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THE EFFECTS OF HABITAT FRAGMENTATION ON POPULATIONS OF THREE SPECIES OF SMALL MAMMALS IN EASTERN KANSAS

We examined the effect of an experimentally fragmented landscape on population processes of three small mammal species over a seven year period (1984–1991). Habitat patches of three different sizes (5 000 m², 288 m², 32 m²) were created in 0.5 ha archipelagos by mowing an old field. The largest species, *Sigmodon hispidus*, had highest densities on large archipelagos (i.e., the archipelagos with large patches), the mid-sized *Microtus ochrogaster* on medium archipelagos and the smallest species, *Peromyscus maniculatus*, on small archipelagos. Persistence rates for *S. hispidus*, *M. ochrogaster* and *P. maniculatus* were generally highest on large archipelagos. *S. hispidus* and *M. ochrogaster* moved more frequently from smaller to larger archipelagos but *P. maniculatus* did not. *S. hispidus* and *M. ochrogaster* had the highest effective population size (N_e) values on large archipelagos, whereas the highest N_e values for *P. maniculatus* were on medium archipelagos. We conclude that a comparative approach is needed to understand the effects of habitat fragmentation on population processes.

Key words. Habitat fragmentation, population dynamics, small mammals, source-sink dynamics.

1. INTRODUCTION

Given the recent concern about the reduction in biological diversity, conservation biologists have directed their efforts towards understanding the effects of habitat fragmentation on population dynamics and genetic structure. As fragmentation increases, it leads to a decrease in the average size of suitable habitat patches and an increase in average distances between patches (Wilcox 1980). This habitat loss and increased insularity can reduce population sizes to such low levels that species go extinct.

Shaffer (1981, 1987) identified four sources of variation that could lead to the extinction of a population: 1) demographic stochasticity due to random events in individual survival and reproduction; 2) environmental stochasticity due to unpredictable change in abiotic (i.e., weather) or biotic (i.e., predators, competitors, parasites) factors; 3) natural catastrophes such as fires and floods, which occur at random intervals; and 4) genetic stochasticity due to genetic drift and inbreeding, which may affect individual survival and reproduction. These four sources of variation may be interconnected and can operate in concert to cause population extinction.

There has been considerable discussion about the relative roles of demographic and genetic factors in causing local extinctions. Lande (1988) suggested that demography has a more immediate role than population genetics in determining minimum viable population sizes. The first step in assessing the potential roles of demographic and genetic factors in population extinction is to examine the effects of habitat fragmentation on population processes and genetic structure.

We studied small mammals in a fragmented landscape to explore the effects of habitat fragmentation on three rodent species at a micro-landscape scale. We have previously reported results of this long-term study for sequential time periods in a series of different publications (Foster and Gaines 1991, Gaines et al. 1992a, 1992b, Robinson et al. 1992). Here we provide a synthesis of these results from seven years of continuous demographic data.

2. METHODS

The study site is the western half of a 12 ha field, 16 km north of Lawrence, Kansas (Fig. 1). In 1984, we created habitat patches of three sizes, 5 000 m², 288 m², and 32 m² by mowing an old field. We regularly mowed the interstitial areas between patches and allowed secondary plant succession to proceed unhindered within patches. For convenience, we define the large patches as "large archipelagos", archipelagos of medium sized patches as "medium archipelagos" and archipelagos of small patches as "small archipelagos". The largest archipelagos (0.5 ha) were comparable to the sizes of enclosures typically used in experimental manipulations of small mammal populations (Johnson and Gaines 1987). We have considered the large archipelagos controls. The medium archipelagos represented increasing levels of fragmentation, followed by the smallest archipelagos, which were the most fragmented.

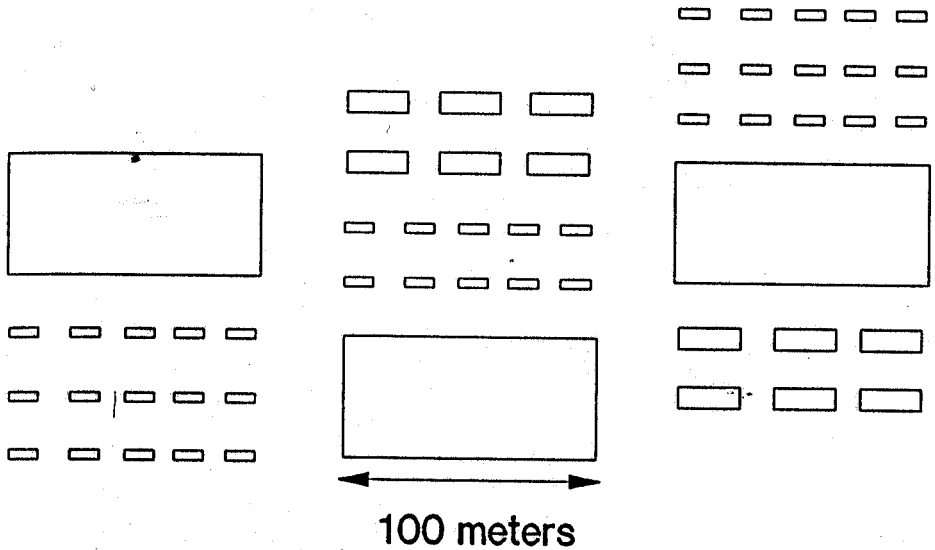


Fig. 1. Diagram of experimental archipelagos. The 40 small patches are each 4 m x 8 m; the 12 medium patches are 12 m x 24 m; the three large patches are 50 m x 100 m. Note that one large patch is a large archipelago; a group of 6 medium patches is a medium archipelago; a group of 15 small patches is a small archipelago

Small mammals were live-trapped bi-weekly. At first capture, individuals were marked with a fingerling fish tag. The following data were recorded the first time an animal was captured in each trapping session: tag number, species, trap location, body mass, sex and reproductive condition. Trap location was recorded for subsequent captures within a trapping session. A detailed description of trapping methods is in Foster and Gaines (1991). The small mammal community consisted predominantly of species that ranged in mean adult body size from large cotton rats (*Sigmodon hispidus*), weighing 135 g, to intermediate-sized prairie voles (*Microtus ochrogaster*) weighing 43 g, to the small deer mouse (*Peromyscus maniculatus*) weighing 20 g. Other species occurring at low densities included *Blarina brevicauda*, *Cryptotis parva*, *Mus musculus*, *Peromyscus leucopus*, *Reithrodontomys megalotis*, and *Sylvilagus floridanus*.

All demographic data over the seven-year period except movements were first separated by season and archipelago size then pooled over all years.

3. RESULTS

In previous work (Gaines et al. 1992a, Gaines et al. 1992b, Robinson et al. 1992) we made the following predictions about the effects of habitat fragmentation on the three species: 1) species will have the highest population.

densities on the largest archipelagos; 2) the highest persistence rates for all species will occur on the largest archipelagos; and 3) there will be more movement of animals from larger to smaller archipelagos than from smaller to larger archipelagos. The underlying assumption for these predictions is that large archipelagos are optimal habitat based on total availability of plants for cover and food, whereas smaller archipelagos are suboptimal.

3.1. DENSITIES

We analyzed the data using a two-way ANOVA with archipelago size and season as main effects (Table 1). Population density for each archipelago (excluding the mowed area) was based on the minimum number alive (MNA). Only 34 *S. hispidus* were trapped on small archipelagos over the seven-year

Table 1.

Mean density (Minimum Number Alive/ha) \pm S.E. by archipelago size for *S. hispidus*, *M. ochrogaster* and *P. maniculatus* estimated from 171 live-trap censuses (1984–1991). Sample sizes are as follows: Fall = 48, Winter = 36, Spring = 47, Summer = 40

Species	Archipelago Size		
	large	medium	small
<i>S. hispidus</i>			
Fall	17.2 \pm 1.9	8.9 \pm 1.7	
Winter	16.2 \pm 2.3	3.4 \pm 1.0	
Spring	5.7 \pm 0.8	0.6 \pm 0.2	
Summer	9.7 \pm 1.4	4.4 \pm 1.0	
Total	12.1 \pm 0.9	4.4 \pm 0.6	
<i>M. ochrogaster</i>			
Fall	28.9 \pm 4.2	62.9 \pm 5.8	62.0 \pm 8.44
Winter	52.5 \pm 8.1	103.1 \pm 10.8	78.8 \pm 10.9
Spring	47.8 \pm 5.3	78.3 \pm 7.1	55.0 \pm 5.9
Summer	37.9 \pm 6.1	69.3 \pm 6.4	87.2 \pm 6.4
Total	41.2 \pm 2.7	77.3 \pm 3.88	69.4 \pm 4.1
<i>P. maniculatus</i>			
Fall	12.0 \pm 1.5	22.9 \pm 3.4	34.1 \pm 4.1
Winter	16.4 \pm 1.6	33.1 \pm 4.7	50.8 \pm 4.8
Spring	13.5 \pm 1.2	34.1 \pm 3.5	43.0 \pm 4.3
Summer	10.3 \pm 1.5	29.8 \pm 5.1	33.1 \pm 5.5
Total	13.0 \pm 0.73	29.7 \pm 2.1	40.0 \pm 2.4

period and had a skewed distribution of density estimates. Thus, *S. hispidus* on small archipelagos were excluded from the density analysis. *S. hispidus* had highest densities on large archipelagos in every season ($F = 58.93$, $p < 0.001$, $df = 1, 334$). Also, densities were significantly lower in the spring due to poor over-wintering survival ($F = 19.04$, $p < 0.001$, $df = 3, 334$). The absolute decline in densities between the winter and spring was much more pronounced on large archipelagos than on medium archipelagos, leading to a significant archipelago size-by-season interaction ($F = 2.94$, $p < 0.05$, $df = 3, 334$). *M. ochrogaster* density was significantly affected by archipelago size ($F = 29.36$, $p < 0.001$, $df = 2, 501$), season ($F = 7.42$, $p < 0.001$, $df = 3, 501$) and the interaction between archipelago size and season ($F = 2.63$, $p < 0.05$, $df = 6, 501$). The highest densities were on the medium archipelagos, followed by small archipelagos with the lowest densities on the large archipelagos. The only exception was in the summer when density was highest on the small archipelagos. Densities of *P. maniculatus* were consistently highest on the small archipelagos, and lowest on large archipelagos for all seasons ($F = 55.16$, $p < 0.001$, $df = 2, 501$). There was also a statistically significant seasonal effect ($F = 5.22$, $p < 0.001$, $df = 3, 501$), but there was no significant archipelago size-by-season interaction.

We correlated density estimates across different archipelago sizes for each species separately. All possible pairwise correlation coefficients were significantly positive ($p < 0.01$, $n = 171$), ranging from $r = 0.256$ for *S. hispidus* on large vs. medium archipelagos to $r = 0.898$ for *P. maniculatus* on medium vs. small archipelagos. Because temporal changes in densities were positively correlated across different archipelago sizes, we pooled the density data for each species to provide an overview of population fluctuations (Fig. 2). *M. ochrogaster* underwent a multi-annual fluctuation with peaks in December of 1987 and 1990. *S. hispidus* and *P. maniculatus* exhibited annual cycles with peak densities occurring in late fall and early winter.

In summary, our analysis of seven years of density data refuted our initial expectation that all three mammal species have the highest densities on the large archipelagos. Instead, the species sorted out on differently sized archipelagos based on body size. However, for *S. hispidus* and *M. ochrogaster*, there was a statistically significant archipelago size-by-season interaction on population density.

3.2. PERSISTENCE RATES

We calculated persistence rates per two weeks by determining the proportion of animals in week t in a given archipelago that were recaptured in week $t + 2$ in that same archipelago (Table 2). The measure of "persistence" incorporates both death and emigration (see below). We weighted the persistence rates by density at t and averaged over seasons on different archipelago sizes for each species and added 0.01 to persistence rates of 0. Arcsin-transformed persistence rates for each species were analyzed using a two-way ANOVA with archipelago size and season as main effects. In *S. hispidus*, persistence rates were higher on large archipelagos ($F = 1977.42$, $p < 0.001$, $df = 1, 2660$) in all seasons except in the spring, when persistence rates on medium archipelagos increased

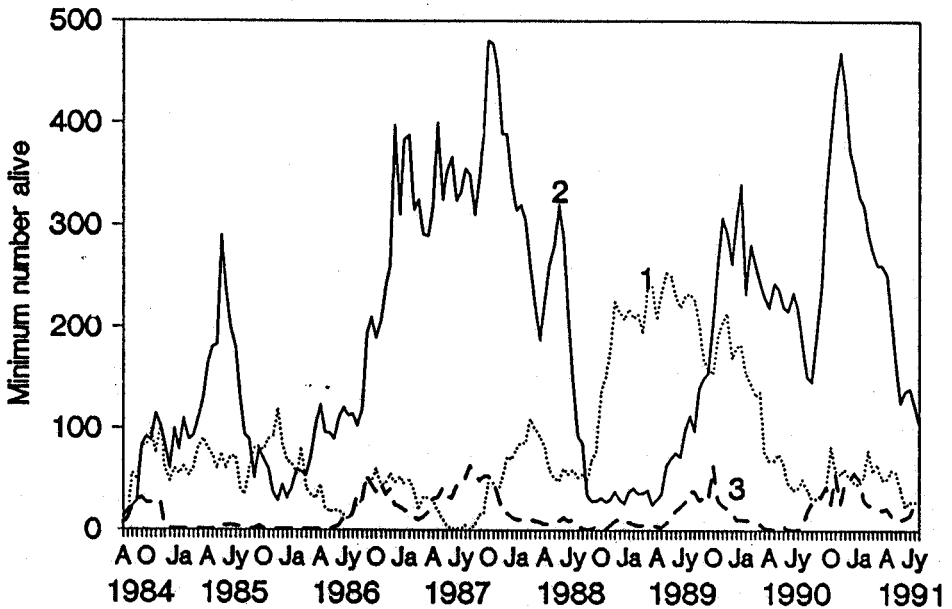


Fig. 2. Population densities (minimum number alive/ha) based on bi-weekly trapping data of *S. hispidus*, *M. ochrogaster* and *P. maniculatus* from 1984–1991
1 – *S. hispidus*, 2 – *M. ochrogaster*, 3 – *P. maniculatus*

dramatically. However, there was a significant archipelago size-by-season interaction ($F = 65.58$, $p < 0.001$, $df = 3$, 2660). Similarly, in *M. ochrogaster*, there was a statistically significant archipelago size effect ($F = 1814.11$, $p < 0.001$, $df = 2$, 15404), seasonal effect ($F = 860.41$, $p < 0.001$, $df = 3$, 15404) and archipelago size-by-season interaction ($F = 488.69$, $p < 0.001$, $df = 6$, 15404). Persistence rates were highest on large archipelagos for all seasons except summer. Moreover, persistence rates were higher on medium archipelagos than on small archipelagos over all seasons. In *P. maniculatus* there were statistically significant effects of archipelago size ($F = 23.04$, $p < 0.001$, $df = 2$, 6544), season ($F = 135.09$, $p < 0.001$, $df = 3$, 6544) and archipelago size-by-season interaction ($F = 53.28$, $p < 0.001$, $df = 6$, 6544). On average, persistence rates for *P. maniculatus* were highest on large archipelagos and were consistently highest on all archipelagos in the winter. It should be noted that the magnitude of the effect of archipelago size on persistence is considerably smaller for *P. maniculatus* than for the two larger bodied species.

In summary, *S. hispidus*, *M. ochrogaster* and *P. maniculatus* generally support our predictions that individuals remain longer on large archipelagos. However, persistence rates in all species were influenced by season.

Table 2.

Mean persistence rates \pm S.E by archipelago size and season for *S. hispidus*, *M. ochrogaster* and *P. maniculatus* estimated from 1984–1991. Sample sizes are the cumulative number of animals captured over a given season

Species	Archipelago Size		
	large	medium	small
<i>S. hispidus</i>			
Fall	.552 \pm .004 (938)	.152 \pm .010 (240)	
Winter	.494 \pm .008 (664)	.319 \pm .033 (154)	
Spring	.527 \pm .009 (334)	.701 \pm .058 (63)	
Summer	.414 \pm .011 (240)	.333 \pm .024 (140)	
Total	.515 \pm .004 (2 176)	.295 \pm .014 (597)	
<i>M. ochrogaster</i>			
Fall	.767 \pm .003 (1 959)	.667 \pm .006 (870)	.602 \pm .005 (835)
Winter	.819 \pm .002 (2 267)	.719 \pm .002 (1 099)	.455 \pm .006 (792)
Spring	.705 \pm .003 (2 623)	.659 \pm .003 (1 060)	.591 \pm .003 (748)
Summer	.521 \pm .006 (1 513)	.664 \pm .003 (805)	.548 \pm .006 (847)
Total	.717 \pm .002 (8 362)	.679 \pm .002 (3 834)	.549 \pm .003 (3 222)
<i>P. maniculatus</i>			
Fall	.449 \pm .007 (812)	.388 \pm .013 (316)	.533 \pm .008 (466)
Winter	.570 \pm .006 (857)	.562 \pm .009 (353)	.544 \pm .009 (522)
Spring	.509 \pm .005 (898)	.379 \pm .011 (461)	.435 \pm .007 (571)
Summer	.472 \pm .008 (582)	.539 \pm .054 (348)	.402 \pm .011 (372)
Total	.503 \pm .003 (3 149)	.463 \pm .005 (1 478)	.482 \pm .004 (1 931)

3.3. MOVEMENT

During the seven-year period some animals switched from one archipelago to another. These animals are here defined as "switchers". An animal had to be captured at least twice in different trapping periods to be a switcher. In some cases switchers moved to a different archipelago only to return in subsequent captures to its initial archipelago. We estimated the proportion of switches in different directions by dividing the number of switches occurring by the total number of potential switches. Potential switches within a trapping period were the number of times an animal was captured within a trapping period, minus one. Potential switches between trapping periods were the number of trapping periods an animal was captured, minus one.

We did not do a contingency test to determine if the proportion of switches is dependent on the direction of switching (from larger to smaller, smaller to larger or to same-sized archipelagos) because the data did not fit a Poisson distribution (Kramer and Schmidhammer 1992). Instead of using chi-squared statistics, we calculated estimates for the percent of animals that switched between consecutive weeks, for each of three directions: from larger to smaller archipelagos, from smaller to larger archipelagos and between archipelagos of the same size. The data were extremely skewed, even after arcsin-transformations, and were analyzed using Kruskal-Wallis tests (corrected for ties) and multiple comparison techniques (Neave and Worthington 1988). However, because the ranked data used in the Kruskal-Wallis tests contained many ties (418 ties of 450 cases for *S. hispidus*, 420 ties of 561 cases for *M. ochrogaster*, and 495 ties of 558 cases for *P. maniculatus*) we also used one-way ANOVAs with T-method multiple comparisons of means (Sokal and Rohlf 1969).

Contrary to our predictions, the trends in the data indicated there was more movement from smaller to larger archipelagos in all species (Table 3). The proportion of *S. hispidus* switching depended on direction ($H = 38.43$, $df = 2$, $p < 0.001$, $F = 53.39$, $df = 2$, $p < 0.001$). Multiple comparison tests indicated the mean proportion of animals switching from smaller to larger was greater than the mean proportions switching in the other directions. In *M. ochrogaster*, the proportion of animals switching was different for each category of switching ($H = 95.22$, $df = 2$, $p < 0.001$, $F = 46.47$, $df = 2$, $p < 0.001$) with the most switching occurring from smaller to larger archipelagos. In *P. maniculatus* the proportion of animals switching depended on direction ($H = 130.22$, $df = 2$, $p < 0.001$, $F = 30.86$, $df = 2$, $p < 0.001$). The multiple comparisons indicated the proportion of animals switching among same-sized archipelagos was less than

Table 3

Mean percent \pm S.E. of animals switching between weeks by direction for *S. hispidus*, *M. ochrogaster* and *P. maniculatus*. The sample size is in parentheses. Weeks with no potential switchers were not used

Species	Direction		
	smaller to larger	larger to smaller	same
<i>S. hispidus</i>	33.08 \pm 5.63 (52)	2.25 \pm 0.54 (150)	4.24 \pm 1.11 (150)
<i>M. ochrogaster</i>	7.88 \pm 0.82 (187)	4.01 \pm 0.45 (186)	0.71 \pm 0.11 (187)
<i>P. maniculatus</i>	16.63 \pm 1.57 (177)	16.29 \pm 1.62 (174)	1.13 \pm 0.22 (182)

the proportion of animals switching from either smaller to larger or larger to smaller archipelagos. However, unlike the other two species, there was no difference between the proportion of animals switching from smaller to larger and larger to smaller archipelagos.

In summary, contrary to our initial expectations, both *S. hispidus* and *M. ochrogaster* switched in greater proportions from smaller to larger archipelagos. However, *P. maniculatus* did not show this counterintuitive effect.

3.4. EFFECTIVE POPULATION SIZE

We examined the evolutionary potential of differently sized archipelagos by estimating the effective population size, N_e . Shields (p. 5: 1987) defined N_e as "the size of an ideal deme that would produce the same level of inbreeding and opportunity for drift as a real population with a specific census size and other characteristics".

We calculated seasonal N_e values for different archipelago sizes using the following formula:

$$N_e = \frac{4 N_m N_f}{(N_m + N_f)}$$

where N_m is the raw, absolute number of breeding males and N_f is the absolute number of breeding females in the deme (Table 4). A "breeding" male was defined as a male with visible, descended testes; a "breeding" female was one with swollen nipples. N_m and N_f were summed over all years for each season to calculate the seasonal N_e , thus there is no variance estimate for N_e . The totals for different archipelago sizes were calculated as harmonic means from the seasonal estimates of N_e , which is appropriate because of the temporal variation in abundance (Lande and Barrowclough 1987).

Two interesting points emerged from the data. First, census densities did not always accurately reflect N_e values. For example, although census densities of *M. ochrogaster* were highest on the medium archipelagos, the N_e values were generally highest on the large archipelagos. Also, *P. maniculatus* had the highest densities on small archipelagos, yet N_e values were highest on the medium archipelagos. These inconsistencies likely reflect three factors: 1) a larger number of breeding adults on larger archipelagos (Gaines et al. 1992b), 2) temporal variation in abundance, 3) temporal and spatial variation in sex ratio. The second interesting point is that N_e values we obtained for prairie voles were higher than those reported for other small mammals (Chepko-Sade et al. 1987).

4. DISCUSSION

An analysis of the effects of habitat fragmentation on the population dynamics of *S. hispidus*, *M. ochrogaster*, and *P. maniculatus* has generated consistent results over a seven-year period. We found that: 1) species sort out on archipelagos of different sizes based on their body size; 2) persistence rates are highest on large archipelagos; and 3) movement occurs generally from smaller

Table 4

The effective population size by archipelago and by season for *S. hispidus*, *M. ochrogaster*, and *P. maniculatus*. Males were considered reproductive if their testes were scrotal. Females were considered reproductive if they were lactating

Species	Archipelago Size		
	large	medium	small
<i>S. hispidus</i>			
Fall	157.0	60.3	3
Winter	11.7	0	0
Spring	29.7	3.3	0
Summer	104.7	31.9	0
Total	29.6	11.4	0
<i>M. ochrogaster</i>			
Fall	292.5	318.1	231.8
Winter	291.5	224.3	100.4
Spring	455.6	329.3	147.4
Summer	311.7	256.4	192.5
Total	326.5	275.1	152.4
<i>P. maniculatus</i>			
Fall	161.2	162.4	105.6
Winter	44.3	57.2	60.8
Spring	150.9	164.8	124.0
Summer	102.6	109.0	39.9
Total	82.3	102.9	66.7

to larger archipelagos. Because the plant community on the archipelagos was undergoing succession (Robinson et al. 1992), and these major trends in our data did not change over time, we conclude that the population dynamics of the three mammal species were not driven by successional dynamics in the vegetation.

Previously (Gaines et al. 1992b), we have hypothesized that the density pattern summarized in Table 1 reflected a rather complex interplay of species-specific autecological requirements, intraspecific interactions in high-quality habitats, and interspecific competition. In particular, we suggested that the spatial dynamics in our experimental landscape manifested source-sink dynamics (Pulliam 1988). A population has a source-sink structure if one subpopulation (the source) has high fitness, tending to grow in abundance, and the other subpopulation (the sink) has low fitness, tending to decline, and there is a net flux of individuals out of the former into the latter.

Consider for instance *S. hispidus* and *M. ochrogaster* on the two larger archipelago sizes. We suggested that *S. hispidus* may require a minimal home range larger than the medium archipelagos and thus be largely restricted as a breeding population to large archipelagos by virtue of its individual requirements. Subordinate individuals might be forced out of these habitats; this forced emigration could sustain a low-density sink population (*sensu* Pulliam 1988) in medium archipelagos. *S. hispidus* aggressively dominates *M. ochrogaster*, which thus tends to be excluded from otherwise suitable sites when *S. hispidus* is present (Glass and Slade 1980). Hence, medium archipelagos, which are sufficient in size to support *M. ochrogaster*, provide competitive refuges from the dominant species. Because *M. ochrogaster* is excluded from the large archipelagos, those archipelagos are by definition sink habitats. However, intraspecific interactions in the high-quality (i.e., medium) archipelagos for *M. ochrogaster* lead to subordinate individuals being forced elsewhere, including into the larger archipelagos. Similarly, *P. maniculatus* would be forced off of medium archipelagos by *M. ochrogaster* to competitive refuges in the small archipelagos.

However, the data reported here makes us somewhat skeptical about this interpretation. For instance, if large archipelagos were indeed sinks for *M. ochrogaster*, we might expect lower persistence rates there (i.e., lower fitness in the presence of the competitive dominant), and also a greater movement rate of individuals from medium to large archipelagos. The latter is observed, but the former is not. Likewise, *S. hispidus* tends to move from smaller to larger archipelagos, contrary to our expectations. Thus, some of our results are consistent with a source-sink interpretation, whereas other results may not be.

A way to assess the source-sink hypothesis would be to measure the net movement into and out of an archipelago. We would predict that in source archipelagos the net movement out of the archipelago would be greater than the net movement into the archipelago. Conversely, in sink archipelagos, the net movement into the archipelago would be greater than the net movement out of the archipelago. We were only able to measure the percent of switches in different directions, which may not be an accurate estimator of movement at the population level. We are currently making estimates of local fitness and net fluxes of individuals and intend to integrate them into a spatially-explicit model.

The best way to test our source-sink and competition hypotheses is to conduct experimental manipulations (Gaines et al. 1992a). By using rodent-proof fences to prevent dispersal, we would expect a species to go extinct on the archipelagos considered sinks and to reach higher densities on the archipelagos considered sources. By excluding presumed dominant species, we would expect the subordinate species to increase in density and alter their movement patterns.

Furthermore, our analysis indicates we need to consider other levels of complexity, which modulate the effects of habitat fragmentation on population dynamics of the small mammals. Five of six possible archipelago size-by-season interactions were significant in affecting the patterns we observed in densities and persistence rates. Thus, the patterns we have observed may result from a complex series of interactions (e.g., sex, age structure, archipelago location

in the landscape, and exposure to predators as animals switch), defying any simple explanation.

The results regarding N_e provide a first glimpse of the genetic structure of populations in this fragmented landscape. The effective population sizes for *S. hispidus* and *P. maniculatus* that we calculated on different archipelagos are comparable with those of other small mammal species, whereas those of *M. ochrogaster* were higher (Chepko-Sade et al. 1987). The next step would be to assess genetic structuring among archipelagos from F_{st} values estimated from protein polymorphisms and mtDNA analysis. We are convinced that a thorough understanding of the extinction process in fragmented landscapes will not occur until conservation biologists investigate more thoroughly the feedback loop between population dynamics and genetic structure.

Finally, Ims, Rolstad and Wegge (1993), suggested that the root vole (*Microtus oeconomus*) can serve as an experimental model system to predict the effects of habitat fragmentation on capercaillie grouse (*Tetrao urogallus*) in boreal forests. Both species have similar space-use patterns in patchy environments. Although observations of Ims, Rolstad and Wegge (1993) are titillating, we believe their results may unfortunately be more of an exception than a rule. For instance, it would be useful to know if other demographic variables such as survivorship, reproduction, and dispersal show similar responses to habitat fragmentation in the two species. If not, the power of the experimental model system for the grouse would be reduced.

The three small mammal species in our system reacted differently to habitat fragmentation, presumably because they are embedded differently in the community with respect to food habitats, competitors, etc. Thus, it would be difficult to use one species we studied to make specific predictions about the responses of another species within the same landscape, let alone to extrapolate to landscapes at larger or smaller scales. However, generalities may emerge by examining the effects of habitat fragmentation in many different environments on many different species. Such generalities should lead to specific predictions that can be tested experimentally and used by land managers.

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