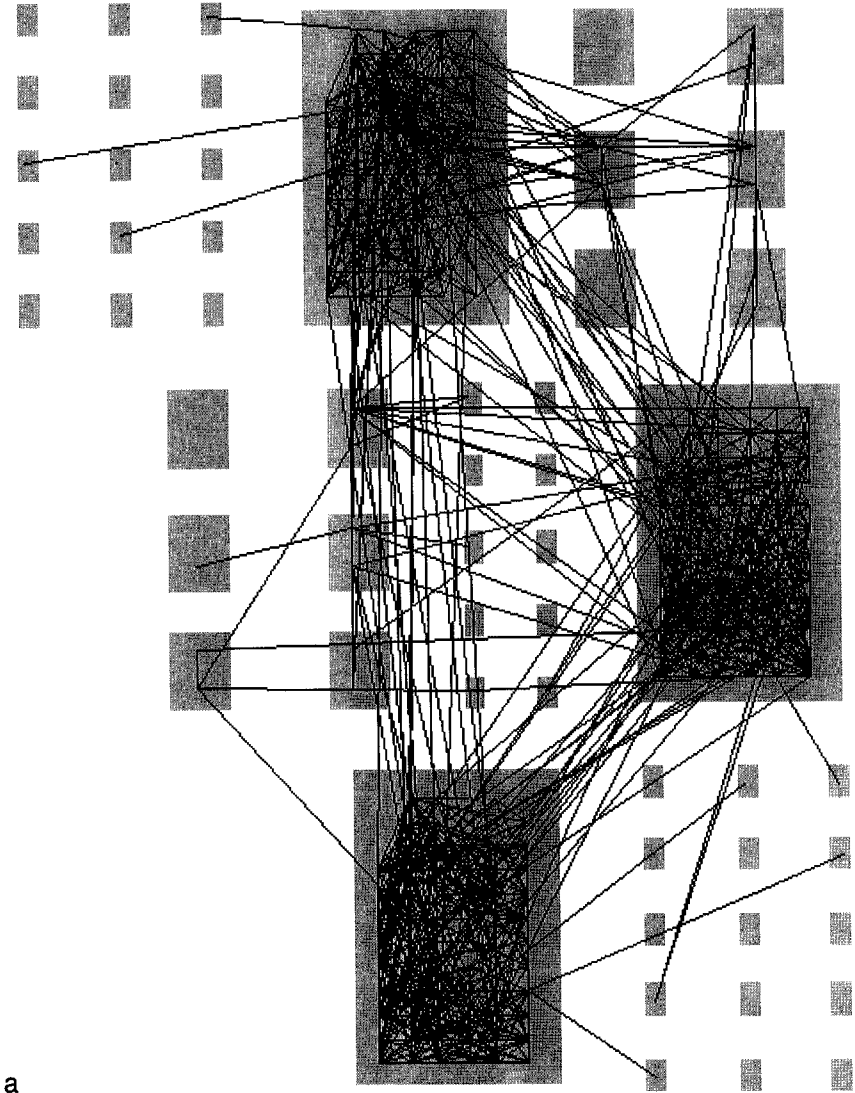
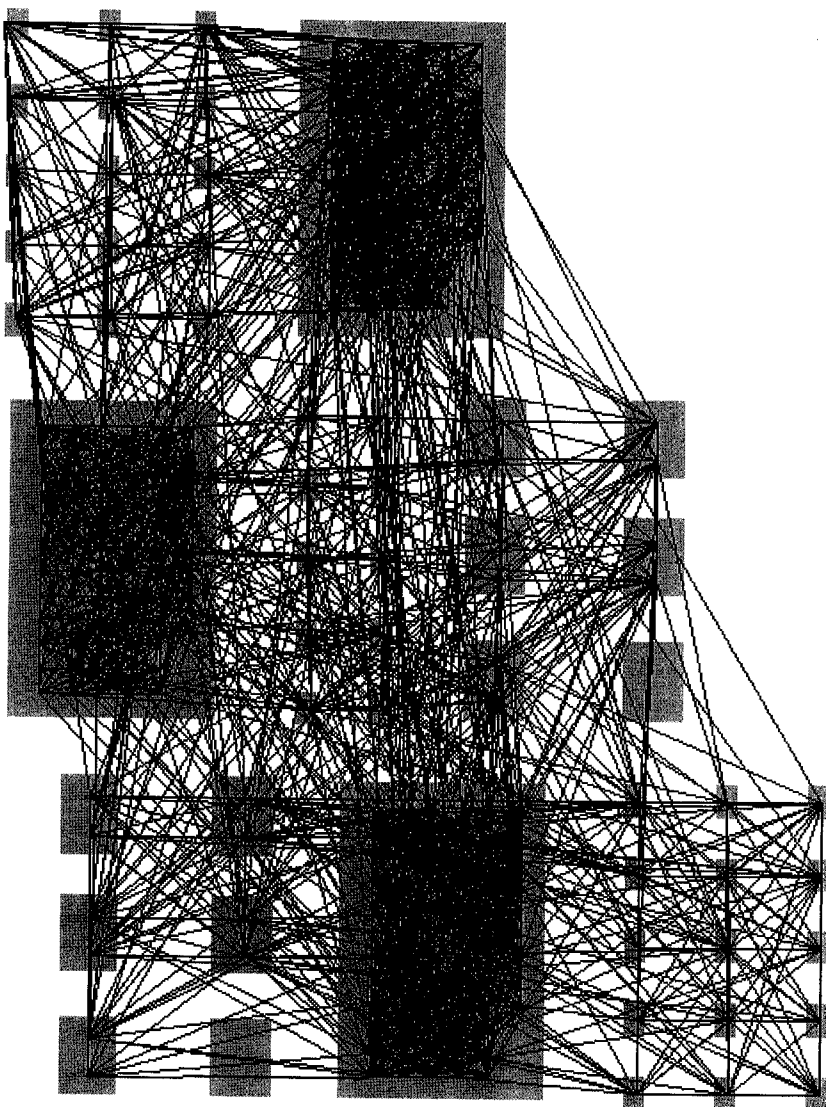


FIGURE 4.2a–c. Movement patterns of each species. These figures were created using a program that first draws the study area, then traces the movements of each individual based on location data from the individual’s trap history.

ous to the fragmented site. For voles and deer mice the results were similar. In voles, 7% of the individuals moved between blocks, whereas 7 of 1702 (0.41%) voles moved between sites. In deer mice, 26% of individuals moved between blocks within the fragmented site, but only 2 of 227 (0.88%) moved between the continuous and fragmented sites.

FIGURE 4.2a-c (*continued*).

The second method of analyzing distance effects on movement focused on movements occurring within the fragmented site. Because distance effects were obvious at distances of 500 m, we wanted to determine whether there were similar trends at smaller scales. We regressed the distance between the centers of blocks with the proportion of animals leaving a block. Because there are directional biases in movement (higher proportions of animals moved from smaller blocks than from larger blocks; Diffendorfer et al. 1995a), we per-

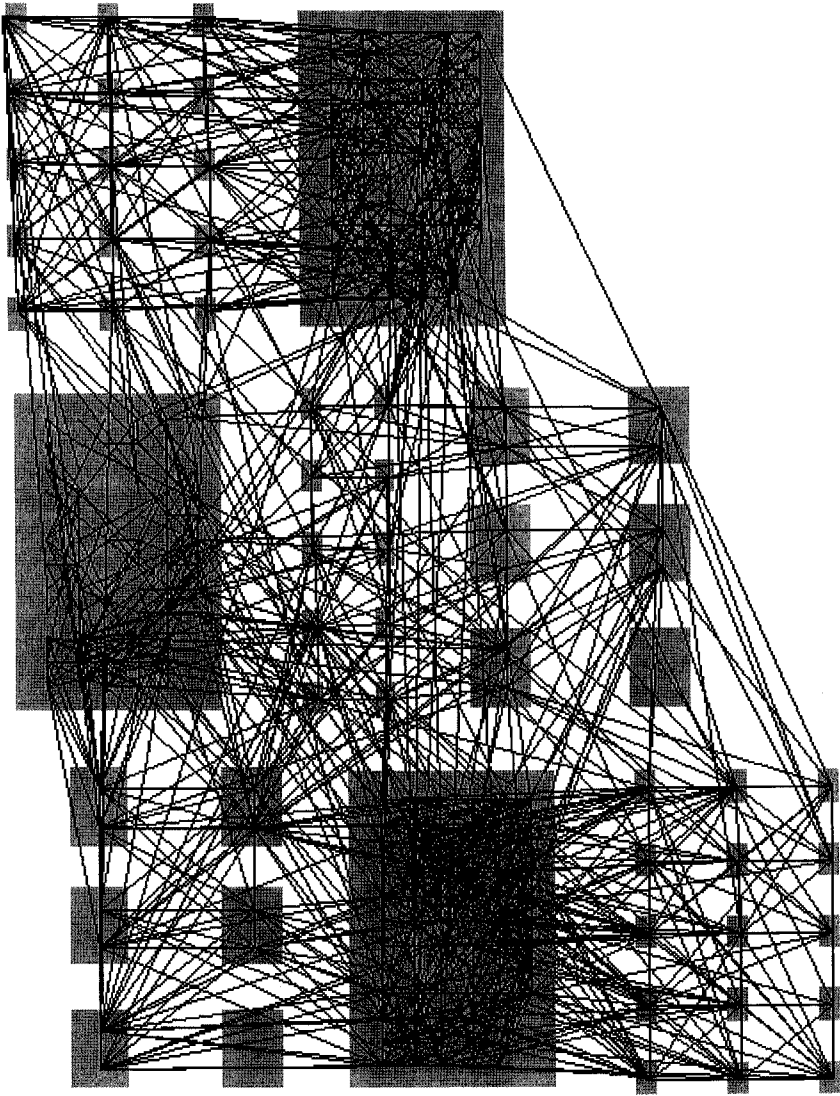


FIGURE 4.2a-c (continued).

formed three separate regressions for each block size. The first regression used all possible combinations of movements from the three large blocks, the second used all possible combinations of movements from medium blocks, and the third used all possible combinations of movements from the small blocks. In all cases, except for cotton rats leaving large blocks, distance was significantly, negatively related to the proportion of animals leaving a block (Table 4.2).

Our mark-recapture data indicate that most individuals in small mammal populations do not move far. The distances separating our blocks were 20 m or more. Even with this short distance, more than 90% of cotton rats and prairie voles and more than 80% of deer mice never moved. Other researchers have found similar low rates of movement in different species. Verner and Getz (1985) calculated that 6.6% of *Microtus pennsylvanicus* and 16.7% of *Microtus ochrogaster* individuals in a 1-ha enclosure with exit tubes dispersed from the area. Tamarin et al. (1984), in an enclosure containing forest and field habitat similarly found that only 98 of 1077 (9.1%) individuals of *M. pennsylvanicus* dispersed to the forest habitat. Beacham (1980) studied *M. townsendii* on plots with fences on three sides separated by a 27–36-m wide mowed strip from a control plot on the fourth side. He found that 15.9% of the individuals in the fenced area moved across the mowed strip and were recaptured on the control site. Finally, Dooley and Bowers (1996) found that only 17% and 3 % of *Peromyscus leucopus* and *M. pennsylvanicus* individuals, respectively, moved between patches separated by 50 m or more. Taken together, these results indicate that in some small mammals, dispersal across areas greater than 100 m are rare.

Rajska-Jurgiel (1992), however, found much higher rates of movement in *Apodemus flavicollis* (33–76%) and *Clethrionomys glareolus* (16–56%) between plots scattered across woodlots separated by 30–100 m. Some of the plots were unfortunately within the same woodlot, making it difficult to determine what proportion of the animals were actually moving across interstitial area. M.S. Gaines (unpubl. data) found high rates of movements of *Sigmodon hispidus* (~60%) and *Orzomyus palustris* (~80%) between hammock islands

TABLE 4.2. Regression equations for the relationship between the probability of leaving a block and the distance between blocks.

| Species | Block size | Constant | Coefficient | R ² adjusted | P-value |
|---------------|------------|----------|-------------|-------------------------|---------|
| Cotton rats | Large | 0.023 | -0.000038 | 0.0 | 0.586 |
| | Medium | 0.232 | -0.001039 | 25.8 | 0.006 |
| | Small | 0.318 | -0.001391 | 19.0 | 0.006 |
| Prairie voles | Large | 0.051 | -0.000180 | 51.0 | <0.001 |
| | Medium | 0.095 | -0.004041 | 35.9 | 0.014 |
| | Small | 0.135 | -0.005608 | 52.4 | <0.001 |
| Deer mice | Large | 0.147 | -0.000595 | 40.9 | 0.001 |
| | Medium | 0.192 | -0.000873 | 62.7 | <0.001 |
| | Small | 0.213 | -0.000873 | 41.7 | 0.001 |

Degrees of freedom in the *F*-test are 20 for large and small blocks and 13 for medium blocks.

separated by approximately 50–150 m. Peles et al. (Chapter 3) have also observed long-distance movements (up to 1.5 km) by *S. hispidus*. Although not the focus of their analyses, rates of movements were high (~75% moved from clear cut patches into other patches or other habitats). In these cases, the species may be interacting with the landscape at a larger spatial scale than the species mentioned above.

The next step in our analyses of movement distances is to apply our field data to models of dispersal (Waser 1985, Buechner 1987, Miller and Carrol 1989). Because many models predict that distance will negatively influence the probability of dispersal to a site, our current results were not unexpected. We need to develop a null model, however, that will allow us to determine if the fragmentation treatment (mowing) has actually influenced dispersal distances. In general, in order to determine if dispersal distances are influenced by fragmentation, there needs to be a null model or an experimental control such as a continuous habitat for comparison (Ims and Yoccoz 1997).

Patch size and geometry can also influence dispersal. Emigration rates from different-sized patches have been analyzed in insects, but not in vertebrates (Ims 1995). Our study allows us to analyze the impacts of patch size on emigration rates. We compared the proportion of individuals moving from a block across the three block sizes using chi-square tests. Individuals must be captured at least twice to have moved, so proportions were calculated from the pool of individuals captured at least twice. The proportion of individuals leaving a block increased as blocks became more fragmented [Cotton rats, ($\chi^2 = 77.29$, $df = 1$, $P < 0.001$); Prairie voles, ($\chi^2 = 57.93$, $df = 2$, $P < 0.001$); Deer mice, ($\chi^2 = 13.44$, $df = 2$, $P = 0.001$; Table 4.3).

According to Ims (1995), there has been no explicit test of patch size effects on rates of emigration in vertebrates. Our study is not a perfect test of such effects because our blocks are not singular patches of different size.

TABLE 4.3. Proportion of individuals moving from a block size for cotton rats, prairie voles, and deer mice.

| Species | Block | | |
|---------------|-----------------|----------------|----------------|
| | Large | Medium | Small |
| Cotton rats | 0.123 (583) | 0.545 (66) | N/A |
| Prairie voles | 0.166 (1412) | 0.244 (627) | 0.307 (709) |
| Deer mice | 0.354 (540) | 0.426 (265) | 0.476 (336) |

Proportions were calculated as the number of individuals which moved from the block and were recaptured elsewhere, divided by the number of individuals captured at least twice on the source block. Numbers in parentheses indicate the total number of individuals captured at least twice.

Instead, our blocks are clusters of similarly sized patches. Our results, however, strongly support a model of dispersal by Stamps et al. (1987). Their model included assumptions such as territoriality, a mortality rate associated with movement, and home ranges, which makes it realistic for small mammal populations. Among other variables, Stamps et al. (1987) measured the impact of the "edge-to-size ratio" (ESR) on emigration. They define the ESR as "... the ratio of the home ranges bordering the habitat boundary, divided by the total number of home ranges in that habitat patch." The prediction is that areas with higher ESR would have higher rates of emigration. In our system, the smaller the block, the higher the ESR, and, as their model predicts, the higher the rate of emigration. These results indicate that it may not be habitat size per se, but rather how the size and shape of a habitat patch affect the distributions of home ranges, which ultimately determines the dispersal rate from the patch.

Density is another factor that may affect dispersal (Gaines and McClenaghan 1980). We found a negative relationship between density and the proportion of individuals leaving a block (Fig. 4.3). We regressed the log of the proportion of individuals leaving any block across the entire fragmented site with the log of the Minimum Number Known Alive (MNKA) on the entire site. In all species, the proportion of individuals moving was negatively related to abundance on the entire site [Cotton rats, $\text{Log}(\% \text{ move}) = -0.72 \text{ Log}(\text{MNKA})$

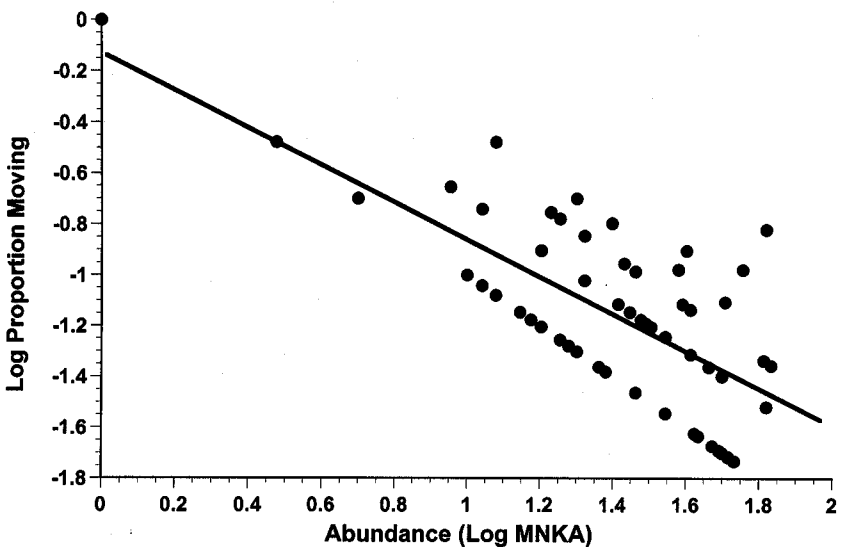


FIGURE 4.3a-c. Regressions between the proportion of individuals leaving any block on the fragmented site and the density over the entire site. At each trapping period, the proportion of individuals moving off a block and the density on the study area were calculated. These values were used in the regression.

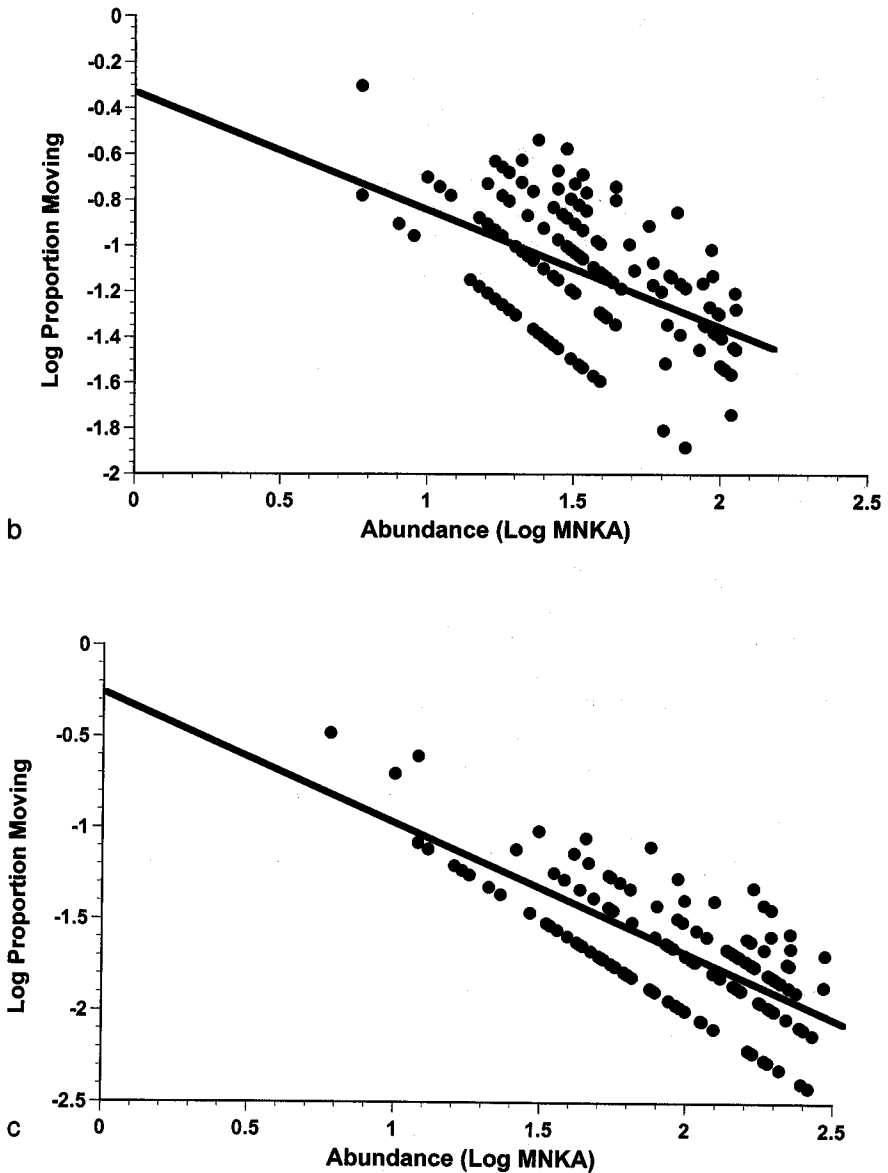


FIGURE 4.3 (continued).

- 0.15, $F = 62.44$, $df = 1, 59$, $P < 0.001$, $R^2(\text{adjusted})=51.0\%$; Prairie voles, $\text{Log}(\% \text{ move}) = -0.71 \text{Log}(\text{MNKA}) - 0.29$, $F = 167.40$, $df = 1, 139$, $P < 0.0001$, $R^2(\text{adjusted})=54.5\%$; Deer mice, $\text{Log}(\% \text{ move}) = -0.51 \text{Log}(\text{MNKA}) - 0.35$, $F = 55.07$, $df = 1, 155$, $P < 0.001$, $R^2(\text{adjusted})=25.9\%$. These analyses may include the same individuals in different abundance estimates because the

data are from the entire site. This negative relationship, however, also held when we analyzed individual blocks separately (i.e., the proportion of individuals leaving Large Block 1 vs. the density on Large Block 1) and when we included animals that moved only one time (true dispersal).

These findings were unexpected because earlier studies of dispersal in microtines (McClenaghan and Gaines 1976, Gaines and Johnson 1984, Verner and Getz 1985) did not indicate a relationship between density and the proportion of individuals dispersing. Similar to our results, Krebs (1992) found a negative relationship between dispersal rates and density in *Microtus townsendii*. In all of our analyses of the relationship between density and dispersal, we pooled all individuals irrespective of sex, age, and reproductive condition. A more detailed analysis of these different categories may illuminate possible mechanisms behind this overall pattern.

The Impact of Movement on Local Demography

We previously reported on the proportion of the abundance of animals on a block accounted for by immigrants and emigrants (Diffendorfer et al. 1996). In general, between 6 and 10% of the average abundance on a block was explained by movement. In addition, the smaller the average abundance on a block, the higher the impact of movement on local abundance. Here we extend these analyses in three ways. First, we screened data for immigrants and emigrants, recalculated demographic variables, and then compared these to unscreened data. Second, we looked at the long-term impacts of dispersers on a block by comparing the total proportion of "animal-weeks" comprised by immigrants on different blocks. Third, we calculated extinction/colonization indices for blocks.

Impacts of Immigration and Emigration on Demographic Variables

We examined impacts of movements on local demographic variables by comparing estimates of Jolly-Seber abundance, survival, and the rate of population change on blocks that have been "screened" for either immigrants and emigrants versus "unscreened" blocks. We screened blocks in two ways. To test effects of immigration on local demography, we removed all trap histories of an individual from a block if that individual immigrated to that block. For example, if an animal was originally on Large Block 1 and immigrated to Medium Block 2, and was captured on Medium Block 2 for the next four trapping periods, then the entire trap history for that animal on Medium Block 2 was removed from the raw data. By doing so, we were placing an imaginary fence around the block, thereby stopping immigration. To test the effects of emigration on a block, we did the opposite. We added trap histories of individuals living on another block to the

block from which they emigrated. We make a number of assumptions when doing these data manipulations. First, we assume that demographic variables are similar across the blocks, so an individual that moved from Large Block 1 to Medium Block 2 has similar demographic statistics on both blocks. This assumption is reasonable for all the demographic variables tested because they do not, on average, differ between the blocks (Diffendorfer 1998).

For each species, we compared screened and unscreened data on each block using paired *t*-tests. We note that this test assumes no correlation in the data, which may not be the case. Given the large number of tests, we will not discuss each separately; instead, we present the statistically significant tests and give general trends.

In all species and across most blocks, both immigration and emigration significantly influenced average abundance (Table 4.4). As might be expected, blocks with immigrants removed had lower average abundances than blocks with unmanipulated data, and blocks with emigrants added had higher average abundances. In voles, abundances averaged over all eight blocks de-

TABLE 4.4. Summary of impacts of movement on demographic variables on each block.

| Species | Movement | Variable | Effect | Number and type of blocks influenced |
|---------------|-------------|--------------|-----------|--|
| Cotton rats | Emigration | Jolly N | Increase | Large ($N = 2$), Medium ($N = 1$) |
| | | Survivorship | Increase | Large ($N = 1$), Medium ($N = 1$) |
| | | Pop. Growth | No effect | |
| | Immigration | Jolly N | Decrease | Large ($N = 3$), Medium ($N = 1$) |
| | | Survivorship | No effect | |
| | | Pop. Growth | No effect | |
| Prairie voles | Emigration | Jolly N | Increase | All blocks |
| | | Survivorship | Decrease | Large ($N = 1$) |
| | | Pop. Growth | Decrease | Large ($N = 2$), Medium ($N = 1$), Small ($N = 1$) |
| | Immigration | Jolly N | Decrease | All blocks |
| | | Survivorship | Decrease | Large ($N = 2$), Small ($N = 1$) |
| | | Pop. Growth | Decrease | Large ($N = 1$), Medium ($N = 2$) |
| Deer mice | Emigration | Jolly N | Increase | All blocks |
| | | Survivorship | Increase | Large ($N = 2$), Medium ($N = 2$), Small ($N = 2$) |
| | | Pop. Growth | No effect | |
| | Immigration | Jolly N | Decrease | All blocks |
| | | Survivorship | Increase | Large ($N = 1$) |
| | | Pop. Growth | Decreased | Large ($N = 1$) |

In all cases, a paired *t*-test was conducted between estimates in which the data were screened versus the untouched data. Screened data had the trap histories of emigrants added back to a block or the trap histories of immigrants removed from a block. Only significant paired *t*-tests are presented ($p < 0.05$).

creased 20% when immigrants were removed, and increased 17% when emigrants were added. In deer mice the values were higher: 35% and 34%, respectively. In cotton rats, average abundances on some blocks were not influenced by movement, but in those that were, the addition of emigrants increased average abundances by 13% and the removal of immigrants decreased abundances by 12%.

The impacts of movement on survivorship showed no discernable trends across species. Adding emigrant trap histories back to blocks increased survivorship estimates in cotton rats on Large Block 3 and Medium Block 2, decreased the estimate on Large Block 3 only for prairie voles, and increased survivorship estimates on all blocks except Large Block 2 and Small Block 3 for deer mice. Removing immigrant trap histories from the blocks did not change survivorship estimates in cotton rats on all blocks; reduced survivorship estimates on Large Block 1, Large Block 3 and Small Block 2 in prairie voles; and increased survivorship on Large Block 1 only in deer mice.

In cotton rats, emigration and immigration did not influence rates of population change. In prairie voles, rates of population change were reduced on Large Block 1 and on all medium blocks when immigrants were removed from the data. Adding trap histories of emigrants back to blocks also decreased population growth rates on Large Blocks 1 and 3, as well as Medium Block 1 and Small Block 3. In deer mice, removing immigrants decreased population growth rates on Large Block 1, but not on other blocks.

We can make some generalizations from these analyses. First, movement influences average abundances on blocks between 10 and 30% with higher values in deer mice, which is the species that moves the most between blocks. These results are higher than those found in Diffendorfer et al. (1996); however, they should not be taken as exact values because our screening process altered probabilities of capture and, hence, indirectly influenced the estimates of abundance. We clearly need a robust and accurate technique for discovering the impact of movement on local populations (Nichols and Coffman, Chapter 14). Second, movement influenced survivorship on less than half of the blocks in all species. In cotton rats, movement impacted survivorship in only 2 of 10 possible cases; in prairie voles, only 4 of 16; and in deer mice, 7 of 16. We suspect that because so few individuals moved between blocks relative to the number of residents on a block, mean survivorship was not affected in most cases. Third, movement in cotton rats and deer mice did not influence population growth rates on all blocks except Large Block 1 in deer mice and both immigration and emigration decreased rates of population growth in prairie voles. We hypothesize that because the patterns of changes in abundance of cotton rats and deer mice were similar across time regardless of movement, rates of population change were not affected. In voles, however, movement (both immigration and emigration) acts in a manner that increases the difference between abundance estimates in consecutive trapping periods on some blocks.

Long-Term Impacts of Movement

In the past we examined the proportion of individuals on a block that were immigrants. Once immigrants arrive on a block, however, they can persist, potentially breed, and therefore contribute to the long-term dynamics of a local population. We assessed the long-term impacts of immigrants by estimating the proportion of "weeks persisted" by all individuals on a block that were made up of immigrants. We estimated weeks persisted by summing the number of weeks persisted by each individual on a block. We divided the total number of weeks persisted by immigrants by the total number of weeks persisted by all individuals on a block to estimate the proportion of weeks persisted by immigrants.

If immigrants arrive on a block and have similar persistence times as residents, then we expect the proportion of weeks persisted by immigrants to be equal to the proportion of individuals on a block that were immigrants. If immigrants persist more or less than residents, then we would expect differences between the proportion of weeks persisted by immigrants and the proportion of individuals that are immigrants on a block. For example, if 10 of 100 individuals on a block are immigrants, then the proportion of immigrants on a block is 0.10. If residents persist 4 weeks and immigrants persist 10 weeks, however, then the proportion of weeks persisted by immigrants is $(10 \text{ weeks} \times 10 \text{ ind.} / 4 \text{ weeks} \times 90 \text{ ind.} + 10 \text{ weeks} \times 10 \text{ ind.})$ is 0.22. We calculated these proportions for each block and then used each block as a replicate and compared the proportions using *t*-tests. For all species, we found no difference between the proportion of weeks persisted by immigrants and the proportion of individuals that were immigrants. These results indicate that immigrants persisted as long as residents.

These results should be viewed with caution for two reasons. First, immigrants may be a different subset of the population, particularly based on earlier results showing sex and age bias in dispersal (Diffendorfer et al. 1995a). Thus, even though immigrants have similar persistence times, they may alter age structure or sex ratios, and hence demography, of the local population. Second, we have not compared capture probabilities between residents and immigrants. If differences do exist in capture probabilities, then our estimates of persistence may be biased.

Extinction/Colonization Dynamics

Given that average abundances across the eight blocks range between 1 and 11 individuals for cotton rats, 7 and 24 individuals for prairie voles, and 3 and 14 individuals for deer mice, chance local extinctions caused by demographic stochasticity and subsequent colonization events should occur. Movement between blocks becomes paramount in local dynamics, because without movement, many of the blocks would not be recolonized. Here we determine if average abundance on a block influenced rates of extinction and colonization. Clark and Rosenzweig (1994) describe maximum likelihood methods for calculating extinction and colonization rates based on surveys through time (annual censuses, regular trapping schedules, etc). We used these methods to estimate probability

of extinctions and colonization per 2 weeks on blocks. An extinction on a block was defined as a sample period when the estimated minimum number known alive was zero. Colonization occurred into blocks that had experienced extinction. This convention indicates that (1) no animals were captured on that block during the trapping period in question and (2) no animals captured previous to the trapping period on the block were captured there at some later time. We regressed the extinction and colonization probabilities against average abundances on the eight blocks (five for cotton rats).

In cotton rats, the probability of extinction (PE) per 2 weeks was negatively related to average abundance on a block, whereas the probability of colonization (PC) was positively related to average abundance ($PE = 0.23 - 0.02$ Jolly N, $F = 7.39$, $df = 1,4$, $P = 0.073$, Adjusted $R^2 = 61.5\%$; $PC = 0.05 + 0.01$ Jolly N, $F = 37.31$, $df = 1,4$, $P = 0.009$, Adjusted $R^2 = 90.1\%$, Fig. 4.4a and b). In voles, all blocks except Medium 1 had extinctions, however, there were no statistically significant relationships between either the probability of extinction or colonization and average abundance on a block. In contrast to cotton rats, deer mice showed a marginally significant negative relationship between the probability of colonization and the average abundance on a block ($PC = 0.77 - 0.03$ Jolly N, $F = 3.80$, $df = 1,7$, $P = 0.099$, Adjusted $R^2 = 28.6\%$, Fig. 4.4c).

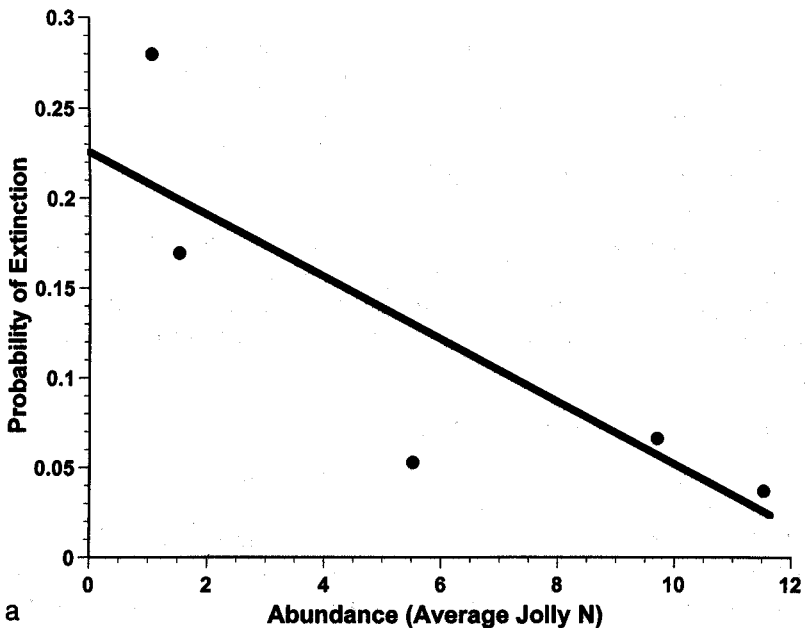
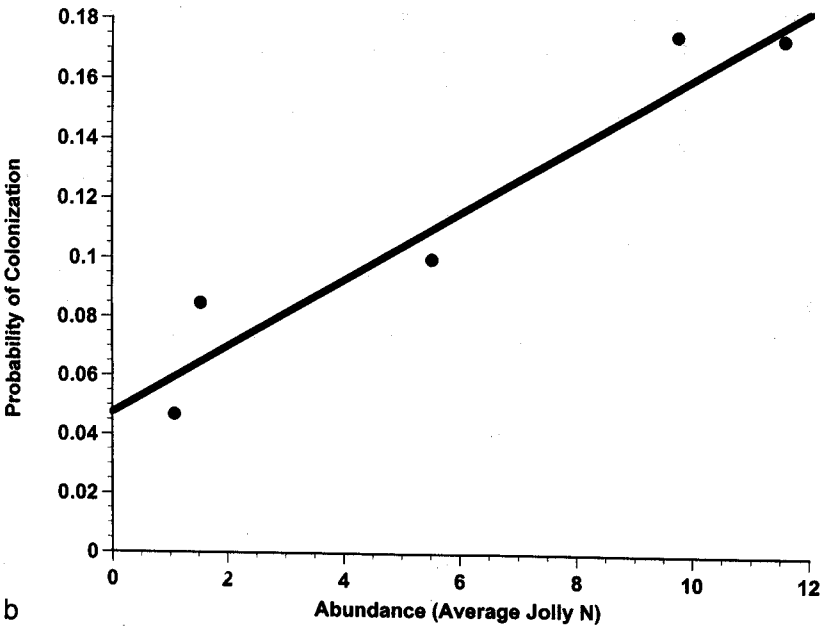
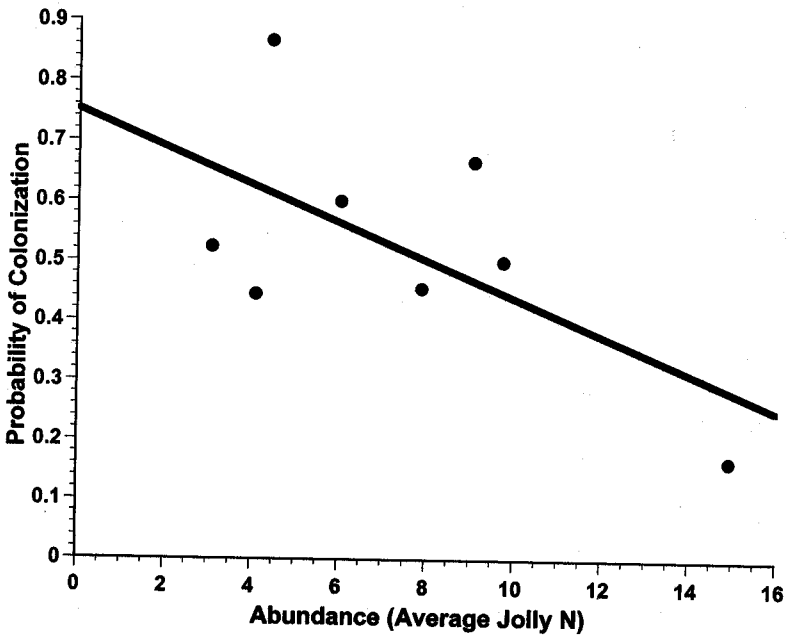


FIGURE 4.4a–c. Regressions between probability of extinction in cotton rats (a), probability colonization in cotton rats (b), and probability of colonization in deer mice (c) against the average abundance on a block. Probabilities of extinction and colonization are per 2 weeks. They were calculated using techniques described in Clark and Rosenswieg (1994).



b



c

FIGURE 4.4a-c (continued).

We expected the probability of extinction to decrease with increasing average abundance. Larger numbers of individuals are more apt to buffer against demographic stochasticity and emigration, causing extinction. We found this relationship in cotton rats, but not in the other species. Because the fragmented site contained only eight blocks, however, the regressions were significant only if the effects were strong. In deer mice, there was a nonsignificant trend for lower probabilities of extinction with higher abundances, but not in prairie voles. The lack of a relationship between extinction probability and average abundance may be due to multiannual cycles on the fragmented site. Processes much larger than the spatial scale of the study site determined the population dynamics at these longer time scales (Diffendorfer et al. 1995b). Hence, we did not see an effect of average abundance on extinction probability because when populations crash towards extinction during declines of the cycle, the differences in abundances between the large and small blocks (23 vs. 7) is not enough to buffer a block from a short-term extinction.

Cotton rats and deer mice had different relationships between the probability of colonization and the average abundance on a block. In cotton rats, the positive relationship is most likely caused by habitat selection. Based on abundances, animals prefer large blocks. We have previously shown source-sink dynamics are not occurring on the site (Diffendorfer et al. 1995a, 1998). Average abundance is thus a reasonable indirect indicator of habitat quality. A dispersing animal attempting to establish most likely encounters both medium and large blocks while moving in the fragmented site. We suggest that an animal is more likely to choose a large block than a medium block. Because large blocks are associated with the highest abundances, we find a positive relationship between average abundance and the probability of colonization. In deer mice, the negative relationship between colonization and average abundance may be caused by territoriality.

Applications for Management at the Landscape Scale

Our goal was to synthesize previous analyses from our studies as well as to present new data that emphasized movements at different scales. We feel doubtful that biologists or land managers who attempt to develop restoration scenarios will find our specific results useful unless they are concerned with management of the particular species we studied. In general, applied conservation work is species or system specific so that natural history and ecological information regarding particular species in particular areas is most useful to local conservation efforts. If ecologists discover responses of species to the patterns of heterogeneity in landscapes, however, then we have at the very least uncovered patterns that managers should consider when making decisions. Furthermore, if we understand the mechanisms behind these responses, then we have created a base of knowledge that managers should find useful. In our study of movement, details such as what sexes or age classes moved,

the timing of movement and the spatial patterns of movement, all varied among the species investigated. These sorts of differences should be expected in most studies because different species evolve different patterns of space use and strategies of dispersal. Despite these differences, however, we found five patterns where (for the most part) the three species we studied had similar responses to the fragmented pattern of our study site.

1. At small scales, when patches were smaller than home ranges, fragmentation reduced the probability of moving between patches over short time scales in two of three species. Other researchers have found similar results. Predation avoidance is one possible reason. In our system, the lack of cover caused by mowing could expose individuals moving across the interstitial areas to higher predation rates. The fact that one species (*P. maniculatus*) did not respond to mowing suggests that connectivity is determined by individual decisions regarding patterns of movement that are species and habitat specific.
2. Distance negatively influenced rates of movement. This result is not surprising. It is also ubiquitous, providing the underpinning of island biogeography theory (MacArthur and Wilson 1967) and the genetic structuring of populations (Wright 1940).
3. Less fragmented blocks had lower rates of emigration. Work on insects has focused on patch size effects on emigration rates (for a review, see Ims 1995) and the results are equivocal. If we interpret our results in terms of a model by Stamps et al. (1987), then one factor that determines emigration rates from our blocks may be the ratio of home ranges on patch edges to the total number of home ranges in the block.
4. We found a negative relationship between population density and the proportion of individuals emigrating in all species. We note that other small mammal ecologists have found either a positive relationship between density and proportional dispersal or none at all. The question of density-dependent dispersal in small mammals is largely unanswered.
5. In all species, movements influenced local demographic variables. As expected, average abundances declined when immigrants were removed and increased when emigrants were added. In most cases, the change caused by movement was approximately 10–30%. Previous work (Diffendorfer et al. 1996) indicates, however, that the relative impacts of movement may be less and that the impacts are greater when abundances are low.

Experimental studies such as those in this book are becoming more frequent and should provide the empirical basis for understanding the impacts of spatial pattern on small mammal distributions and abundances. As patterns

emerge from these studies (like the five we report here) they need to be compared with other studies of small mammals and across taxa (Bowers and Matter 1997). The next step is to begin unraveling the mechanisms causing the responses we are finding to spatial heterogeneity.

If we hope to increase our understanding of how spatial mosaics influence ecological processes, then there needs to be a tighter link between theory and empirical work. Much of the theory currently available to landscape ecologists consists of models with simple organisms in simple landscapes or of simulations that focus on population or metapopulation responses to changes in the spatial attributes and connectivity of habitat patches. These types of simulations repeatedly alter the structure of a hypothetical landscape, then predict rates of extinctions or population demography over the entire area (Harrison and Fahrig 1995). These models might be useful as tools for conservation strategies and large-scale prediction, but the majority of studies presented in this book, including ours, do not mesh well with such theory. This is because the experiments are limited to only one landscape (i.e., we cannot repeatedly reconfigure our landscapes easily), and focus primarily on individual, not population- or community-level responses (See Dooley and Bowers 1996 for additional discussions on patch theory).

Another body of ecological theory focuses on individuals and strategies in heterogeneous landscapes and predicts population-level responses. Examples include source-sink dynamics (see Dias 1996 for review), the balanced dispersal model (McPeck and Holt 1992), models of habitat selection in heterogeneous landscapes (Morris 1992, 1995), and models of dispersal from patches (Stamps et al. 1987). This flavor of "Spatial Ecology" is better for empiricists to use because the models are more tractable. These models, however, do not make predictions at larger scales of entire landscapes like the simulation models discussed earlier. It is critical that individual responses to changes in spatial heterogeneity be incorporated into landscape-level theory. In so doing, models that make landscape-level predictions could be grounded in empirically testable assumptions.

It behooves empiricists to relate their findings to theory. In our case, higher rates of movement from more fragmented blocks support a model by Stamps et al. (1987) that predicts higher rates of movement as the ratio of home ranges on the edges of patches increases. The model by Stamps et al. (1987) needs further testing because it may explain a general mechanism for predicting dispersal rates in fragmented systems. As another example, one of us (Diffendorfer 1998) completed a series of analyses that used data from the fragmented site to test balanced-dispersal (McPeck and Holt 1992) and source-sink models (Dias 1996). The data indicate that individuals in our landscape are choosing to move between blocks in a manner that maximizes their fitness and equilibrates fitness across space (Diffendorfer 1998). Assuming an ideal free distribution in a spatially heterogeneous system may be the appropriate null model for small mammals.

Neither theory nor empirical data will make sense unless they are embedded in the appropriate context of space and time (Wiens 1976, 1995, Allen and Hoekstra 1992, Levin 1992, 1993, Wiens et al. 1993). Ecologists will

“talk by” one another until they make predictions and collect data at similar scales (Murphy 1989). Following Ims (1995), we have outlined three scales to study movements. Before any generalities regarding species responses to spatial mosaics can emerge, ecologists must recognize the role of scale in their studies of population demography (Stiling et al. 1991, Doak et al. 1992, Crist and Wiens 1994), community structure (Thorhallsdottir 1990, Palmer and White 1994), and energy flow through ecosystems (Kolasa 1989, Holling 1992).

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Literature Cited

- Abramsky, Z., O. Ovadia, and M.L. Rosenzweig. 1994. The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: an experimental field study. *Oikos* 69:318–326.
- Allen, T.F.H., and T.W. Hoekstra. 1992. *Toward a unified ecology*. Columbia University Press, New York, New York.
- Beacham, T.D. 1980. Dispersal during population fluctuations of the vole, *Microtus townsendii*. *Journal of Animal Ecology* 49:867–877.
- Bowers, M.A., and S.F. Matter. 1997. Landscape analyses of density-patch size relationships in mammals: a review of the literature. *Journal of Mammalogy* 78:999–1013.
- Bowers, M.A., K. Gregario, C.J. Brame, S.F. Matter, and J.L. Dooley Jr. 1996. Use of space and habitat by meadow voles at the home range, patch and landscape scale. *Oecologia* 105:107–115.
- Brown, J.S. 1996. Coevolution and community organization in three habitats. *Oikos* 75:193–206.
- Buechner, M. 1987. A geometric model of vertebrate dispersal: tests and implications. *Ecology* 68:310–318.
- Clark, C.W., and M.L. Rosenzweig. 1994. Extinction and colonization processes: parameter estimates from sporadic surveys. *The American Naturalist* 143:583–596.
- Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
- Crist, T.O., and J.A. Wiens. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. *Oikos* 69:37–46.
- Danielson, B.J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. *The American Naturalist* 138:1105–1120.
- Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. *Evolutionary Ecology* 6:399–411.
- Dias, P.C. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* 11:326–330.
- Diffendorfer J.E. 1998. Testing models of source-sink dynamics and balanced dispersal. *Oikos* 81:417–433.

- Diffendorfer, J.E., M.S. Gaines, and R.D. Holt. 1995a. Habitat fragmentation and the movements of three small mammals (*Sigmodon hispidus*, *Microtus ochrogaster*, and *Peromyscus maniculatus*). *Ecology* 76:837–839.
- Diffendorfer, J.E., N.A. Slade, M.S. Gaines, and R.D. Holt. 1995b. Population dynamics of small mammals in fragmented and continuous old-field habitat. Pages 175–199 in W.Z. Lidicker, editors. *Landscape approaches in mammalian ecology and conservation*. University of Minnesota Press, Minneapolis, Minnesota.
- Diffendorfer, J.E., R.D. Holt, N.A. Slade, and M.S. Gaines. 1996. Small mammal community patterns in old fields: distinguishing site-specific from regional processes. Pages 421–466 in M.L. Cody and J.A. Smallwood, editors. *Long-term studies of vertebrate communities*. Academic Press, San Diego, California.
- Doak, D.F., P.C. Marino, and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theoretical Population Biology* 41:315–336.
- Dobrowolski, K., A. Banach, A. Kozakiewicz, and M. Kozakiewicz. 1993. Effect of habitat barriers on animal populations and communities in heterogeneous landscapes. Pages 61–70 in R.G.H. Bunce, L. Ryskewski and M.G. Paoletti, editors. *Landscape ecology and agroecosystems*. Lewis Publishers, Boca Raton, Florida.
- Dooley, J.L., and M.A. Bowers. 1996. Influences of patch size and microhabitat on the demography of two old-field rodents. *Oikos* 75:453–462.
- Fretwell, S.D., and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Gaines, M.S., and L.R. McClenaghan Jr. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics* 11:163–196.
- Gaines, M.S., and M.L. Johnson. 1984. A multivariate study of the relationship between dispersal and demography in populations of *Microtus ochrogaster* in eastern Kansas. *The American Midland Naturalist* 111:223–233.
- Gautestad, A.O., and I. Myrsterud. 1993. Physical and biological mechanisms in animal movement processes. *Journal of Applied Ecology* 30:523–535.
- Gottfried, B.M. 1982. A seasonal analysis of small mammal populations in isolated woodlot islands. *Canadian Journal of Zoology* 60:1660–1664.
- Hanski, I., and M.E. Gilpin. 1991. Metapopulation dynamics: a brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3–16.
- Hansson, L., L. Fahrig, and G. Merriam. 1995. Mosaic landscapes and ecological processes. Chapman and Hall, London, United Kingdom.
- Harper, S.J., E.K. Bollinger, and G.W. Barrett. 1993. The effect of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). *Journal of Mammalogy* 74:1045–1055.
- Harrison, S., and L. Fahrig. 1995. Landscape pattern and population conservation. Pages 293–308 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, United Kingdom.
- Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs* 62:447–502.
- Holt, R.D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181–208.
- Holt, R.D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 in R.E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois.

- Ims, R.A. 1995. Movement patterns related to spatial structure. Pages 85–109 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, UK.
- Ims, R.A., and N.G. Yoccoz. Studying transfer processes in metapopulations: Emigration, migration, and colonization. Pages 247–265 in I. Hanski and M. Gilpin, editors. *Metapopulation biology*. Academic Press, San Diego, California.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London* 330:175–190.
- Kolasa, J. 1989. Ecological systems in hierarchical perspective: breaks in community structure and other consequences. *Ecology* 70:36–47.
- Krebs, C.J. 1992. The role of dispersal in cyclic rodent populations. Page 160–176 in N. Stenseth and W.Z. Lidicker, editors. *Animal dispersal: small mammals as a model*. Chapman and Hall, London, United Kingdom.
- La Polla, V.N., and G.W. Barrett. 1993. Effects of corridor width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecology* 8:25–37.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Levin, S.A. 1993. Concepts of scale at the local level. Pages 7–19, in J.R. Ehrlinger and C.B. Field, editors. *Scaling physiological processes: leaf to globe*. Academic Press, San Diego, California.
- MacArthur, R.H., and E.O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.
- McClenaghan, L.R., Jr., and M.S. Gaines. 1976. Density-dependent dispersal in *Sigmodon*: a critique. *Journal of Mammalogy* 57:758–759.
- McLaughlin, J.F., and J. Roughgarden. 1993. Species interactions in space. Page 89–98 in R.E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois.
- McPeck, M.A., and R.D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *The American Naturalist* 140:1010–1027.
- Miller, G.L., and B.W. Carroll. 1989. Modeling vertebrate dispersal distances: alternatives to the geometric distribution. *Ecology* 70:977–986.
- Morris, D.W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology* 6:412–432.
- Morris, D.W. 1995. Habitat selection in mosaic landscapes. Pages 110–135 in L. Hansson, L. Fahrig, and G. Merriam editors. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, United Kingdom.
- Murphy, D.D. 1989. Conservation and confusion: wrong species, wrong scale, wrong conclusions. *Conservation Biology* 3:82–84.
- Ostfeld, R.S., S.T. A. Pickett, M. Shachak, and G.E. Likens. 1996. Defining the scientific issues. Pages 3–10 in S.T.A. Pickett, R.S. Ostfeld, M. Shachak, and G.E. Likens, editors. *The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity*. Chapman and Hall, New York, New York.
- Palmer, M.W., and P.S. White. 1994. Scale dependence and the species-area relationship. *The American Naturalist* 144:717–740.
- Pulliam, R.H. 1988. Source, sinks and population regulations. *The American Naturalist* 132:652–661.
- Pulliam, R.H., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *The American Naturalist* 137:S51–S66.

- Rajska-Jurgiel, E. 1992. Demography of woodland rodents in fragmented habitat. *Acta Theriologica* 37:73-90.
- Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and S.D.M. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789-799.
- Stamps, J.A., Buechner, M., and V.V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *The American Naturalist* 129:533-552.
- Stiling, P., A. Throckmorton, J. Silvanima, and D.R. Strong. 1991. Does spatial scale affect the incidence of density-dependence? A field test with insect parasitoids. *Ecology* 72:2143-2154.
- Tamarin, R.H., Reich, L.M., and C.A. Moyer. 1984. Meadow vole cycles within fences. *Canadian Journal of Zoology* 62:1796-1804.
- Thorhallsdottir, T.E. 1990. The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology* 78:884-908.
- Verner, L., and L.L. Getz. 1985. Significance of dispersal in fluctuating populations of *Microtus ochrogaster* and *M. pennsylvanicus*. *Journal of Mammalogy* 66:338-347.
- Waser, P.M. 1985. Does competition drive dispersal? *Ecology* 66:1170-1175.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7:81-120.
- Wiens, J.A. 1995. Landscape mosaics and ecological theory. Pages 1-26 in L. Hansson, L. Fahrig, and G. Merriam, editor. *Mosaic landscapes and ecological processes*. Chapman and Hall, London, United Kingdom.
- Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369-380.
- Wolff, J.O., E.M. Schaubert, and D.W. Edge. 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. *Conservation Biology* 11:945-956.
- Wright, S. 1940. Breeding structure of populations in relation to speciation. *The American Naturalist* 74:232-248.