

## THE EFFECTS OF HABITAT FRAGMENTATION ON SMALL MAMMAL POPULATIONS

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**Abstract.** We examined the population dynamics of small mammals in an experimentally fragmented, successional field over three years. Patches of three sizes (32 m<sup>2</sup>, 288 m<sup>2</sup>, and 5000 m<sup>2</sup>) were censused at biweekly intervals, and data for the three common species were grouped by patch size and analyzed for relative population density, persistence of individuals, and patterns of movement among patches. The three species sorted by patch size, with the largest (*Sigmodon hispidus*) most abundant on the largest patches, the smallest (*Peromyscus maniculatus*) most abundant on the smallest patches, and the intermediate-sized (*Microtus ochrogaster*) most abundant on medium patches. Our explanation for this spatial pattern in density involves the interplay of source-sink dynamics and interspecific interactions. Persistence times for the two larger species were highest on large patches, but *P. maniculatus* persisted equally well on all patch sizes. Eighty-five percent of individual moves for all species occurred within a patch size. Individuals that dispersed between patch sizes tended to move towards a larger size patch. Our results suggest that in the future, metapopulation theory and analyses of habitat fragmentation should consider in more detail the effects of intra- and interspecific density-dependent interactions.

### INTRODUCTION

The growing interest in the effect of habitat fragmentation on evolutionary and ecological processes is generated in part by concerns about the fate of threatened and endangered species such as the spotted-owl (*Strix occidentalis caurina*) (Lande 1988, Doak 1989) and the checkerspot butterfly (*Euphydryas editha*) (Ehrlich and Murphy 1989) whose habitats are becoming increasingly fragmented. To ensure the preservation of many species, conservation biologists will need an improved understanding of how natural populations function when they are reduced and disconnected.

Metapopulation theory provides a framework for analyzing the persistence of species in fragmented habitats and should prove useful in elucidating the conservation

implications of fragmentation. Following Levins (1980), Hanski and Gilpin (1991) defined a metapopulation as "a set of local populations which interact via individuals moving among populations." Most models of metapopulations incorporate local extinctions followed by recolonization by individuals moving from extant populations. Spatial heterogeneity in the environment may cause differences in habitat quality among populations within a metapopulation. Populations in higher quality habitats may contain a surplus of animals that can disperse to neighboring populations. Populations can thus persist in low quality habitats due to the colonization of individuals from higher quality habitats. Holt (1985) and Pulliam (1988) describe populations that produce a surplus of dispersing animals as "sources" and populations in suboptimal habitat maintained by dispersal as "sinks."

Fragmented landscapes containing an array of different patch sizes may lead to source-sink population dynamics. For most species there should be a minimum patch size below which a population cannot persist without immigration. The existence of source-sink population structure has been documented in annual plant species (Keddy 1981, Kadmon and Shmida 1990) but there is little evidence for source-sink population structure in small mammals.

We made a series of predictions concerning the effects of patch size on small mammal density, persistence, and direction of dispersal. We assumed larger patches would be of higher quality and support source populations, whereas smaller patches would be of poorer quality and represent sink populations. If so, larger patches should have higher densities than smaller patches. Because sink populations will be subject to extinctions and recolonizations, we predicted that smaller patches would have greater variation in population density over time than larger patches. Moreover, individuals on larger patches should have higher persistence rates than on smaller patches because of better habitat quality. Finally, because sink populations can be sustained only by immigration, we predicted more dispersal from larger to smaller patches than from smaller to larger.

We tested these predictions using mark-recapture data from a fragmented landscape, created by mowing a successional field into an archipelago of semi-isolated patches varying over two orders of magnitude in size.

#### *Study site*

The study site is half of a 12 ha field on the University of Kansas' Nelson Environmental Study Area (NESA), 16 km north of Lawrence, Kansas (Fig. 1). In 1984, habitat patches of three sizes, 5000 m<sup>2</sup>, 288 m<sup>2</sup> and 32 m<sup>2</sup>, were created by mowing an old field. The shortest distance between any two patches was 15 m. We mowed interstitial areas between patches at biweekly intervals during the growing season and allowed secondary plant succession to proceed unhindered within patches.

The rationale for patch sizes and arrangement was based on a consideration of the biology of the species on the study area. The largest patches (0.5 ha) were comparable to the sizes of enclosures typically used in experimental manipulations of small mammal populations (Johnson and Gaines 1987). Archipelagos equal in size to large patches are the basic unit of measurement in our fragmented landscape. The archipelagos of medium sized patches represent an increasing level of fragmentation, followed by the archipelagos

of the smallest patch sizes which are most fragmented. This design enabled us to assess the effects of increasing levels of habitat fragmentation on small mammal populations. Data reported here are for the period from September, 1987 to April, 1990.

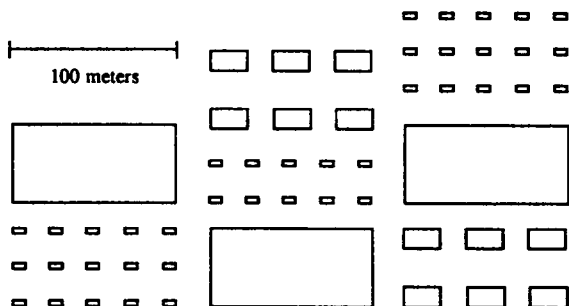


Fig. 1. Diagram of experimental patches. The 40 small patches are each 4 m x 8 m; the 12 medium patches are 12 m x 24 m; the three large patches are 50 m x 100 m.

The three small mammal species that accounted for most captures over the duration of the study were the hispid cotton rat (*Sigmodon hispidus*), the prairie vole (*Microtus ochrogaster*), and the deer mouse (*Peromyscus maniculatus*). These three small mammal species range widely in body size from the hispid cotton rat with an average adult body mass of 135 g, the prairie vole 43 g, and the deer mouse 20 g.

Old field succession of the plant community in the study site has followed the familiar pattern documented throughout the central United States (Bazzaz 1968, Collins and Adams 1983). Substantial changes in the plant community composition occurred during the first three years of succession (1984-1987) but the rate of change greatly slowed thereafter as perennial forbs and invading woody species replaced annual species. Analysis of vegetation data show that patch size did not markedly affect plant species composition (Holt et al. 1991). Thus, plant data can be ignored as a covariate in analyzing the mammal data.

## METHODS

We assessed the effects of patch size on the population dynamics of each small mammal species using mark-recapture methods. A detailed description of the arrangement of the traps on the patches and the field protocol is given in Foster and Gaines (1991). Briefly, animals were live-trapped with Sherman traps for 2 consecutive days every 2 weeks. Each new animal was marked with a fingerling fish tag upon first capture. At first and all subsequent captures the following data were recorded: ear tag number, trap location, species, body mass, sex, and reproductive condition.

## RESULTS

The population densities expressed as the minimum number alive for three small mammal species are presented in Table 1. We did not use the Jolly-Seber model to estimate population density because of large standard errors associated with density estimates, which were due to low trappability on all patch sizes. The overall trappability for the three species were as follows: *S. hispidus* 40.5%, *M. ochrogaster* 52.7%, and *P. maniculatus* 34.9%. Using the minimum number alive to estimate population density also maintains consistency with Foster and Gaines (1991). The population densities were adjusted for differences in the number of traps in each patch. Since the trap density in small patches was approximately 31 per 1000 m<sup>2</sup> and medium and large patches had a trap density of 14 per 1000 m<sup>2</sup>, population density estimates on small patches were reduced by a factor of 0.45.

TABLE 1. Comparison of mean  $\pm$  1 SE population (number/ha) densities for three species of small mammals, according to patch size, estimated from 67 bi-weekly live-trap censuses, 1987-1990. Density estimates are minimum number alive (MNA) per unit habitable area.

Species	n*	Small patches	Medium patches	Large patches
<i>Sigmodon hispidus</i>	375	0.5 $\pm$ 0.4	3.7 $\pm$ 0.8	12.2 $\pm$ 0.3
<i>Microtus ochrogaster</i>	1424	61.9 $\pm$ 1.2	77.7 $\pm$ 2.2	49.4 $\pm$ 0.7
<i>Peromyscus maniculatus</i>	751	64.6 $\pm$ 1.4	49.1 $\pm$ 1.3	17.6 $\pm$ 0.4

\*n = Total number of individuals of each species.

Our prediction that population density would be higher on large patches was verified for *S. hispidus* but falsified for *M. ochrogaster* and *P. maniculatus*. Based on the density data, the species sort into different patches by body size. The species with the largest body mass, *S. hispidus*, was most common on the large patches ( $F_{2,198}=47.64$ ,  $P<0.0001$ ) and the species with the smallest body mass, *P. maniculatus*, was most common on the small patches ( $F_{2,198}=43.72$ ,  $P<0.0001$ ). *Microtus ochrogaster*, which has an intermediate body mass, was most common on the medium sized patches ( $F_{2,198}=5.89$ ,  $P<0.005$ ).

We tested the prediction that smaller patches would have a greater variance in density over time by first grouping patches by size. For each time period, the data shown

in Fig. 2 are running coefficients of variation in the minimum number alive (MNA) over consecutive trapping periods. The coefficient of variation in MNA at time  $t$  was calculated from a mean and standard deviation for all MNA's from time 1 to time  $t$ .

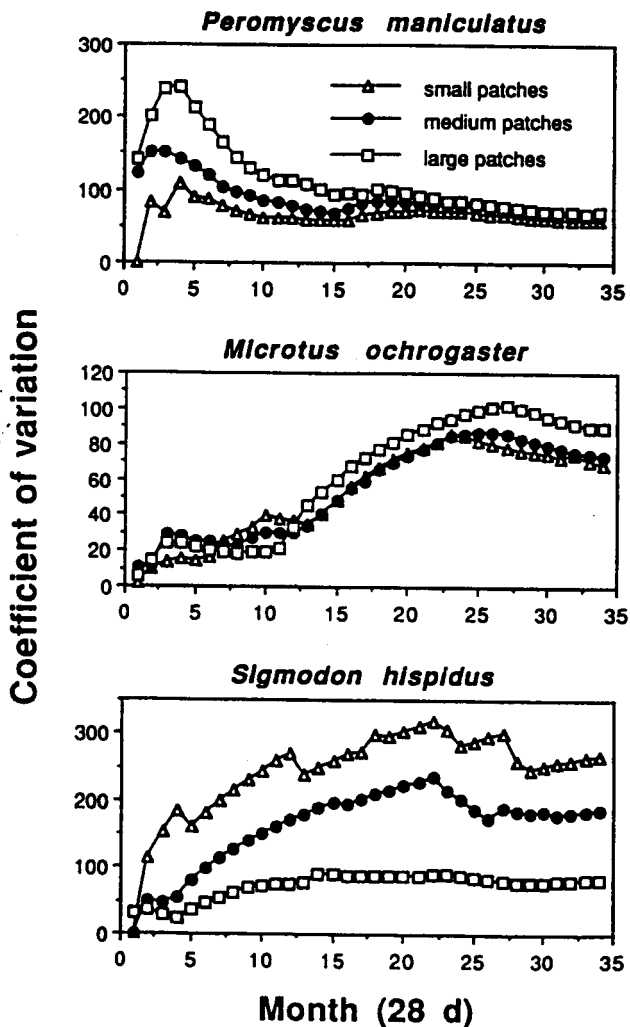


Fig. 2. The running variance in density on different sized patches over time for each species.

The standardized variance on all sizes of patches increased over time then stabilized for *S. hispidus* and *M. ochrogaster*. Conversely, the variance in *P. maniculatus* exhibited a rapid increase followed by a decline and eventual stabilization. For *S. hispidus*, differences in variance between patch sizes support our prediction with the variance being lowest in the large patches and highest in small patches. The variance in density for *M. ochrogaster* was generally higher in the large patches than in medium and small patches. Initially for *P. maniculatus*, the variance in density in large patches was higher than the small and medium patches, but the variance in all patches converged with time.

Persistence rates for *S. hispidus* and *M. ochrogaster* (Table 2) support our prediction that individuals remain longer on large patches. Both *S. hispidus* ( $F_{2,389} = 5.74, P < 0.01$ ) and *M. ochrogaster* ( $F_{2,1577} = 34.6, P < 0.01$ ) individuals persisted longer on large patches compared to small patches. There were no significant differences for *P. maniculatus* ( $F_{2,879} = 0.16, P > 0.5$ ).

TABLE 2. Mean  $\pm$  1 SE individual persistence times for each species according to patch size. Persistence of an individual is the duration in weeks between the first and last periods trapped, plus one. Sample sizes are given in parentheses.

Species	Persistence time (weeks)		
	Small patches	Medium patches	Large patches
<i>Sigmodon hispidus</i>	1.00 $\pm$ 0.00 (10)	2.54 $\pm$ 0.55 (41)	6.16 $\pm$ 0.45 (340)
<i>Microtus ochrogaster</i>	5.15 $\pm$ 0.35 (385)	7.91 $\pm$ 0.51 (350)	10.46 $\pm$ 0.42 (844)
<i>Peromyscus maniculatus</i>	8.21 $\pm$ 0.66 (263)	7.73 $\pm$ 0.78 (223)	7.76 $\pm$ 0.55 (390)

We analyzed movements by calculating the proportion of individuals moving within an archipelago of the same size patches and between archipelagos of different size patches (Table 3). The within category includes the proportion of individuals that move within a large patch, within an archipelago of medium patches, and within an archipelago of small patches. The between category includes the proportion of individuals that move to a different sized patch. An animal that changes patch size will, by definition, have to move to a different sized archipelago. In addition, any animal that moved from small to large and back to small, or conversely, large to small and back to large, was excluded from the analysis.

A greater proportion of individuals moved within a patch size compared to individuals moving between patch sizes (Table 3). In comparing movement between patch sizes, there was a greater proportion of individuals moving from small to larger

TABLE 3. Total proportion of individual movements within and between patches of different sizes. The numbers of individuals are in parentheses.

Species	Direction of movements		
	Within a patch	Between patch sizes	
		to smaller	to larger
<i>Sigmodon hispidus</i>	0.946 (194)	0.019 (4)	0.034 (7)
<i>Microtus ochrogaster</i>	0.862 (600)	0.056 (43)	0.082 (63)
<i>Peromyscus maniculatus</i>	0.774 (260)	0.083 (28)	0.143 (48)
Totals	0.845 (1054)	0.060 (75)	0.095 (118)

patches than from large to smaller patches for all species. After testing for homogeneity with a G-test, the movements of all species were pooled. The pooled movement data showed there were statistically significant differences ( $G = 9.66$ ,  $df = 1$ ,  $P < 0.05$ ) with a greater proportion of individuals moving from small to large size patches than vice versa.

## DISCUSSION

The density differences in Table 1 can be explained in the context of source-sink dynamics. Medium and small patches may be too small to sustain an individual of *S. hispidus*, so this species was forced to live on large patches. The low density of *S. hispidus* populations in the smaller patches may have consisted of transient individuals, an interpretation consistent with the low individual persistence rates on medium and small patches (Table 2). Therefore, small and medium patches may have contained sink populations maintained by immigration from large patches. *S. hispidus* may have been a competitive dominant in this system. Laboratory experiments have demonstrated it was superior in aggressive interactions with *M. ochrogaster* (Terman 1974). Consistent with this hypothesis, many studies have shown that *M. ochrogaster* densities declined when *S. hispidus* was abundant in natural populations (Glass and Slade 1980, Fleharty and Olson 1969, Frydenhall 1969). We also found a statistically significant negative correlation between the population densities of these two species in summer ( $r = -0.52$ ,  $P < 0.01$ ). We found a statistically significant negative correlation between *S. hispidus* and *P. maniculatus* population densities ( $r = -0.33$ ,  $P < 0.05$ ) over all seasons indicating *S. hispidus* may be dominant to *P. maniculatus*.

Variance in *S. hispidus* density in the different sized patches also supported the hypothesis that large patches had source populations of *S. hispidus* and that small patches had sink populations. The variance in density over time was lowest in the large patches and highest in the small patches. This result was expected because *S. hispidus* on small and medium patches (sink populations) underwent periodic extinctions and recolonizations that increased the variance in density.

Because *S. hispidus* was rare in the small and medium patches, both *M. ochrogaster* and *P. maniculatus* may have had refuge from competition in these smaller patches. If *M. ochrogaster* were dominant to *P. maniculatus* (based on its larger body mass), *M. ochrogaster* may have had to settle on the next best available habitat, medium patches. Our assumption that *M. ochrogaster* is dominant to *P. maniculatus* is supported by a negative correlation between densities of the two species ( $r = -0.31$ ,  $P < 0.05$ ). The small patches may have been too small to support a resident population of *M. ochrogaster*. Densities of *M. ochrogaster* were generally highest on medium patches and variance in density over time was lowest on medium and small patches during the end of the study. Since persistence rates of *M. ochrogaster* were highest in the large patches, we conclude if a prairie vole was able to establish a home range in a large patch, it had a high probability of persisting there. It seems that smaller patches may have been sink populations for *M. ochrogaster* and the large and medium patches may have been source populations.

*Peromyscus maniculatus* may have had a refuge from competition from both species in the smallest patches. The high population density of *P. maniculatus* on the small patches could have been due to this species' ability to exploit the interstitial mowed areas more effectively than the other species (Foster and Gaines 1991), which in turn, allowed it also to exploit the small patches. The *P. maniculatus* in low densities on the larger patches could have been a sink population maintained by individuals dispersing from small patches and the interstitial area. It is interesting that there was no patch size effect on persistence rates for this species, and that the variance in density on the three patch sizes converged as they decreased over time. These results suggest that *P. maniculatus* was exploiting the fragmented landscape in a very different manner than *S. hispidus* and *M. ochrogaster*.

In a source-sink system, it should be possible to determine which habitat is a source by assessing biases in the direction of known dispersal events. The movement data from capture-recapture methods indicated that there was a greater proportion of individuals moving from smaller to larger patches for all three species (Table 3). Mackelberg and Hallet (1991) obtained a similar result in their study of the responses of *Microtus montanus* to habitat fragmentation in a grassland in southeastern Washington. If the larger patches were sinks for *M. ochrogaster* and *P. maniculatus*, there should have been more movement from smaller to larger patches, which is consistent with our results. However, using the same argument for *S. hispidus*, there should have been more movement from larger to smaller patches, which we did not observe.

Our movement data needs to be viewed with caution for several reasons. First, the movement based on trapping data was confounded with survivorship. For example, since survivorship was highest on large patches for *S. hispidus* and *M. ochrogaster*, we may have been more likely to trap individuals that moved from smaller to larger patches than from larger to smaller patches, where individuals may disappear before they are



captured. Second, the number of trap locations varied among patch sizes. There were more traps on large and medium patches compared to the small patches. This difference in trapping effort may have biased our data in favor of movement towards larger patches because it would have been more likely to capture animals there. However, the average occupancy in traps was generally less than 50% on all patches, which makes this explanation less plausible. Finally, the percent movement may reflect the cumulative number of captures of the three species on the different patches. If the cumulative number of captures was highest in the smaller patches for *M. ochrogaster* and *P. maniculatus* there may be a greater number of individuals moving from smaller to larger patches due to chance. This was not the case because the highest number of cumulative captures for all species was on the large patches.

The best way to test our hypothesis that source-sink structure interacts with interspecific competition to generate the population dynamics of the three species in our fragmented habitat will be to conduct experimental manipulations. If large patches are source populations and smaller patches are sinks for *S. hispidus*, inhibiting dispersal between them should lead to abnormally high densities on large patches and extinction of *S. hispidus* on the smaller patches. We intend to test this prediction by surrounding different sized patches with rodent-proof fences. Similar types of experiments inhibiting dispersal can be done with the other species. If interspecific competition is responsible in part for the patterns we observe, then excluding *S. hispidus* from large patches should result in an increase of *M. ochrogaster* on these patches. Similarly, excluding both *S. hispidus* and *M. ochrogaster* from large patches should result in an increase of *P. maniculatus*. We can selectively exclude certain species by manipulating openings in the fences. We plan to complement these experiments with radiotelemetry data on individual movements between patches for different species.

The question remains, what are the implications of our results to conservation biology? Some ecologists have claimed that the same processes affected by habitat fragmentation on smaller spatial scales are affected similarly at larger spatial scales. Ims (1990) and Stenseth (1990) suggested that small rodents in small-scale fragmented landscapes can serve as "Empirical Model Systems (EMS)" for larger mammals living in areas fragmented by human activity. Similarly, J. A. Wiens (*personal communication*), believes that it might be possible to use information obtained at a micro-landscape level to make predictions about larger scales. It is appealing to extrapolate processes that occur at a microscale to large scale phenomena using small mammals, because they are easy to manipulate experimentally, and the population dynamics of some species have been thoroughly studied. However, generalizing about population dynamics from small to larger landscapes may be possible only if ecological processes scale linearly with area. As area increases, the complexity of biotic and abiotic interactions increases, making a linear relationship between small and large scale ecological processes unlikely.

Our results suggest it may even be difficult to generalize about the effects of habitat fragmentation on different small mammal species living in the same area. The three species in our system responded in very different ways to fragmentation in our micro-landscape. These different responses presumably reflect slight differences in autecological requirements compounded by competitive interactions. It is imperative that more attention be given to these factors if we hope to understand how species utilize fragmented landscapes.

Finally, the results we obtained from 1987-1990 on the effects of patch size on density and persistence rates of *S. hispidus*, *M. ochrogaster*, and *P. maniculatus* species are consistent with those obtained by Foster and Gaines (1991) from 1984-1987. This consistency indicates that, at this point in time, secondary succession has not been a major factor in determining the distribution and abundance of these three species. It is interesting that population densities of a fourth small mammal species, *Reithrodontomys megalotis* (western harvest mouse), decreased steadily from 1984-1987, and were at low numbers at the end of the Foster and Gaines (1991) study. In this study the species disappeared completely. The decrease in *R. megalotis* was concomitant with a decrease in annual grasses. It is possible that given enough time, the other species may be affected by changes in the plant community.

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