

Population Dynamics of Small Mammals in Fragmented and Continuous Old-Field Habitat

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Early empirical work pertinent to habitat fragmentation was motivated by island biogeography theory and generally focused on descriptive, community-level patterns of extinctions and species diversity as functions of patch size or isolation (for reviews, see Diamond 1984; Simberloff 1988). Island theory was used to predict the optimal design of reserves; this attempted use of ecological theory has led to continuing debate (Beckon 1993; Gilpin 1988; Quinn and Hastings 1987). However, there is growing recognition that habitat fragmentation acts via ecological processes that affect population dynamics (McCallum 1992; Ostfeld 1992; Pulliam and Danielson 1992) and therefore local abundance (Fahrig and Paloheimo 1988), viability (Fahrig and Merriam 1985; Lande 1987; Roff 1974), and community organization (Holt 1985, 1993). Moreover, ecologists are increasingly becoming aware of how profoundly landscape patterns and mesoscale processes can influence local population dynamics and community structure (Hansson, Chap. 2; Holt 1993; Lidicker, Chap. 1).

As in other areas of ecology, properly designed experiments could be useful in analyzing habitat fragmentation. But in practice such experiments are difficult to design and execute, for several reasons. First, the spatial scale at which habitat fragmentation affects ecological processes is often too large to allow adequate replication or controls in experimental designs (but see Lord and Norton 1990). Second, studies of habitat fragmentation are motivated by conservation issues and so are often done "after the fact." A researcher may not sample a forest before it is cut, but instead must deal with remnants from an already fragmented system. For these reasons, most studies of habitat fragmentation in the past have understandably tended to describe patterns and could only indirectly infer the underlying causal mechanisms. However,

ecologists are increasingly using experimental landscapes as model systems for addressing landscape-level questions (Barrett et al., Chap. 8).

Moreover, increasing attention has recently been paid to the demographic mechanisms involved in habitat fragmentation (Barrett et al., Chap. 8; Brown and Ehrlich 1980; Fahrig and Paloheimo 1987; Foster and Gaines 1991; Gaines et al. 1992a,b, 1994; Haila et al. 1993; Harper et al. 1993; Harrison et al. 1988; Henderson et al. 1985; Kareiva 1987, 1990; Laurance, Chap. 3; Lovejoy et al. 1984; Peltonen and Hanski 1991; Soulé et al. 1992; van Apeldoorn et al. 1992; Wegner and Merriam 1979). These studies indicate that habitat fragmentation can have far-reaching and sometimes unexpected effects on populations and communities that are mediated through effects on demographic parameters.

In this chapter, we describe the results of an experimental system in which fragmentation has been imposed on a landscape to investigate the effects of habitat fragmentation on basic population dynamics in old-field habitats in eastern Kansas. Our basic approach is to combine data from two ongoing long-term studies of small-mammal populations in old-field habitats. One study focuses on a continuous area of habitat, the other on a fragmented system (Fig. 9.1). We will compare temporal trends in abundance, survival, sex ratios, and reproduction for three common small-mammal species (*Sigmodon hispidus*, *Microtus ochrogaster*, and *Peromyscus maniculatus*). Populations in the continuous habitat can be considered "controls," which allows us to make more powerful inferences about the influence of habitat fragmentation on population processes than are permitted by comparisons among patches within the fragmented system (Foster and Gaines 1991; Gaines et al. 1992a,b, 1994). This chapter represents the first attempt to synthesize these long-term data sets to provide a perspective on the overall effects of habitat fragmentation on small-mammal demography.

Earlier analyses from the fragmented site enable us to predict the abundance patterns we may expect when we compare the two sites. The most striking result from the fragmented area study is the clear relationship between body size/block size and density, which has been evident for 7.7 years (Fig. 9.2). Here, "blocks" are defined as spatial units 50 m x 100 m in extent, with clusters of either 15 small patches, six medium patches, or one large patch. The largest-bodied species (*S. hispidus*) has its highest densities on large blocks and is rarely found on blocks of the other sizes. Similarly, the medium-sized species (*M. ochrogaster*) has its highest densities on the blocks with medium-sized patches, and the smallest-bodied species (*P. maniculatus*) has its highest densities on the blocks of small patches. We found

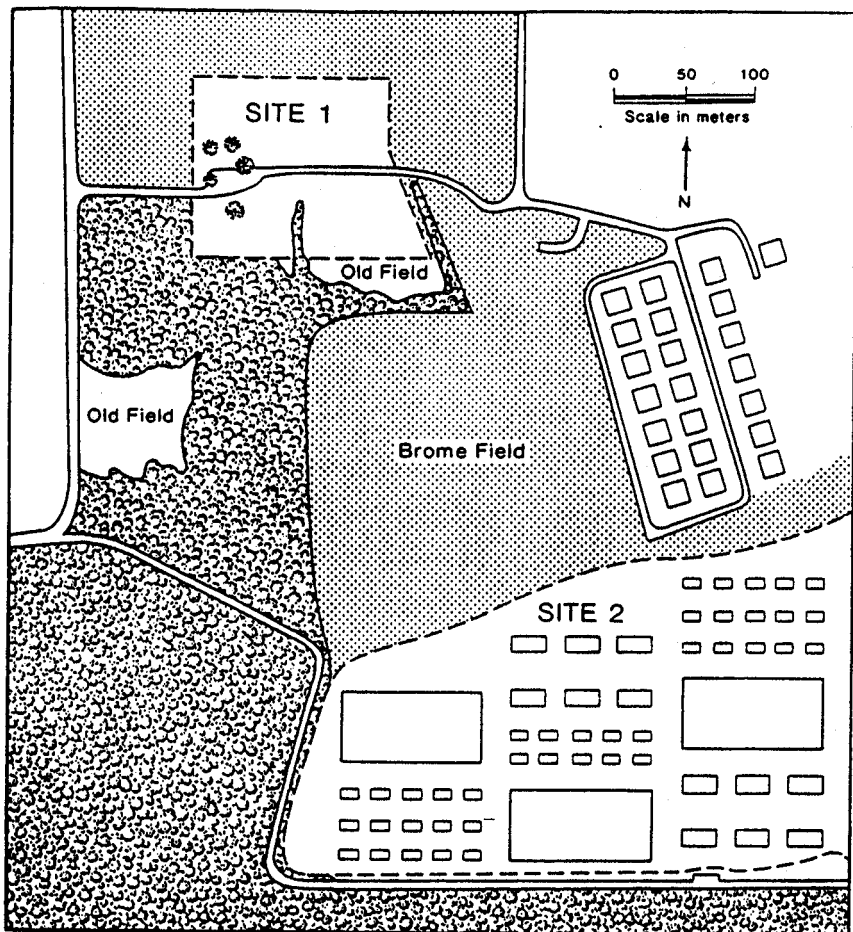


Fig. 9.1. Diagram of the two study sites at the Nelson Environmental Study Area 12 km northeast of Lawrence, Kansas. The continuous area (site 1) is approximately 1.9 ha. The experimentally fragmented system (site 2) has approximately 1.9 ha of successional old-field habitat contained within a total area of 6.9 ha.

this result surprising, because we initially expected all three species to reach their highest densities on the largest blocks. Clearly, the three species have responded to the imposed habitat fragmentation in different ways.

Our working hypothesis for the observed density trends combines consideration of species-specific ecological requirements and interspecific competition (Gaines et al. 1992a,b). We hypothesized that the larger-bodied *S. hispidus* is restricted to the large blocks because it cannot find sufficient

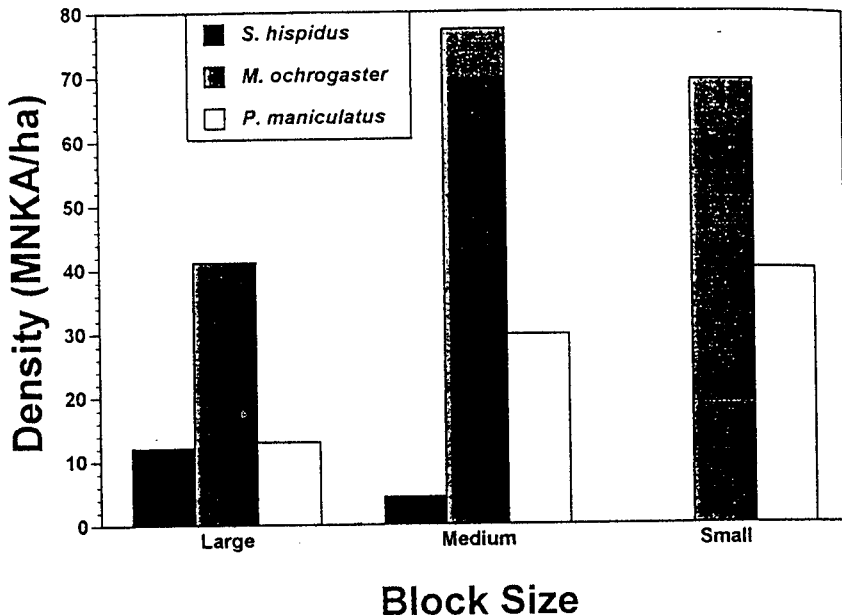


Fig. 9.2. Average density (minimum number known alive [MNKA] per hectare) by block size for *Sigmodon hispidus*, *Microtus ochrogaster*, and *Peromyscus maniculatus*. Data are means of 7.7 years (August 1984 to May 1992) of mark-recapture records on the fragmented study site.

resources to sustain itself on smaller blocks. This habitat restriction in turn provides *M. ochrogaster* with a competitive refuge from *S. hispidus* on the medium and small blocks, thus permitting higher densities there than on large blocks; the likelihood of competition, particularly interference, is suggested from previous studies on the interaction between *S. hispidus* and *M. ochrogaster* (Glass and Slade 1980; Terman 1978).

Competition may explain the patterns observed for *P. maniculatus* as well. *M. ochrogaster* has lower densities on the small blocks than on the medium-sized blocks presumably because, as with *S. hispidus*, the small blocks do not have enough habitat to sustain individuals. *P. maniculatus* may therefore reach its highest densities on small blocks where it can avoid competition with both *S. hispidus* and *M. ochrogaster* (Abramsky et al. 1979; Grant 1971, 1972; Redfield et al. 1977). Furthermore, unlike the other two species, *P. maniculatus* also uses the mowed interstitial areas separating the old-field patches (Foster and Gaines 1991), and thus it may not experience the small amounts of unmowed habitat on the small blocks as isolates.

Given this working hypothesis regarding the underlying processes shap-

ing the densities of the three species on the fragmented area, we made the following species-specific predictions about the abundances on the two study sites being compared: (1) *S. hispidus* should have higher abundances on the continuous site, because it will have more available habitat there than in the fragmented system. (2) *M. ochrogaster* should have higher abundances on the fragmented site, because it provides competitor-free space not available in the continuous area. (3) *P. maniculatus* should have greatest abundances on the fragmented site, because it too may have a competitive refuge there.

Materials and Methods

The study sites are located at the Nelson Environmental Study Area, 12 km northeast of Lawrence, Kansas. The sites at their closest points are no more than 500 m apart and are separated by a brome (*Bromus* sp.) field and low woods (Fig. 9.1). Work on the continuous area was started in 1973 by N. Slade and continues today. This 1.9 ha area is divided by a small dirt road running east-west. The north side of the plot was an abandoned farm field, and the south side was an abandoned pasture and hay field. The southern half of the study site also contains a fencerow with bushes and small trees running north-south.

The fragmentation study began in 1984 when an abandoned agricultural field was disked and allowed to enter secondary succession. Since then, regular mowing between the rectangular habitat patches has created blocks of successional habitat (Fig. 9.1). The habitat patches in the 6.9 ha fragmented site are arranged in three types of blocks. The three large blocks each consist of a single 50 m \times 100 m patch. Two medium blocks each include six 12 m \times 24 m patches. Of the three small blocks, two consist of 15, and one of 10, 4 m \times 8 m patches. The total amount of habitat on the fragmented area is 1.87 ha, nearly identical to the area of old-field habitat on the continuous study site.

Trapping regimes on the two study sites differed. The continuous area contained 98 trap stations, spaced 15 m apart, each with two traps. Traps were checked monthly for three consecutive mornings and the intervening afternoons. The fragmented system contained a total of 287 traps distributed at 267 locations and was trapped twice monthly for two consecutive mornings and the intervening afternoon. Thus, the continuous area had a lower trap density than the fragmented area and was trapped only once a month, compared to twice a month on the fragmented site, although trapping sessions on the continuous area lasted an extra afternoon and morning.

To make comparisons between the two sites, we ignored the difference in trap densities and corrected for the difference in trapping periods. Differ-

ences in trap densities could bias our comparisons if traps became saturated when abundances were high; however, even at high numbers, total captures in a trapping session were rarely more than 60% of the possible capture opportunities. Thus, trap densities should have relatively little influence on comparisons between the sites. To make the temporal structure of the two data sets similar, we deleted every other consecutive trapping session from the raw data on the fragmented site and the last afternoon and morning from the raw data on the continuous site. With this trimming, both data sets represent monthly trapping sessions of two mornings and one afternoon.

We have sufficient data on *S. hispidus*, *M. ochrogaster*, and *P. maniculatus*, the three most abundant species, to make demographic comparisons between the sites. For *S. hispidus* and *M. ochrogaster*, the data begin in the fall of 1984 and continue to the spring of 1991. *P. maniculatus* were not individually marked on the continuous area until the winter of 1989, so we were forced to analyze a smaller data set for this species.

Using Fortran programs developed by C. J. Krebs, we estimated the monthly minimum number known alive (MNKA) and Jolly-Seber survivorship for both entire populations and the resident subsets (residents were defined as individuals captured in at least two monthly trapping periods). Since residents, by definition, survived at least one month, our survival estimates for residents are positively biased but comparable across sites. MNKA estimates could be biased if animals had different probabilities of capture on the two sites. We calculated the probability of capture by dividing the number of animals captured in a trapping session by the MNKA for that session. We also calculated monthly sex ratios and the percentage of animals that were reproductive. Males with descended testes were considered reproductive. Females that were captured with young, were obviously pregnant, or had a clearly open pubic symphysis were considered reproductive. We also classified females as reproductive if they had any two of the following three characteristics: nipples medium or larger, a perforate vagina, or a slightly open pubic symphysis. Transients were counted by subtracting the number of resident animals from the total number of animals present.

All data were analyzed with general linear models in which site, year-season, and sex (depending on the dependent variable) were entered as independent variables (using MINITAB). Treating each three months as a unique block of time (i.e., the year-season variable) focused the analysis on differences between sites while adjusting for seasonal and annual changes in populations. Our procedure was analogous to a paired-comparison *t*-test, but

with comparisons being made within each block of time and with sex included as an additional independent variable.

We restricted our analysis to adults when we calculated the percentage of reproductively active individuals, and we considered each sex separately. Adulthood was determined by body mass of at least 60 g for *S. hispidus*, 25 g for *M. ochrogaster*, and 11 g for *P. maniculatus*.

Estimates of the percentages of reproductive adults were weighted by the number of animals handled in a particular trapping period for analysis. Estimates of sex ratios, survivorship, and percentage of transients were weighted by the MNKA estimates for that trapping period. In some cases, data were missing for a particular year-season. If so, we removed that year-season from the analysis and proceeded with a smaller sample size.

Results

Abundances

Abundances of *S. hispidus* for both the total population and the resident subset varied significantly over time (total population, $F = 12.92$; residents, $F = 12.10$; $df = 30, 124$; $p < 0.001$ in both cases) (Fig. 9.3). Seasonal variation was strong; abundances were highest in the summer and fall and lowest in the winter and spring, and there were some differences among years. Temporal patterns of variation were similar between sites (total population, $r = 0.644$, $n = 31$, $p < 0.001$), but the sites did not maintain the same rank order of abundances through time (significant site by year-season interaction; total population, $F = 2.81$; residents, $F = 3.86$, $df = 30, 124$; $p < 0.001$ in both cases).

Despite this temporal variation, *S. hispidus* had higher average abundances on the continuous site than on the fragmented site. The means and standard errors are as follows: for the continuous site—total population, 20.27 ± 0.20 ; residents, 15.06 ± 0.14 ; for the fragmented site—total population, 14.82 ± 0.20 ; residents, 9.08 ± 0.14 (total population, $F = 12.10$; residents, $F = 29.9$; $df = 1, 124$; $p < 0.001$ in both cases). These differences in abundances at the two sites resulted from differences during population peaks (in four years in particular); population sizes were similar on both sites during periods of low numbers (Fig. 9.3a).

Both the total population and the resident subset of *M. ochrogaster* also varied temporally in abundances (total population, $F = 25.09$; residents, $F = 36.56$; $df = 30, 124$; $p < 0.001$ in both cases) (Fig. 9.4). Unlike *S. hispidus*, however, abundances of *M. ochrogaster* did not show strong annual cycles but did show obvious multiannual cycles; peak abundances were reached on

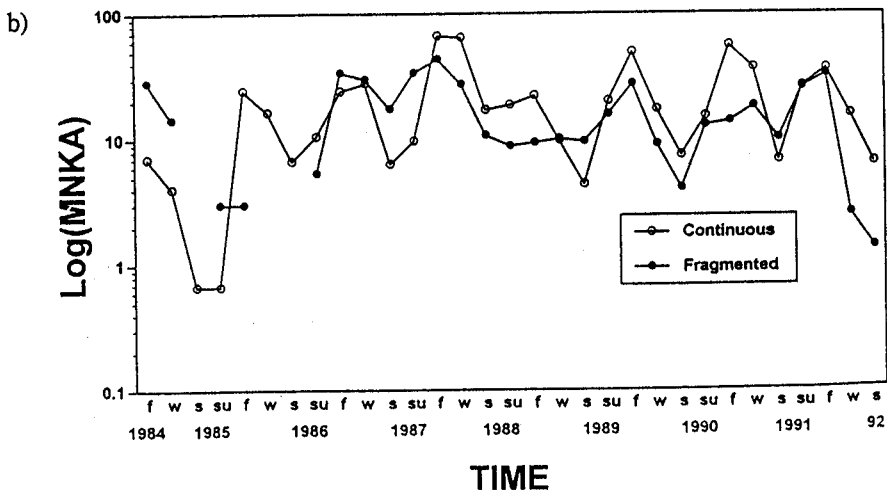
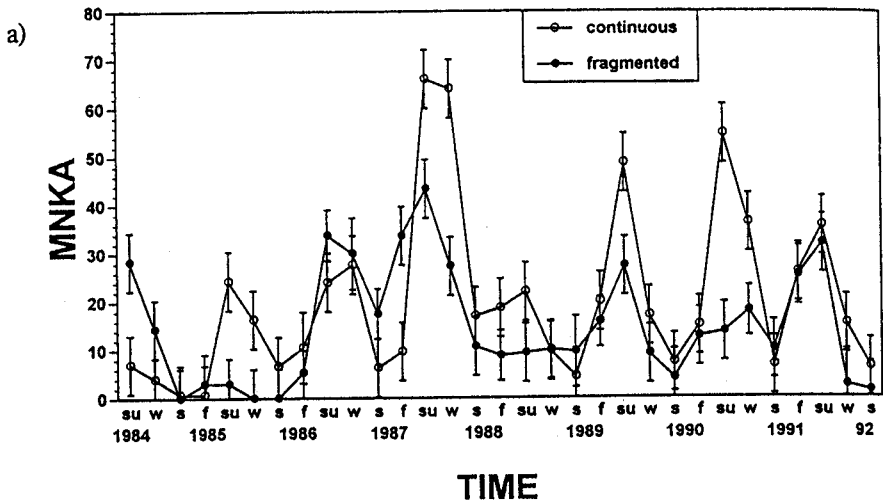


Fig. 9.3. Seasonal average minimum number known alive (MNKA) (a) and log of the seasonal MNKA (b) for *Sigmodon hispidus* on the continuous and fragmented sites from 1984 to 1992. Error bars show the standard errors of the means calculated from the mean squared error from the general linear model.

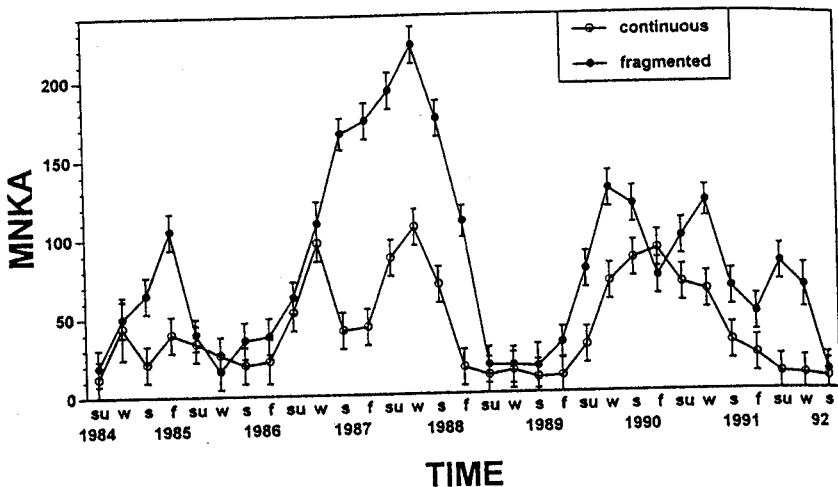
both sites in the fall of 1987 and again in the winters of 1989 and 1990. These patterns of variation in abundance were similar between sites (total population, $r = 0.74$, $n = 31$, $p < 0.001$), but relative differences in abundances changed through time, leading to a significant site by year-season interaction (total population, $F = 6.66$; residents, $F = 9.57$; $df = 30, 124$; $p < 0.001$ in both cases). Despite variation in which site had the highest numbers, on average *M. ochrogaster* abundances were twice as high on the fragmented site as on the continuous site. Means and standard errors are as follows: for the continuous site—total population, 40.73 ± 0.39 ; residents, 32.65 ± 0.29 ; for the fragmented site—total population, 82.18 ± 0.37 ; residents, 66.50 ± 0.27 (total population, $F = 192.42$; residents, $F = 228.5$; $df = 1, 124$; $p < 0.001$ in both cases). In general, *M. ochrogaster* abundances were greater on the fragmented site than on the continuous site but, as with *S. hispidus*, peak abundances differed between sites far more than did low numbers (Fig. 9.4a).

Like the other two species, *P. maniculatus* varied in abundance (both total and resident populations) over time (total population, $F = 14.98$; residents, $F = 24.77$; $df = 12, 51$; $p < 0.001$ in both cases) (Fig. 9.5). No seasonal trends were evident, although abundances on the fragmented site peaked in 1989. Variation in *P. maniculatus* abundances through time was not correlated between the sites ($r = 0.035$, $p = 0.911$), and there was a significant site by time interaction (total population, $F = 13.47$; residents, $F = 22.28$; $df = 12, 51$; $p < 0.001$ in both cases). *P. maniculatus* abundances on the fragmented area declined from a peak in 1989; the peak was not observed on the continuous site, which resulted in mean abundances three times higher on the fragmented site than on the continuous site. Means and standard errors are as follows: for the continuous site—total population, 12.15 ± 0.24 ; residents, 9.14 ± 0.90 ; for the fragmented site—total population, 36.71 ± 0.24 ; residents, 27.61 ± 0.90 (total population, $F = 166.64$; residents, $F = 210.15$; $df = 1, 51$; $p < 0.001$ in both cases). MNKA (y) and number of captures (x) on the continuous site were strongly related ($R^2 = 0.916$; $y = 0.884 + 0.528x$; $t = 23.84$; $df = 52$; $p < 0.001$). We used this regression equation to estimate MNKA from the number of captures prior to 1989, when MNKA estimates were not available for the continuous site. We found that *P. maniculatus* abundances were generally higher on the fragmented site, and not solely as a result of the solitary peak observed on the fragmented site (Fig. 9.5).

Capture Probability

The probability of capture varied over time but not between sites for *S. hispidus* ($F = 4.74$, $df = 27, 109$, $p < 0.001$) and *M. ochrogaster* ($F = 1.73$,

a)



b)

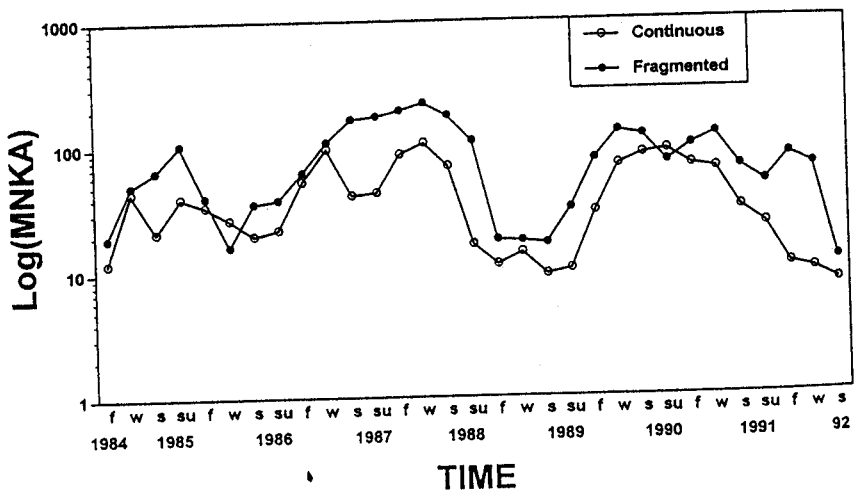


Fig. 9.4. Seasonal average minimum number known alive (MNKA) (a) and log of the seasonal MNKA (b) for *Microtus ochrogaster* on the continuous and fragmented sites from 1984 to 1992. Error bars show the standard errors of the means calculated from the mean squared error from the general linear model.

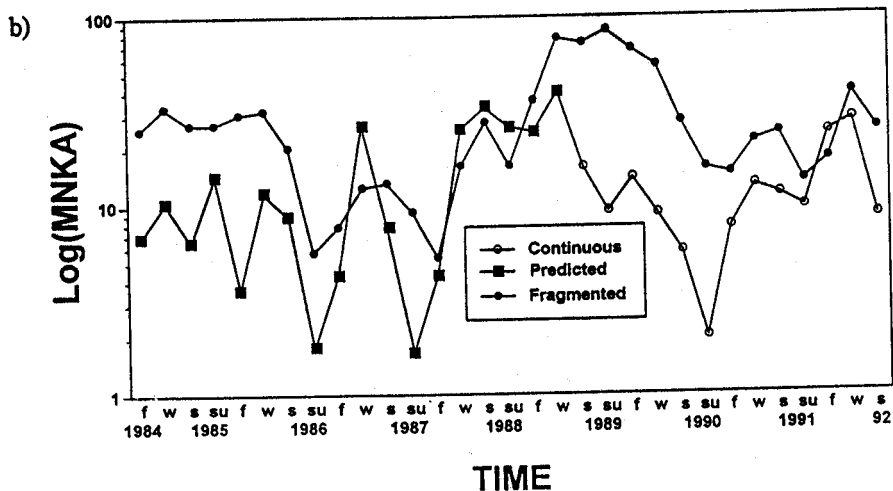
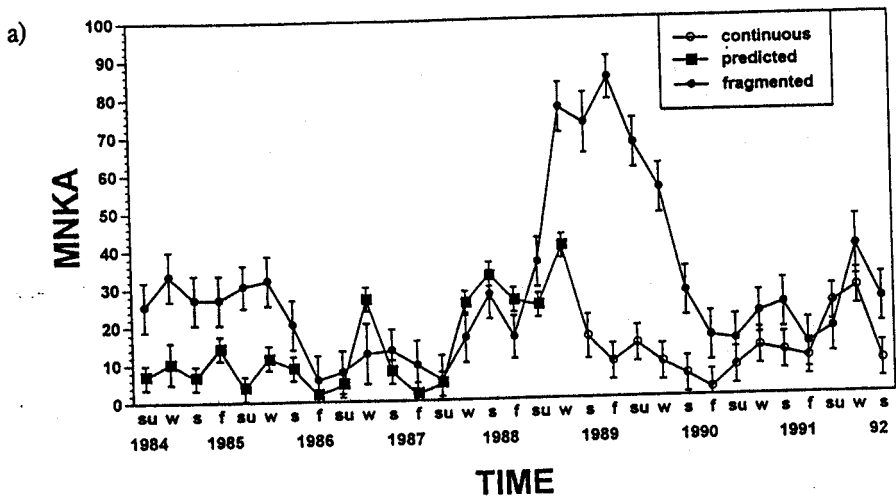


Fig. 9.5. Seasonal average minimum number known alive (MNKA) (a) and log of the seasonal average MNKA (b) for *Peromyscus maniculatus* on the continuous and fragmented sites from 1984 to 1992. Error bars show the standard errors of the means calculated from the mean squared error from the general linear model. The squares on the continuous-site time series are estimates from a regression of MNKA on the number of captures.

df = 30, 124, $p = 0.019$). For *P. maniculatus*, the average probability of capture was higher on the continuous site (0.93 ± 0.034) than on the fragmented site (0.75 ± 0.019) ($F = 20.33$, df = 1, 50, $p < 0.001$), a trend opposite to that expected if capture probability affects abundance.

Survivorship

We estimated survivorship for both the entire population and the resident population. *S. hispidus* survivorship for the total population did not differ by site or sex but changed through time, i.e., year-season ($F = 1.48$, df = 26, 200, $p = 0.071$). Because year-season was the only significant independent variable in the model, we tested whether season alone could account for the temporal variation in survivorship by comparing residual sums of squares from a simple model with only season as the independent variable with those from a more complex model with year-season as the independent variable (Draper and Smith 1981). The complex model produced a significant increase in the model's fit ($F = 2.08$, df = 23, 281, $p = 0.003$). Hence, both year and season were statistically important in explaining the variation in survivorship.

Survivorship of the total population was highest in spring and lowest in summer (Table 9.1). Resident *S. hispidus* survivorship varied only with year-season ($F = 2.11$, df = 24, 261, $p = 0.002$). Unlike total *S. hispidus* survivorship, there was no difference in the amount of variation in resident survivorship explained by the model with year-season as the independent variable compared to the model with the season variable alone, indicating that season explained most of the variation in resident survivorship. Survivorship of residents varied seasonally ($F = 5.58$, df = 3, 282, $p < 0.001$) but in different ways than for the total population (Table 9.1). Unlike the total population, resident survivorship was highest in the fall and lowest in the winter.

As with *S. hispidus*, survivorship for the total *M. ochrogaster* population varied only over time ($F = 3.38$, df = 30, 238, $p < 0.001$). Furthermore, a model with year-season as the independent variable fit the data significantly better than a model with just season ($F = 3.640$, df = 27, 331, $p < 0.001$). Thus, *M. ochrogaster* survivorship varied with both year and season. On average, survivorship was highest in the fall and winter and lowest in the spring and summer (Table 9.1). Resident *M. ochrogaster* survivorship also varied with time ($F = 3.66$, df = 30, 235, $p < 0.001$) and, as with the total population, a model with year-season fit the data better than a model with season alone ($F = 3.33$, df = 27, 328, $p < 0.001$). Resident survivorship was

Table 9.1. 28-day Jolly-Seber survivorships (mean \pm one standard error) by season for total and resident populations of *Sigmodon hispidus*, *Microtus ochrogaster*, and *Peromyscus maniculatus*

Species	Total population	<i>N</i>	Resident population	<i>N</i>
Season				
<i>S. hispidus</i>				
Fall	.582 \pm .022	98	.805 \pm .021	84
Winter	.582 \pm .029	78	.685 \pm .023	78
Spring	.696 \pm .029	60	.714 \pm .038	60
Summer	.472 \pm .049	86	.786 \pm .035	74
<i>M. ochrogaster</i>				
Fall	.744 \pm .020	98	.856 \pm .017	98
Winter	.767 \pm .018	90	.861 \pm .015	90
Spring	.676 \pm .020	88	.759 \pm .017	88
Summer	.641 \pm .021	86	.787 \pm .019	86
<i>P. maniculatus</i>				
Fall	.639 \pm .036	36	.798 \pm .032	36
Winter	.723 \pm .057	36	.824 \pm .030	36
Spring	.454 \pm .041	36	.604 \pm .033	36
Summer	.663 \pm .047	38	.856 \pm .030	26

also highest in the fall and winter and lowest in the spring and summer (Table 9.1).

P. maniculatus survivorship also varied over time ($F = 3.37$, $df = 12, 116$, $p < 0.001$). However, total *P. maniculatus* populations had higher average survivorship on the fragmented site (0.62 ± 0.022) than on the continuous site (0.51 ± 0.041) ($F = 5.09$, $df = 1, 116$, $p = 0.026$). To determine whether year-season was a better predictor of survivorship than season alone, we ran a model including site and either season or year-season. The overall fit to the data did not differ between the two models, indicating that season explained the variation in survivorship as well as did year-season. Average survivorship for the total population varied in similar patterns on both grids, with highest survivorship in the winter and lowest in the spring. Spring survivorship on the continuous site was 1.5 times lower than on the fragmented site, which led to a significant difference in survivorship between the grids (Table 9.1). Survivorship of residents did not differ between sites. As with the other two species, resident survivorship varied with time ($F = 3.07$, $df = 11, 84$, $p = 0.002$). Resident survivorship changed with season, and year-season was a better predictor of survivorship than season ($F = 2.786$, $df = 8, 120$, $p = 0.007$). Residents had highest average survivorship in the summer and lowest in the spring (Table 9.1).

Table 9.2. Percentage of male *Sigmodon hispidus*, *Microtus ochrogaster*, and *Peromyscus maniculatus* in the continuous and fragmented study sites

Species	Study Site			
	Continuous	N ^a	Fragmented	N ^a
<i>S. hispidus</i>	.573 ± .017	1,867	.450 ± .016	1,433
<i>M. ochrogaster</i>	.500 ± .009	3,678	.443 ± .006	7,979
<i>P. maniculatus</i>	.473 ± .021	458	.519 ± .012	1,426

^aSince the general linear models were weighted by the minimum number known alive (MNKA), *N* represents the total MNKA summed over all trapping sessions (mean ± one standard error).

Sex Ratios

S. hispidus sex ratio varied over time ($F = 1.60$, $df = 27, 109$, $p = 0.047$) (Fig. 9.6a) but in different patterns at each site, leading to a significant site by year-season interaction ($F = 3.04$, $df = 27, 109$, $p < 0.001$). On average, *S. hispidus* populations in continuous habitat were male-biased compared to those in the fragmented habitat ($F = 27.99$, $df = 1, 109$, $p < 0.001$) (Table 9.2). In *M. ochrogaster* populations, sex ratio varied with year-season ($F = 2.62$, $df = 30, 124$, $p < 0.001$) (Fig. 9.6b) and in different ways on each site ($F = 2.49$, $df = 30, 124$, $p < 0.001$). Populations in the fragmented habitat were on average female-biased ($F = 27.92$, $df = 1, 124$, $p < 0.001$) (Table 9.2). In *P. maniculatus* populations, sex ratio varied in different patterns on each site over time, resulting in a significant site by year-season interaction ($F = 2.37$, $df = 12, 50$, $p = 0.017$).

Reproduction

The proportions of adult female *S. hispidus* and *M. ochrogaster* that were judged to be reproductive changed over time (*S. hispidus*, $F = 3.14$, $df = 24, 87$, $p < 0.001$; *M. ochrogaster*, $F = 4.37$, $df = 30, 121$, $p < 0.001$). Higher proportions of female *S. hispidus* and *M. ochrogaster* were reproductive on the continuous habitat than on the fragmented habitat (*S. hispidus*, $F = 3.69$, $df = 1, 87$, $p = 0.058$; *M. ochrogaster*, $F = 9.60$, $df = 1, 121$, $p < 0.001$) (Table 9.3). The proportion of reproductive *S. hispidus* males varied with time ($F = 4.23$, $df = 25, 92$, $p < 0.001$). For male *M. ochrogaster*, the proportion varied over time and in different patterns on each site ($F = 2.39$, $df = 30, 119$, $p < 0.001$). The average proportions of reproductive male *S. hispidus* and *M. ochrogaster* were similar between sites. The proportion of reproductive male *P. maniculatus* changed with time ($F = 4.37$, $df = 12, 49$, $p < 0.001$), but on average, greater

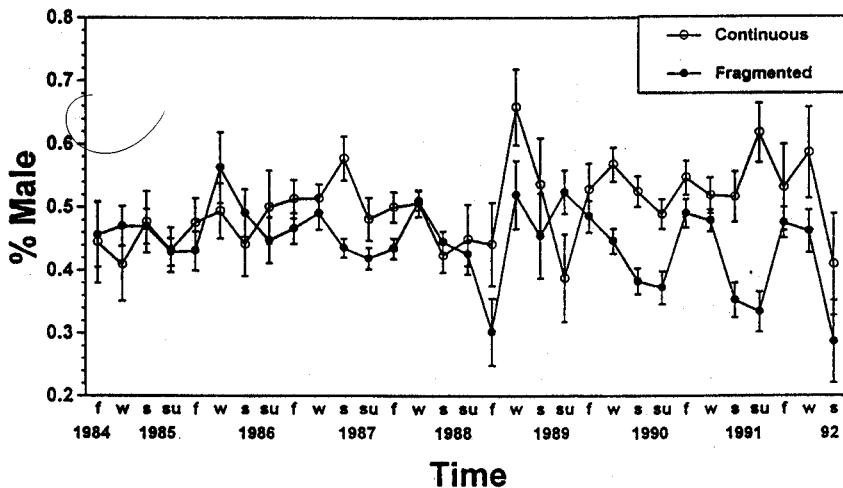
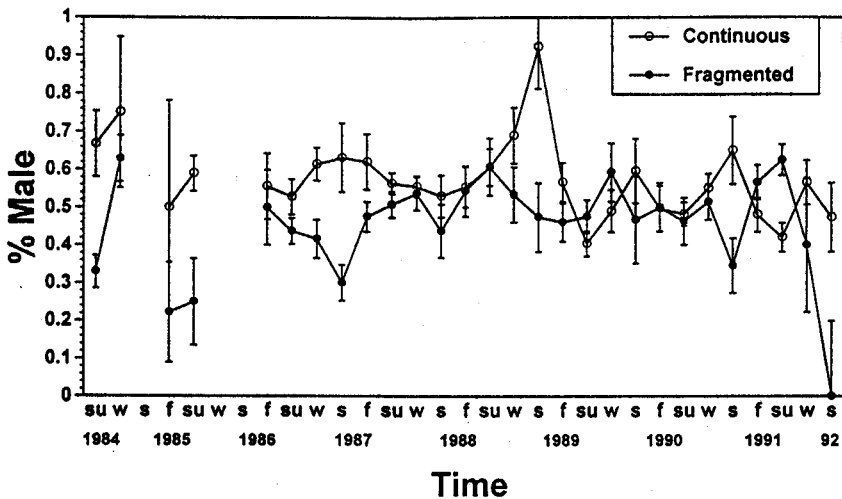


Fig. 9.6. Seasonal sex ratio estimates for *Sigmodon hispidus* (a) and *Microtus ochrogaster* (b) on the continuous and fragmented sites from 1984 to 1992. Error bars show the standard errors of the means calculated from the mean squared error from the general linear model.

Table 9.3. Percentage of reproductively active adult male and female *Sigmodon hispidus*, *Microtus ochrogaster*, and *Peromyscus maniculatus* trapped in continuous and fragmented sites

Species Site	Male	N ^a	Female	N ^a
<i>S. hispidus</i>				
Continuous	.425 ± .048	565	.399 ± .055	478
Fragmented	.431 ± .059	316	.216 ± .046	366
<i>M. ochrogaster</i>				
Continuous	.741 ± .030	1,224	.637 ± .035	1,191
Fragmented	.787 ± .019	2,250	.510 ± .022	2,820
<i>P. maniculatus</i>				
Continuous	.486 ± .058	163	.442 ± .058	159
Fragmented	.638 ± .037	437	.336 ± .029	424

^aSince general linear models were weighted by the number of adult animals captured in a trapping session, *N* represents the total number of adults captured (mean ± one standard error).

proportions of males were reproductive in the fragmented habitat than in the continuous habitat ($F = 4.83$, $df = 1, 49$, $p = 0.003$) (Table 9.3). The proportion of reproductive *P. maniculatus* females varied with time ($F = 6.16$, $df = 12, 49$, $p < 0.001$) but not by site.

Transients

In *S. hispidus*, the proportion of transient individuals (those animals captured only in a single month) varied over time ($F = 6.69$, $df = 26, 108$, $p < 0.001$). However, populations in the fragmented area tended to have a higher average proportion of transients (0.346 ± 0.026) than those on the continuous site (0.287 ± 0.023) ($F = 2.98$, $df = 1, 108$, $p = 0.087$). In *M. ochrogaster*, the proportion of transients varied with time ($F = 4.16$, $df = 30, 108$, $p < 0.001$) but not by site.

In *P. maniculatus*, the proportion of transients varied with time ($F = 2.60$, $df = 12, 50$, $p = 0.009$), and the pattern of variation differed among the sites ($F = 2.27$, $df = 50, 75$, $p = 0.021$). The proportion of transients remained fairly constant on the fragmented site, fluctuating from 0.18 to 0.42. On the continuous site, the proportion of transients showed seasonal trends, decreasing over winter and then rising to high levels in spring or fall. Transience on the continuous site ranged from 0.07 to 0.67. Although the average proportion of transients was the same for the two sites (0.29), *P. maniculatus* population on the continuous area had more than three times the temporal variance in the proportion of transients as populations on the fragmented site (contin-

ous, $s^2 = 0.00027$; fragmented, $s^2 = 0.00085$; one-tailed $F = 3.148$, $df = 12, 12$, $p = 0.028$).

Discussion

Fragmentation influenced species abundances in the manner we predicted when we projected from the spatial patterns in abundance within the fragmented area alone. *S. hispidus*, the largest-bodied species, had higher abundances in the continuous area, whereas the two smaller-bodied species had higher abundances in the fragmented system.

The critical question is, by what demographic processes has habitat fragmentation influenced these differences in abundance? In *S. hispidus*, abundance differences are attributable to the large differences in peak abundances between sites. *M. ochrogaster* had consistently higher abundances, particularly peak abundances, on the fragmented site. *P. maniculatus* had consistently higher abundances on the fragmented site, and densities were less variable than those for the other species. These findings are intriguing. We can use the other demographic data presented to distinguish among plausible processes by which habitat fragmentation influences population dynamics.

If the observed abundance differences were primarily due to differences in the amount of available habitat, disentangled from other ecological processes, then the demographic variables we measured should have been equal between sites. However, our data revealed species-specific differences between the sites in demographic variables, despite similar total amounts of habitat. Apparently, habitat fragmentation leads to species-specific demographic responses, independent of simple area effects.

Sigmodon hispidus

Abundance differences between the sites for *S. hispidus* resulted primarily from higher peaks on the continuous site. These higher peaks indicate times of higher per capita growth rates on the continuous site. We infer higher growth rates from a plot of log MNKA versus time, which shows a consistently steeper slope on the continuous site as populations climb from seasonal lows (Fig. 9.3b).

A number of distinct demographic processes could cause the observed site differences in per capita growth rates for *S. hispidus*. First, higher birth rates on the continuous grid could result in higher growth rates and thus abundances. A higher proportion of females were reproductive on the continuous site. The restriction of activity to the three large blocks in the fragmented site may prevent access to the level of resources needed to sustain

high reproductive rates. Furthermore, medium and small patches may be too small to support reproduction. However, abundances of females on smaller patches are too low to definitively test this hypothesis.

Second, movements and social interactions could influence abundances. The continuous site could experience more immigration or less emigration than the fragmented site. The higher percentage of transients on the fragmented site could result from differences either in survival or in dispersal. Since survival rates of residents were similar across the sites, we assume that the differences in transience indicate that fragmentation likely influences movement behavior. Patch geometry could also influence the consequences of intraspecific interference: the greater edge-to-interior ratios on the fragmented site might intensify territorial behavior, because edge provides territorial boundaries that are defensible at low costs, permitting more effective defense of nonedge borders. This could reduce the number of territories per unit area. If so, then subordinate animals would be more prone to leave the fragmented site as conditions became crowded, and potential immigrants would have a more difficult time establishing in patches. The trend toward higher percentages of transients in the fragmented area supports this scenario.

Third, abundances on the fragmented site may not reach the high values seen on the continuous site simply because there is less available habitat overall. Presumably because of its large body size, *S. hispidus* cannot use medium or small habitat blocks for long-term survival and reproduction (see Gaines et al. 1992a,b, 1994). Excluding the medium and small blocks, the fragmented site has 22.7% less habitat available than the continuous area. Average total abundances were 26.9% less on the fragmented site than on the continuous area, which suggests that the decrease in usable habitat may account for much of the difference between sites. However, average resident *S. hispidus* abundances were nearly 40% lower on the fragmented area. The difference between total and resident populations reflects the greater transience observed on the fragmented site and further indicates that habitat fragmentation reduces numbers more than can be accounted for merely by the reduction in suitable area.

In summary, habitat fragmentation reduces *S. hispidus* populations in three distinct demographic ways. First, it lowers the proportion of reproductively active females, resulting in higher per capita growth rates and thus higher maximal abundances in favorable years on the continuous site. Second, a greater proportion of animals are transient on the fragmented system, indicating that animals leave faster or stay shorter amounts of time there

Third, because few individuals can occupy the smaller blocks of habitat, there is less total habitat available on the fragmented site.

Microtus ochrogaster

We hypothesized that competitor-free space on the fragmented site should lead to higher abundances of *M. ochrogaster* there than on the continuous site. The average abundance of *S. hispidus* on medium blocks is one (1.29 ± 0.25) per block, and this species has been captured on the small patches only 33 times in 7.7 years. Medium and small blocks represent 22.7% of the available habitat on the fragmented site, yet they account for 42.6% of the average *M. ochrogaster* abundance. Thus, in the absence of *S. hispidus*, *M. ochrogaster* seems capable of achieving higher densities on the smaller blocks (Gaines et al. 1994). This block-specific effect makes a significant contribution to the overall population size of this species on the fragmented site.

As with *S. hispidus*, some of the differences between sites for *M. ochrogaster* resulted from high peak abundances on the fragmented site that did not occur on the continuous site. However, unlike with *S. hispidus*, plots of log MNKA versus time indicate that per capita growth rates during periods when *M. ochrogaster* was rebounding from population lows were similar between the grids and hence do not explain the differences in peak abundances we observed between the sites (Fig. 9.4b). Thus, we must find other explanations for the peak abundance differences.

If for a given series of trapping periods, abundances are, on average, higher on the fragmented site, and if per capita growth rates are similar in both sites, then the population on the fragmented site will grow to higher levels. This effect may have occurred in our system, but in many cases the low pregrowth abundances were roughly equal in both sites. It seems more likely that the differences in abundance reflect differences in "carrying capacity" rather than in maximal growth rates.

Our findings that adult sex ratios are female-biased on the fragmented site and that the proportion of reproductive females is higher on the continuous site merit further discussion. Female-biased sex ratios may reduce the proportion of reproductive females if *M. ochrogaster* is monogamous (Carter and Getz 1993). Movement between blocks is male-biased (J. E. Diffendorfer, unpub. data). If dispersal is correlated with these movements, then fragmentation may increase male dispersal and thus skew the sex ratio toward females. It seems doubtful that this effect could fully explain the differences in mean abundance, because the percentage of transients does not differ between the grids.

Per capita female reproduction may be greater on the continuous site for reasons similar to those suggested above for *S. hispidus*. Small and medium-sized patches may not be ideal breeding habitat for *M. ochrogaster*. Furthermore, the higher edge-to-interior ratios on the fragmented site may indirectly reduce the number of female territories by sharpening the effectiveness of interference and thus reduce reproductive activity, particularly for subordinate individuals.

In summary, the per capita population growth rates of *M. ochrogaster* when rebounding from low numbers are similar on fragmented and continuous sites. Yet these voles reach higher abundances on the fragmented site because they ultimately achieve higher peak densities there, we suspect mainly because 23% of the fragmented site (i.e., the medium and small patches) is competitor-free. Testing this hypothesis will require further work.

Peromyscus maniculatus

P. maniculatus showed the greatest positive response to fragmentation, with average abundances nearly three times higher on the fragmented site. However, this may be misleading, because more than 50% of the average MNKA can come from the interstitial or matrix area (Foster and Gaines 1991). Including the interstitial area, the fragmented site contains approximately 6.9 ha of mowed and successional vegetation. Extrapolating total abundance in the continuous habitat (1.9 ha) to an area of 6.9 ha results in an abundance of 44, slightly higher than observed on the fragmented site. However, we only set traps in 1.87 ha of the 6.9 ha on the fragmented site. Thus we may have underestimated density for the fragmented site because we had no traps in nearly three-quarters of the habitat available. If we use the finding of Foster and Gaines (1991) that about 50% of the *P. maniculatus* population was found in the interstitial matrix areas, then the overall abundances of *P. maniculatus* on the entire fragmented site ($36.6 \times 2 = 73.2$) would be higher than the abundance on a continuous site of equal size (44.1). Thus, *P. maniculatus* abundances on the fragmented area appear to be higher than the abundances on a continuous site regardless of how we interpret the data.

The higher abundances of *P. maniculatus* on the fragmented site may result from the abundant food supply in the interstitial area. Furthermore, *P. maniculatus* faces no competitors in the interstitial area and hence, like *M. ochrogaster*, has a huge area of competitor-free space not found on the continuous site.

The increased habitat area and reduced competition are reflected, we suggest, in higher average survivorship and higher percentage of reproductive

males for the total *P. maniculatus* population on the fragmented site compared to the continuous site. However, despite the higher survivorship and male reproductive activity, a plot of log MNKA versus time gave no evidence of higher per capita growth rates on the fragmented site. The higher percentage of reproductive males on the fragmented site may result from the general increase in resources available in the interstitial areas.

P. maniculatus was the only species for which the probability of capture differed between sites. The lower probability of capture on the fragmented grid fits our scenario of many individuals spread out over the entire 6.9 ha fragmented site, with traps covering only 1.87 ha. Our results agree with those of Sietman et al. (1994), who found that *P. maniculatus* was common in old-field habitats, native tallgrass prairie, and mowed hay fields. This species probably views our system as a complex of two major habitat types, namely, old-field patches interspersed in a "sea" of lower-quality "turf" habitat.

The percentage of transients fell every winter and rose in the spring and summer on the continuous site but not on the fragmented site. This suggests that larger, continuous areas may be better overwintering habitat for *P. maniculatus*. If so, then the percentage of transients should be lower on large blocks than on smaller blocks in the fragmented site. Although we have not analyzed percentage of transience by block size, persistence rates appear to be higher on large blocks than on smaller blocks (Gaines et al. 1994), indicating that animals stay longer on large blocks. Thus, the smaller patches of habitat in the fragmented area may have higher transience than large blocks.

An important direction for future work in the fragmented system is analysis of how the demographic effects documented here and elsewhere (Foster and Gaines 1991; Gaines et al. 1992a,b, 1994) reflect underlying processes such as resource availability, social interactions (R. Pierotti and P. Wilson, pers. comm.), individual movement patterns (J. E. Diffendorfer, unpub. data), spacing behavior (Kozakiewicz and Szacki, Chap. 5), and risk of predation (Oksanen and Schneider, Chap. 7)—all of which are likely to vary as a function of the degree of habitat fragmentation (Hansson, Chap. 2).

Conclusions

Our data show that species respond differently to fragmentation, not just in overall abundance, but also in detailed demographic parameters. For *S. hispidus*, fragmentation reduced habitat availability and was associated with fewer reproductively active females and an increase in transience. These factors collectively influence population growth rates and ultimately the magnitude of peaks in abundances. For *M. ochrogaster*, fragmentation seems to

lower female reproductive rates, but this is likely offset by an easing of competitive pressure from *S. hispidus*; the net result is that *M. ochrogaster* abundances are higher on the fragmented site. For *P. maniculatus*, habitat fragmentation actually creates suitable competitor-free habitat, which increases survivorship and reproductive activity, resulting in a higher *P. maniculatus* population in the fragmented area.

Our comparison of continuous and fragmented habitats raises a number of interesting unanswered questions. For example, the differences between the sites in sex ratios of *S. hispidus* and *M. ochrogaster* and in the percentage of reproductive adults (for at least one sex) in all three species indicate underlying variation between the sites that we cannot yet explain. Designing experiments and field protocols to interpret these patterns will be difficult. However, understanding individual demographic responses is essential to deepening our understanding of habitat fragmentation. Moreover, our analyses have focused on only a single, rather coarse landscape attribute—patch size. Other attributes, such as patch configuration and landscape arrangement, are likely to have significant effects on total population responses, reflecting spatial influences on individual demographic parameters (Barrett et al., Chap. 8).

Doak et al. (1992, 332) observed that “few theoretical or empirical studies treat fragmentation in a way that would satisfy the concerns most conservation biologists have about habitat fragmentation.” We feel more can be gleaned from experimental model approaches in studies of habitat fragmentation. The contributions by Barrett et al. (Chap. 8) and Laurance (Chap. 3) reinforce this conclusion, albeit from different perspectives. Experimental approaches are necessarily conducted at modest spatial scales, relative to those of concern for conservation biology and landscape ecology (Lidicker, Chap. 1). Nonetheless, experimental systems can sharpen the descriptive, pattern-oriented, and modeling approaches usually required for broad, landscape-level analyses.

Summary

This chapter describes how habitat fragmentation influences temporal trends in abundance and an array of demographic parameters for three small-mammal species, *S. hispidus*, *M. ochrogaster*, and *P. maniculatus*. From August 1984 to May 1992, we collected capture-recapture data on a single continuous area spanning 1.9 ha of successional old-field habitat and on patches of successional old-field habitat of varying size but totaling 1.87 ha. Numbers of each species varied over time and between sites. MNKAs in the continuous

and fragmented areas averaged 20.3 and 14.8, respectively, for *S. hispidus*, 40.7 and 82.2 for *M. ochrogaster*, and 12.2 and 36.7 for *P. maniculatus*; the differences between the two sites in mean abundances were statistically significant ($p < 0.05$) for all three species. Survival rates varied with season for all species but were different between areas ($p < 0.10$) only for *P. maniculatus*, which showed higher survival on the fragmented area. Survival among resident individuals was less variable; it was not significantly different in the two areas ($p > 0.30$); and it was about 15% greater than survival among the total populations (including transients). Transients made up 32% of *S. hispidus*, 23% of *M. ochrogaster*, and 29% of *P. maniculatus* populations regardless of habitat; thus, all abundance differences were caused by differences in abundances of resident animals. *Sigmodon* and *Microtus* males were proportionally more common on the continuous site. Greater proportions of *S. hispidus* and *M. ochrogaster* females were reproductive in continuous habitat, whereas male *Peromyscus* were more likely to be scrotal in the fragmented area.

Our results are consistent with the idea that fragmentation has distinct effects on each species. Fragmentation reduced the amount of habitat available to *S. hispidus* and thereby may offer *Microtus* a competitive refuge from *Sigmodon*. *P. maniculatus* may be attracted to the closely mowed and competitor-free interstices between habitat patches and hence in effect inhabit an area much larger than the sum of our old-field patches. Our results underscore the value of experimental field studies in analyzing the processes influenced by habitat fragmentation.

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