Oecologia (1996) 108:182–191

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Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals

Received: 13 February 1995 / Accepted: 6 April 1996

Abstract Habitat fragmentation involves a reduction in the effective area available to a population and the imposition of hard patch edges. Studies seeking to measure effects of habitat fragmentation have compared populations in fragments of different size to estimate an area effect but few have examined the effect of converting open populations to closed ones (an effect of edges). To do so requires a shift in spatial scope – from comparison of individual fragments to that of fragmented versus unfragmented landscapes. Here we note that large-scale, "controlled" studies of habitat fragmentation have rarely been performed and are needed. In making our case we develop a simple computer simulation model based on how individual animals with home ranges are affected by the imposition of habitat edges, and use it to predict population-level responses to habitat fragmentation. We then compare predictions of the model with results from a field experiment on *Peromyscus* and *Microtus*. Our model treats the case where home ranges/territories fall entirely within or partially overlap with that of sample areas in continuous landscapes, but are restricted to areas within habitat fragments in impacted landscapes. Results of the simulations demonstrate that the imposition of hard edges can produce different population abundances for similar-sized areas in continuous and fragmented landscapes. This edge effect is disproportionately greater in small than large fragments and for species with larger than smaller home ranges. These predictions were generally supported by our field experiment. We argue that large-scale studies of habitat fragmentation are sorely needed, and that control-experiment contrasts of fragmented and unfragmented microlandscapes provide a logical starting point.

Key words Habitat fragmentation · Edge effects · Home range · Landscape ecology · Small mammals

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Introduction

The areal reduction, segregation, and isolation of subpopulations into habitat fragments (i.e., patches) is thought to have many harmful biological effects ranging from the genetic to the community level (e.g., Usher 1987; Quinn and Hastings 1988; Simberloff 1988; Ims and Stenseth 1989; Saunders et al. 1991). Fragmentation of habitats has been heralded as "perhaps the single most significant challenge to the development of models applicable to wildlife management, if not ultimately to the survival of wildlife altogether" (Temple and Wilcox 1986). There are two main effects of habitat fragmentation: the large-scale, destruction of suitable habitat, and the isolation of remaining fragments. Few would argue that habitat destruction is harmful to most species of concern. What most of the discussion revolves around is the extent to which populations in remaining habitat fragments are affected by isolation (see Simberloff 1988).

Most research on habitat fragmentation has focused on responses of organisms to fragment/patch area (e.g., Whitcomb et al. 1981; Turchin 1982; Lynch and Whigham 1984; Fahrig and Merriam 1985; Lovejoy et al. 1986; Temple and Wilcox 1986; Kareiva 1987; Van Dorp and Opdam 1987; Temple and Cary 1988; Quinn et al. 1989; Foster and Gaines 1991; Verboom et al. 1991; Bierregaard et al. 1992; Robinson et al. 1992). Such studies typically make inference via correlative relationships among fragments or use larger fragments as ad hoc controls for smaller ones, the reason being that large patches are more representative of conditions in a continuous habitat situation than smaller fragments.

Beyond fragment-area effects are those attributable to the creation of distinct habitat boundaries. Fragmented landscapes comprise a mosaic of habitable areas, embedded in a matrix that is largely uninhabitable. Individuals living within habitats demarcated by "hard" edges would be expected to have different movement and dispersion patterns than those in more continuous, unfragmented areas (Stamps et al. 1987). The orientation and positioning of individuals relative to fragment edges may be viewed as being largely separate from general population responses to fragment areas. There is, in fact, a spatial hierarchy over which effects of habitat fragmentation can be studied – from local responses of individuals to fragment edges, to population and community responses at the fragment and whole landscape scales (Kotliar and Wiens 1990). While single-scale studies that use individual fragments as the unit of observation can yield information relating to general features of fragments (Pickett and Thompson 1978; Wilcox 1980; Burgess and Sharpe 1981; Harris 1984; Usher 1985; Soule 1986), they are limited when it comes to detailing responses to habitat fragmentation at larger or smaller scales (Vance 1984).

The issue is one of patchiness and scale. There is, in fact, no one correct scale over which habitat fragmentation effects should be measured (e.g., Levin 1992). Wiens et al. (1985) suggested that understanding how individuals respond to habitat discontinuities could provide a mechanistic basis for scaling individual-level responses upwards to account for larger-scale patch and landscape patterns. More specifically, understanding how individual animals are affected by the imposition of hard patch edges might provide a first step in evaluating larger-scale responses to habitat fragmentation. An approach that uses responses of individuals to edge habitats to evaluate larger-scale population ones might target fragmented and unfragmented landscapes as reference points (i.e., experimental units) rather than individual fragments.

Our ongoing field studies on small mammals have forced us to confront these issues. We are conducting one of the first control-treatment field experiments on habitat fragmentation using two species with different space-use requirements – the meadow vole, *Microtus pennsylvanicus*, (mean body mass approx. 42 g), which has relatively small home ranges, and the white-footed mouse, *Peromyscus leucopus* (22 g), with home ranges about four times larger. Comparisons are made between an unfragmented, continuous (control) landscape within which are 13 trapping grids of three sizes (1.0, 0.25, and 0.0625 ha), and an identical landscape with the same number/sizes/configuration of trapping grids but where all inter-grid areas are mowed, thereby creating a landscape of fragmented, isolated patches. But what are the expectations? We initially planned to use the null hypothesis that grids and fragments of the same size would have comparable population abundances. However, this seems unrealistic since an area sampled in a continuous habitat matrix is larger and the distribution of individuals on and off grids more even, in an areal sense, than that in a similar-sized fragment whose hard edges limit the dispersion and movement of individuals. To address this problem we first use computer simulations to construct null expectations of how the dispersion of individuals might be affected by the introduction of patch boundaries, and then scale these results up to make an inference about effects of habitat fragmentation at the landscape scale. We then test the predictions of the model with data from our field experiment, and extrapolate our results to make general predictions concerning responses to habitat fragmentation based on home range: habitat fragment area ratios. Finally, we discuss some of the limitations inherent in conducting large-scale experiments of the type described here.

Materials and methods

Study site

We conducted our field study from June 1993 through October 1994 at the University of Virginia's Blandy Experimental Farm (BEF), Clarke County, Virginia, USA (ca. 78°00°W, 39°00 N). BEF comprises croplands, pasture, old-fields, the Orland E. White Arboretum, and assorted woodlots. Our study site was a 45-ha old-field bounded by U.S. highway 50, an adjacent field of similar vegetation structure, the Arboretum, and a small woodlot. Prior to 1987 the field served as a pasture (with yearly mowings) for more than 20 years; from 1987 to the summer of 1991 the field served as a site for several studies focusing on small mammals (see Bowers and Dooley 1993; Dooley 1993; Bowers et al. 1996). In 1993–1994 the field supported a mosaic of tall/dense stands of thistle (*Carduus* spp.) along with various mixtures of lower growing dicotyledons (i.e., *Daucus carota*, *Ambrosia*, and *Galium*) and grasses (*Festuca*, *Dactylis*, *Lolium*, and *Poa*).

Rodent community

The rodent community comprised two common species: white-footed mice (*Peromyscus leucopus*) and meadow voles (*Microtus pennsylvanicus*); house mice (*Mus musculus*) and deermice (*Peromyscus maniculatus bairdii*) comprised less than 1% of the resident individuals and are not considered further here. See Bowers and Dooley (1993) and Dooley (1993) for more detailed accounts of the biology of *Microtus pennsylvanicus* and *Peromyscus leucopus* in the study field.

Landscape design

We used mowing to create two "microlandscapes": a 20-ha fragmented landscape with 13 unmowed patches embedded in a

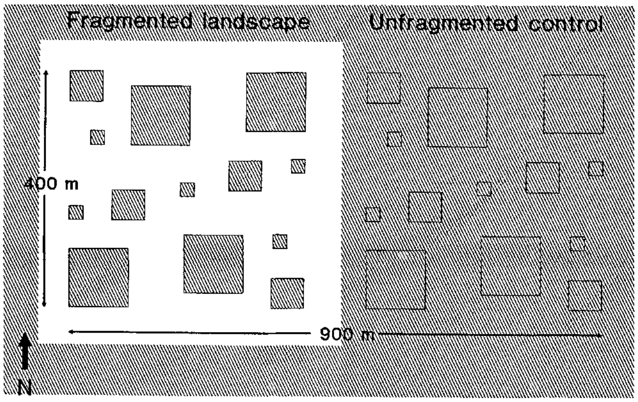

Fig. 1 Landscape design used in our field study. Inhabitable areas for small mammals are unmowed (*shaded*) and uninhabitable areas are mowed (*unshaded*). There are four replicates of three patch sizes (1.0, 0.25, and 0.0625 ha) positioned in four satellite groups within each landscape type – one that is fragmented by regular mowing and the other that is unmowed and serves as a continuous habitat control. The array of patch sizes and the dispersion of patches is identical in the two landscapes. Interpatch distances within a satellite grouping is 50 m; the overlap of patches juxtaposed to one another within a satellite group is 25 m

mowed matrix; and an identically sized continuous-habitat (control) landscape that was not mowed (Fig. 1). Each landscape included four replicates of medium (50×50 m; 0.25 ha) and large (100×100 m; 1.0 ha) and five small (25×25 m; 0.0625 ha) fragments (in the mowed landscape) or grids (in the continuous habitat landscape). All fragments/grids were separated by mowed, "uninhabitable" areas (fragmented) or unmowed vegetation (control) of at least 50 m. Except for mowing, the number, sizes and dispersion of fragments/grids was identical for the two landscapes. Mowing in the fragmented landscape was initiated in May 1993 and was repeated throughout 1993 and 1994 when vegetation reached 20 cm in height. Previous work demonstrated that mowing effectively converted suitable small mammal habitats to unsuitable ones and that individuals did not occupy home ranges within mowed areas (see Bowers and Dooley 1993; Dooley 1993). Consequently, habitat patches were demarcated by hard and grids by soft edges (see Stamps et al. 1987), and each represented a largely separate entity within their respective landscapes.

Justification for the design of the microlandscapes (i.e., the size, dispersion, shape, interpatch distances, and degree of replication) was based on a 2-year study of rodent abundances and movement patterns in the field, details of which are given elsewhere (see Bowers and Dooley 1993; Dooley 1993; Dooley and Bowers 1996). Briefly, we determined that 50-m mowed areas would be adequate to create a system of largely independent patches; and that patches of 1.0 ha, 0.25 ha, and 0.0625 ha would create a range of sizes over which rodent abundances may vary.

Estimates of rodent abundance

Small mammals inhabiting patches in the fragmented and grids in the continuous habitat landscape were censused via capture/recapture methodology bimonthly during the summer months and monthly during the rest of the year (weather permitting). Two folding Sherman live traps were placed at 938 stations spaced at 12.5-m intervals both in patches and grids. Traps were baited with peanut butter wrapped in wax paper, set in the evening, checked at first light, and then closed for the day. Captured animals were fitted with a metal eartag, toe clipped, and released. For each capture we recorded eartag and toe number, trap location, species, age, sex, reproductive condition, and weight. Traps were left open between trap sessions to allow free exploration and aeration.

We alternated trapping sessions between the two landscapes (in 1993) or trapped paired halves of each landscape per trap session (in 1994); traps were run three consecutive nights per trap period, with traps closed over hot mid-day periods during summer months. Over the 17-month study period, we completed 15 censuses of the patches/grids in both landscapes.

Rodents were classified as residents if they remained on a patch/grid for more than one census period; shorter-term inhabitants or those that moved between patches/grids were classified as transients. Age class determinations were based on weight using a cut-off (juveniles below, adults above) of 14 g for *Peromyscus* and 22 g for *Microtus*. Rodent abundances were estimated for each patch/grid and for each of the 15 census periods using the Lincoln model and according to the criteria outlined in Menkens and Anderson (1988) and Skalski and Robson (1992).

A simple computer model of habitat fragmentation

Statement of the problem

Our study was designed so that the abundance of small mammals in habitat fragments of a particular size could be directly compared to similar sized grids in the continuous habitat (control) landscape. However, such comparisons are awkward if not inappropriate for animals with activity areas because the area available to a population will be greater – in an areal sense – for grids embedded in a continuous habitat matrix than for habitat fragments of the same size (see Otis et al. 1978). Our computer simulation model was designed to explore this problem qualitatively and quantitatively.

Description of the model

Our model was conceptually and operationally simple and was designed to be directly comparable to our field experiment. We used a 100×100 cell array to represent a 500×500 m (25 ha) landscape; the distance between two adjacent grid points represented 5 m. Within the landscape matrix we designated locations for one 1.0 ha (100×100 m), four 0.25 ha (50×50 m), and 16 0.0625 ha (25×25 m) grids, separated from each other by distances of at least 50 m. The number, sizes, and configuration of grids within the landscape was held constant over all simulations. Unlike in our field design, however, the total area for each grid size was constant at 1.0 ha in order to reduce the error due to "sampling" different sized areas.

We used a random number generator to assign activity centers of 100 animals per simulation to locations within the landscape matrix; an activity radius parameter in the model determined how far home ranges extended outwards from activity centers. We considered activity radii of 0, 5, 10, 15, 20, and 25 m (i.e., from stationary species to those with home ranges/territories of 0.008–0.20 ha), as well as radii of 8 m and 16 m that are comparable to the approximately 200 and 800 m^2 home ranges of *Microtus* and *Peromyscus*, respectively, in our field (see Dooley 1993; and Bowers et al. 1996).

Each simulation tallied population abundance for the 21 grids or patches, summed over similar patch/grid sizes. An animal was counted as a resident depending on the degree to which its home range overlapped with that of patches/grids, and according to whether the landscape was fragmented or continuous (see below). Since 50 m separated sample areas, and these areas were at least 50 m from the edge of the landscape, individuals resided in no more than one fragment/grid, and fragments/grids on the edges of the landscape potentially included as many home ranges as those in the middle.

We used the general landscape design (see above) to simulate both continuous and fragmented landscapes. In the case of unfragmented landscapes, animals occupied areas both within and outside grids; in the case of the fragmented landscape, animals inhabited only areas within fragments (areas between grid fragments were assumed to be uninhabitable). Different rules were used to determine population abundance in grids or patches: any individual whose home range overlapped with that of a grid in the continuous habitat landscape was included in estimates of abundance; the presence/absence of an individual in habitat fragments was determined by the proportion of its home range area within the fragment to that in uninhabitable areas outside. The model assumes that home range size, regardless of the background habitat template, is rigid within but variable among species. We reasoned that animals whose home ranges were mostly outside of fragments would be eliminated from the fragmented landscape, while those with extensive overlap with fragments would become patch residents. We ran the simulations using the value of ≥66% home range overlap with grid fragments as a threshold determining if individuals persisted and were counted as residents; individuals with lower degrees of overlap (<66%) were eliminated from the grid and landscape. Using the figure of 66% overlap for residency was not arbitrary but followed Ims et al. (1993), who showed that female *Microtus* had home ranges in habitat fragments approximately 70% the size of those in more continuous habitats. Requiring greater overlaps for residency status would have the effect of increasing the difference between abundances in patches and grids, while requiring lower overlap for residency would reduce differences.

We performed two sets of simulations: one set that used 100 simulations for both fragmented and control landscapes for six different activity areas (see above; a total of 1200 simulations); and another set of 500 simulations for each landscape type that used activity radii comparable to that of *Microtus* and *Peromyscus* in the field (8 and 16 m, respectively; see Dooley 1993; Bowers et al. 1996). We tested both fragment-area (within a simulation) and landscape (between-simulation) effects. Output variables included: (1) numbers of resident individuals censused in each of the three grid/patch sizes; and (2) fragment:grid ratios in abundance.

Quantitative comparisons of field and simulation data required several steps. First, we calculated average fragment:grid abundance ratios for the summer breeding periods in 1993 and 1994 for *Peromyscus* and *Microtus* in small, medium, and large fragments/grids. Next we compared these actual ratios to the distribution of ratios generated from 500-paired simulations of abundances from fragmented and control landscapes, and tallied the number of runs with ratios less than, equal to, or greater than that observed. Finally, we used *t*-tests to compare the observed mean ratios in abundance to the mean and standard deviation of the ratios generated via simulation.

Results

Computer simulations

Simulations showed that fragment:grid abundance ratios varied with the size of area considered and with the size of activity ranges (Fig. 2). For sedentary species (activity radius = 0.0), abundances in fragments and grids of comparable size were no different: i.e., fragment:grid abundance ratios averaged 1.0 over all sample areas. With increasingly larger activity radii, differences in abundances between fragments and grids became increasingly different: fragment:grid ratios of <1.0 for medium and large areas and <0.50 in comparisons of small areas. Specific results included: (1) fragment:grid ratios in abundance that were <1.0 for all species with activity radii >0; (2) greater differences in abundances between similar-sized sample areas in fragmented and continuous landscapes for species with large than small activity areas; and (3) greater landscape-scale differences in abundance for smaller than larger sample areas. Since all these comparisons used the same areas, and the same number of individuals, the different results are attributable to the imposition of patch edges and a sample area by activity radius interaction.

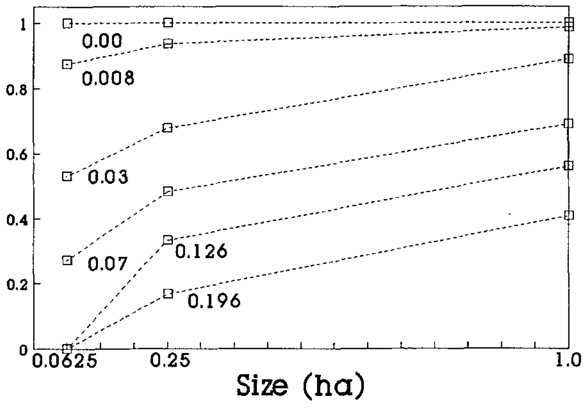

Fig. 2 Results of computer simulations showing fragment:grid ratios in abundance for small, medium and large fragments/grids (on the X-axis), and for six species with home range sizes of 0.00, 0.008, 0.03, 0.07, 0.126 and 0.196 ha. Each plotted ratio represents the mean of 100 simulations for each sample area and home range size. Ratios <1.0 reflect the bias associated with the imposition of hard patch edges

Hence, the simulations suggest the effect of isolating small patches from a continuous habitat matrix was greater than isolating large patches and the overall effect of fragmentation was greater for species with larger than smaller activity areas. Small areas within a continuous habitat matrix had higher population abundances than large grids but in fragmented landscapes large patches had higher abundances than small ones. Proportionately then, the effect of habitat fragmentation was negatively related to home range size:fragment area ratio (see Fig. 3).

Field data

We captured 2569 *Microtus* and 378 *Peromyscus* individuals over both landscapes during 15 trapping sessions. We categorized 187 and 976 resident *Peromyscus* and *Microtus*, respectively; the remaining individuals were classified as transients. We captured an average of 169 ± 56 (SD) and 15 ± 8 resident *Microtus* and *Peromyscus*, respectively, per week in the fragmented landscape and 216 ± 52 and 78 ± 23 in the continuous habitat control. In that the model focused on resident animals with well-defined home ranges, and not transients, we restrict the following analyses of the field data to include just residents. Highest resident abundances for both species were observed in large grids in the control landscape and the lowest in small fragments (Fig. 4). Habitat fragmentation reduced the absolute and relative densities of *Peromyscus*

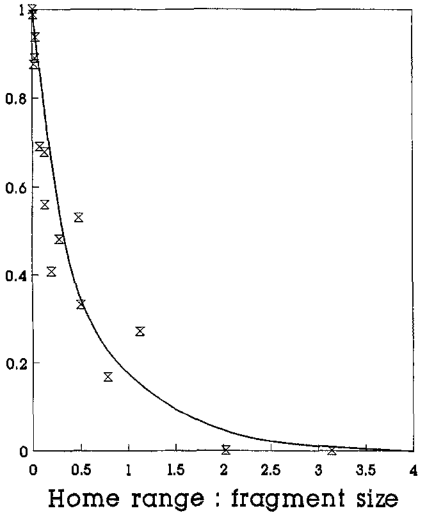

Fig. 3 Scaling relationship between the home range:fragment area ratio (on the X-axis), and the predicted reduction in abundances that accompany habitat fragmentation (fragment/grid abundances as a percentage on the Y-axis). Plotted values represent the mean value of 100 simulations for each combination of six home range sizes and three fragment/grid sizes (number of points = 18; see text for details). The "best fit" equation was $Y = 0.15X^{-1.03}$, $R^2 = 0.59$)

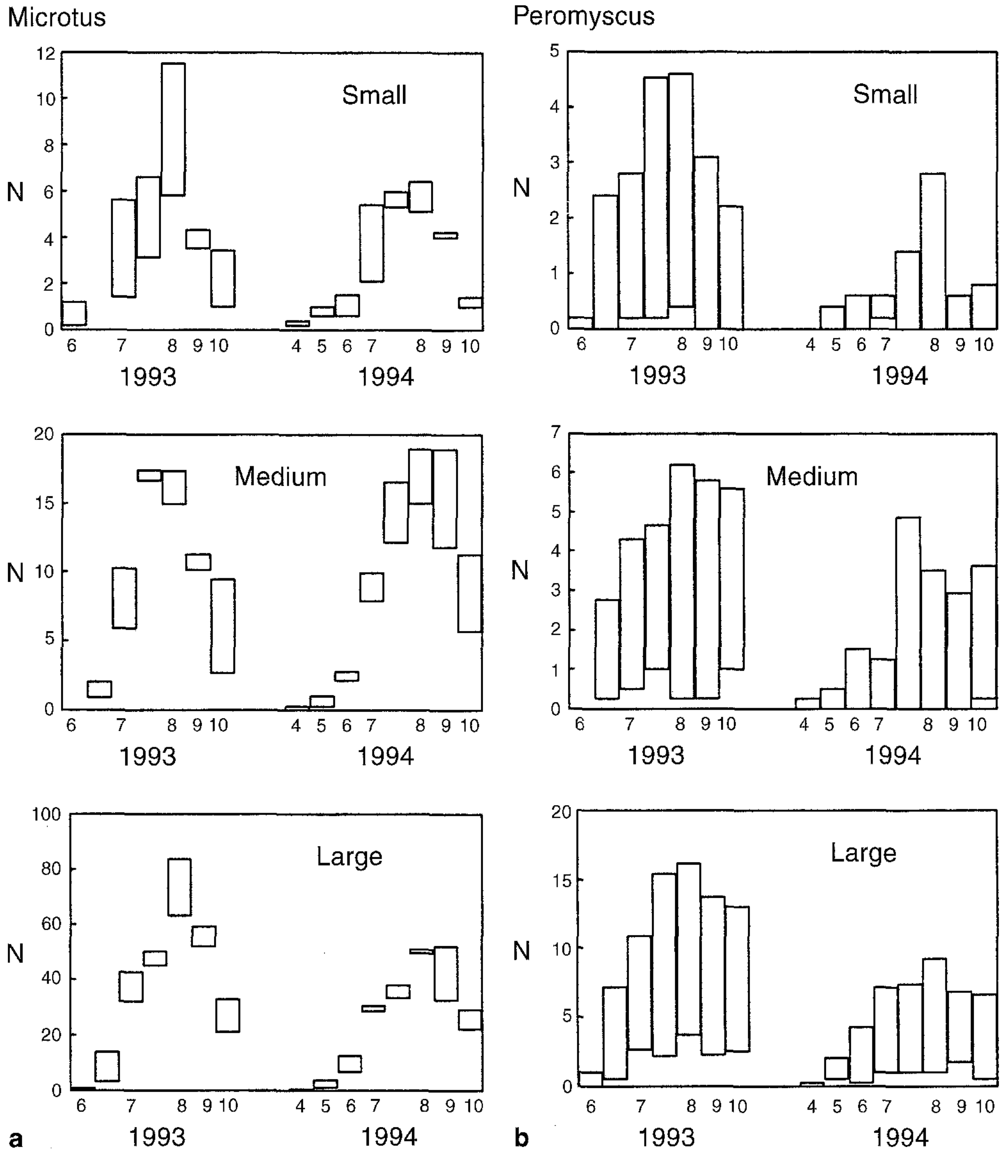

Fig. 4a, b Results of the field experiment showing small mammal abundances in grids (*top of bars*) and fragments (*bottom of bars*) in small, medium, and large grids/fragments for *Microtus* (**a**) and *Peromyscus* (**b**) over 15 census periods in 1993 and 1994; numbers on *X*-axis represent months within years. Values represent the mean abundance of residents (not transients) over replicate grids/fragments for each complete census

(with larger home ranges) in all fragments to a much greater degree than for *Microtus* (with small home ranges; see Fig. 4). Repeated measures ANOVA showed that abundances of resident *Peromyscus* (using four censuses during the breeding season in June–August 1993 and another four in 1994) were significantly lower in small ($f_{1,8}$ = 26.61, $P < 0.001$), medium ($f_{1,6}$ = 22.68, $P < 0.003$), and large ($f_{1,6}$ = 7.34, $P < 0.04$) fragments than in comparable-sized grids; average abundances of *Microtus* were also lower in fragments than grids but the differences were less marked: small ($f_{1,8}$ = 4.23, $P < 0.07$), medium ($f_{1,6}$ = 0.5, $P < 0.55$), and large ($f_{1,6}$ = 0.6, $P < 0.50$). Fragment:grid ratios in abundance were much lower for *Peromyscus* (from 7 to 26%) than *Microtus* (48–98%) and were lowest for both species in small grids/patches, and higher in medium and large ones (Table 1).

Both the Lincoln estimator and the statistical analyses of abundances assume that subpopulations within grids (in the control) and fragments (in the treatment landscape) were closed and independent. This means that inter-grid and inter-fragment movements should have been infrequent. This, in fact, appeared to be the case: i.e., of 1826 individuals captured more than once over the 2-year study, only 43 were observed to move between fragments and 71 between grids.

Match between expected and observed results

Computer simulation results predicted that differences in population abundance between fragments and grids would be more expressed for species with larger home ranges and for smaller sampling areas than larger ones. These predictions are qualitatively supported by analyses of actual population abundance from the control and fragmented landscapes: *Peromyscus*, with larger home ranges, showed the greatest difference in abundance between fragments and grids while *Microtus*, with smaller

Table 1 Comparison of observed fragment:grid abundance ratios for *Peromyscus* and *Microtus* for small, medium and large fragments/grids with that predicted via simulation using home ranges sizes of 800 and 200 m^2, respectively. Tabled values include (from left to right) the mean observed fragment:grid ratio predicted via simulation (±SD), and for each summer, the mean estimated abundance in fragments and grids, the actual observed abundance ratio, and the number of simulated ratios less than (<), equal to (=), and greater than (>) that observed. Actual ratios that differed from that predicted via simulation (using *t*-tests, and *P*=0.05) are indicated by an *asterisk*

Species/ patch	Predicted ratio±SD	1993					1994				
		X abundance fragment/grid	=Observed ratio	N simulations			X abundance fragment/grid	=Observed ratio	N simulations		
				<	=	>			<	=	>
Peromyscus											
Small	0.15±0.11	0.24/2.90	=0.08	240	35	225	0.06/1.36	=0.04	85	42	390
Medium	0.28±0.15	0.50/3.60	=0.14	37	8	455	0.00/2.78	=0.00*	0	13	487
Large	0.56±0.18	2.25/10.11	=0.26*	30	0	470	0.85/6.98	=0.12*	3	4	493
Microtus											
Small	0.47±0.18	2.31/4.79	=0.48	228	0	272	3.76/4.31	=0.87*	472	8	20
Medium	0.70±0.20	7.81/9.24	=0.84	367	0	133	9.28/12.02	=0.77	299	0	201
Large	0.80±0.18	29.81/37.17	=0.80	203	35	262	30.65/31.74	=0.98	360	0	131

home ranges, showed only trends in the direction predicted (Fig. 4). A second prediction, that abundances would differ most markedly for smaller than larger fragments/grids, was also consistent with the field observations.

Simulation results tailored to the two target species were comparable to those measured in the field (Table 1). More specifically, the actual reduction in abundance between fragments and grids for *Microtus* could not be distinguished from that predicted by the simulations in five of six cases, while actual responses of *Peromyscus* in the field were similar to the simulations in three of six comparisons. Significant deviations between simulated and observed results involved higher *Microtus* abundance ratios than predicted in comparison of small fragments:grids in 1994, and lower-than-expected abundance ratios for *Peromyscus* in medium and large fragments: grids in both years.

Discussion

We have three goals in this paper: (1) to make the case that landscape-level tests of habitat fragmentation have rarely been performed and are needed; (2) to provide a heuristic demonstration of how the imposition of patch edges interacts with spatial usage requirements of individuals to affect population abundance at the patch and landscape scale; and (3) to identify some of the problems inherent in conducting landscape-scale tests of habitat fragmentation.

The edge effect we document here might be considered largely methodological, but there are important biological ramifications as well. The methodological problem involves differences in the physical area occupied by census sites and area they effectively sample. For mobile animals, the techniques used to estimate population abundances treat an area that is defined abstractly and largely according to probabilities. "Captured" individuals might be categorized as those whose home ranges/territories are totally confined to the census area, or those whose home ranges include, to varying degrees, a mix of areas in the sample area and areas nearby. More formally, Otis et al. (1978) argue that if $A(W)$ represents the total area censused by a grid in a continuous habitat matrix, the area sampled is a function of both the area within the grid proper (A) and the area in a surrounding boundary strip of width W (where individuals live off the grid but are still likely to be captured). The relationship is

$$A(W) = A + PW/c + \pi W^2/c$$

where P is a linear measurement of the grid dimensions and c is a conversion factor to express PW and W^2 in units of A; $\pi W^2/c$ is the boundary area at the corners of grids. While there are a number of ways of estimating the width of the boundary strip, W (see Otis et al. 1978), it is essentially a measure of home range diameter.

In a habitat fragment with hard patch edges the area within which animals live is well-defined, discrete and densities can be estimated with confidence. Thus, for grid fragments

$$A(W) = A$$

The upshot is that the imposition of hard patch boundaries around trapping grids reduces the area sampled by ($PW/c + \pi W^2/c$). The difference in the area sampled between comparably sized grids in continuous and fragmented landscapes will vary with size of A relative to that of ($PW/c + \pi W^2/c$): i.e., the difference will be greatest when grid areas are small and home ranges large. This, in fact, is what our simulations and field data show. Accounting for differences in sample areas between fragments and grids can be extremely important. For example, if the abundances of *Microtus* are converted to densities, via the adjustments recommended by Otis et al. (1978; see above), small fragments switch from having lower to having higher densities than small grids (Dooley and Bowers, unpublished manuscript).

Our results suggest that there are scaling relationships between spatial usage patterns of individuals and the size of habitat fragments (i.e., home range area:fragment size ratio; see Fig. 3) that might be used to predict responses to habitat fragmentation. In fact, it provides one of the first models that details species responses to habitat fragmentation. We predict that the large-scale destruction of habitats, and the creation of patches with hard edges, will eliminate proportionately more individuals whose home range:fragment area ratio is relatively large than for species where it is smaller (Fig. 3; see also Foster and Gaines 1991). For species where the ratio is >0.5, the edge effect detailed here will be especially marked; species whose home ranges are much smaller than fragments (ratios of <0.05) will be relatively little affected. These predictions are entirely consistent with our field observations that the species with the larger home range (*Peromyscus*) showed more marked responses to habitat fragmentation (especially in small habitat fragments) than the species with smaller home ranges (*Microtus*). Specifically, the smaller the patch relative to the activity area of a species, the larger the sampling area bias, and the greater the effect of creating hard habitat edges.

The reduction in effective sampling area can be viewed as a first-order effect of habitat fragmentation and a sort of null hypothesis for evaluating differences in abundance between fragmented and unfragmented landscapes. The sampling/area bias may be particularly important when comparing abundances across habitat fragments and grids of different size. Small patches have proportionately more edge than larger patches, and, as we have shown here, small sampling areas record relatively high abundances in continuous habitats and relatively low abundances in fragmented landscapes. Large patches, by comparison, have proportionately less edge, and differences in abundance between an isolated large fragment and a comparable area in a continuous habitat matrix will be less. Basically, this is another pathway by which hard patch edges affect populations (for others see Whitcomb et al. 1981; Lovejoy et al. 1986; Stamps et al. 1987; Temple and Cary 1988; Bowers and Dooley 1993). Other studies suggest that small fragments may have lower population densities because of high emigration:immigration ratios, high rates of predation, or other edge effects that decrease the quantity/quality of the more suitable interior habitats (Yahner 1988). Our model and field work show that even in the absence of such effects population abundances in fragments will be lower than that in similar-sized areas in unfragmented habitats.

We view the edge effect as a first-order response to habitat fragmentation because it revolves around the total area available to a population. Other responses to fragmentation may confound, exaggerate or otherwise modify effects related to imposition of edges. For example, in the 2nd year of the field study, *Microtus* abundances were much higher in small fragments than the simulations predicted (fragment:grid ratios of approx. 1:1; see Table 1). Foster and Gaines (1991) also noted that several small mammal species occurred at higher-than-expected densities on small habitat fragments. We suggest two possible reasons for this. First, it may be that small patches are of lower quality, that dominant individuals prefer larger patches, and that subdominants are relegated from larger patches to smaller ones; and – in that the subdominants will be less territorial – higher abundances may result. Alternatively, Bowers et al. (1996) suggest that *Microtus* females with home ranges on patch edges are of larger body size, they reproduce more frequently, and have longer residence times than those in continuous habitat mosaics – all suggesting edge habitats may be of higher quality than non-edges. Hence, small patches with high proportions of edge may represent relatively high-quality habitats capable of supporting high rodent abundances. The point is that there is not just a single fragmentation effect, and introducing hard edges may not only affect the effective area available to a population but may alter habitat quality (for better or worse) as well. In such cases, the simple, single-effects model developed here will provide only a starting point for evaluating responses to habitat fragmentation.

The truncating effect of hard-habitat edges could also work within species to alter demographic make-up over patches of different size and between continuous and fragmented landscapes. In animals with polygynous breeding systems, adult males may have home ranges several times larger than females or juveniles. Consequently, males may be affected to a much greater degree by the creation of hard patch edges than females, and these differential responses could create marked differences in demographic structure and breeding systems between fragmented and continuous landscapes. For example, in our field experiment the proportion of male resident *Peromyscus* in habitat fragments averaged 60% (±41; SD) in the 1st year after mowing and only 28% (±21) in the 2nd year – comparable figures for grids were 64% (±19) in the 1st year and 48% (±24) in the 2nd year. While repeated measures ANOVA showed these landscape differences in sex ratio to be only suggestive ($f_{1,15} = 2.91$, $P = 0.11$), they are in the general direction of fewer males in fragmented than unfragmented landscapes.

Our model also assumes that the dispersion and size of home ranges is relatively similar between fragmented and continuous landscapes, but it is known for some species that home range dispersion patterns become modified under fragmentation. For example, Lovejoy et al. (1986) showed for understory birds in the Amazon that when a portion of the habitat is destroyed, birds become concentrated in nearby and adjacent areas (fragments) retaining suitable habitats. Lovejoy et al. (1986) reported greater crowding effects in smaller than larger fragments and noted that the influx of a constant number of individuals will produce greater proportional and absolute changes in smaller than larger fragments. The crowding of displaced individuals into remaining habitat fragments is essentially the inverse of what our model predicts. One similarity is that both scenarios are based on what happens at the landscape scale when a portion of the habitat matrix is destroyed and hard edges are created (for further discussion see Stamps et al. 1987).

Individuals respond to habitat heterogeneity at both the within- and the between-home range scales (Van Horne 1982). Home range suitability is affected by factors both intrinsic and extrinsic to the home range (Stamps et al. 1987), and the interplay between the two determines landscape patterns of population density and demography (Van Horne 1982; Wiens et al. 1993). However, because of the lack of experimental data using landscape-scale comparisons (controls), we know very little concerning how intrinsic features of home ranges, and especially individual space use requirements, affect species responses to habitat fragmentation (Ims et al. 1993). It is quite clear, however, that home ranges on the edge of patches are often larger and/or more exclusive than those in the center (see Stamps et al. 1987 for review) and that the general pattern varies with the size/shape of patches and the type of surrounding habitat. Our study suggests that animals whose territories are on the edge of patches with hard edges will have fewer neighbors than those in the center of patches or those living in continuous habitat landscapes. If the number of neighbors determine territorial costs, and the costs determine territory size, one would predict that individuals with territories on the edges of hard edged patches will be larger than those living in areas with more neighbors (Krebs 1971; Wiens 1973). Hence, the edge effect detailed here may influence both the relative number of individuals on fragments versus control areas as well as variation in territory sizes both within and between landscape types. Though several of the studies cited above (especially Krebs 1971; Wiens 1973; Stamps et al. 1987) have documented the same edge effect we have here, the focus of such studies has been more on individual-level rather than population effects.

A recently proposed paradigm for landscape ecology is to examine ecological phenomena over a hierarchy of spatial scales – look to higher scales for significance, but to lower scales for mechanism (O'Neill et al. 1986; Levin 1992; Wiens et al. 1993). Habitat patches/fragments usually characterize axes of habitat heterogeneity at an intermediate-scale, and studies of habitat fragmentation have typically followed a single-scale, patch-based orientation. However, the notion of what constitutes a patch is a vague and relative one, and there is a hierarchy of "patchiness" that extends below and above most entities considered as representing patches (Kotliar and Wiens 1990). For example, in our studies we have documented small mammal responses to variation in vegetation within habitat fragments (Bowers and Dooley 1993; Dooley and Bowers 1996), to variation in features of whole fragments (Dooley 1993; Dooley and Bowers 1996), and, in this paper, to phenomena at the above-fragment, landscape scale. Even distinguishing patch-level from landscape-scale responses is problematic because, in part, neither entity has been adequately defined in the literature (Kotliar and Wiens 1990). For example, it is clear that both *Peromyscus* and *Microtus* moved longer distances, more frequently, in the continuous habitat control than in the fragmented landscape. Does this then imply that the continuous landscape was operating more as a 20-ha patch than a landscape? No matter how large the spatial scale considered in a study, there will always be a larger scale over which effects could have been evaluated. The challenge then is to identify model species and systems where studies of large-scale phenomena can be practically performed and their results reasonably extrapolated to larger scales (i.e., the "ecological model system"-"microlandscape" approach championed by Wiens et al.1993). A number of studies on small mammals have, in fact, successfully employed such an approach (see Foster and Gaines 1991; Harper et al. 1993; Ims et al. 1993; Barrett et al. 1995; Diffendorfer et al. 1995).

It is clear that the methods by which organismal responses to spatial heterogeneity are studied at one scale may not work at larger scales. Consider the case of observational units and their replication. If individual home ranges were the focus of inquiry, a field study like ours could have sample sizes in the tens-to-hundreds (see Bowers et al. 1996); tests of fragment size effects, however, would include a maximum of only four or five replicate fragments; and tests at the landscape scale, with one continuous and one fragmented habitat matrix, would be unreplicated. Comparing fragments in one landscape to grids in the other, as we have done here, is an obvious case of pseudoreplication (Hurlbert 1984). A compounding problem is that as larger spatial scales are considered, large-scale gradients in exogenous factors become increasingly important (Levin 1992), further limiting the sort of inferences that can be made. For example, one reason why the fragment:grid ratios for *Peromyscus* were so much lower than the simulations predicted may have involved large-scale gradients in vegetation – i.e., more suitable areas in the continuous than the fragmented landscape. So even when landscape-scale experiments can be performed, it is likely that they will be pseudo-replicated and "quasi-experimental" in design (Hargrove and Pickering 1992).

This is not to say that landscape-scale studies of habitat fragmentation are without value. We, in fact, argue that they are currently a critical missing piece limiting the further development of a general theory of habitat fragmentation (see Stenseth 1985). Given that fragmentation will occur and will undoubtedly increase in the future (Forman 1987; Groom and Schumaker 1993), it is vital that scientists learn as much as possible, using the most rigorous methods available so that future land-management decisions can be based on real relationships and not unsubstantiated speculation (Hopkins and Saunders 1987). While we acknowledge the severe limitations inherent in treatment-control, landscape-scale studies like ours, we also believe they offer one means of quantifying larger-scale effects of habitat fragmentation that heretofore have not been considered.

Acknowledgements We thank E.F. Connor, S.L. Pimm, C.F. Sacchi, and an anonymous reviewer who made valuable comments on an earlier version of the manuscript. This research was supported by NSF grant DEB-920772

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