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Michael A. Bowers · Kristina Gregario
 Courtney J. Brame · Stephen F. Matter
 James L. Dooley Jr.

Use of space and habitats by meadow voles at the home range, patch and landscape scales

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Abstract Using capture/recapture methods, we examined the spatial usage patterns of *Microtus pennsylvanicus* within and between experimentally created habitat patches of three sizes (1.0, 0.25 and 0.0625 ha) and between a 20-ha fragmented and a 20-ha continuous habitat landscape. We tested the prediction that home ranges near patch edges would be qualitatively different from those in patch interiors, and that the edge:interior habitat ratio could be used to make predictions concerning the dispersion and spatial use of individuals occupying different sized patches and between landscapes with different habitat structure. We found adult females on patch edges to have larger and more exclusive home ranges, larger body sizes, longer residence times, and to reproduce at a higher frequency than those in patch interiors. These “edge effects” also appeared to be largely responsible for the greater proportion of larger, reproductive females we found in small than larger patches and in the fragmented than in the continuous habitat (control) landscape. The selection of higher quality edge habitats by dominant females and the relegation of sub-dominants to patch interiors provides an explanation for the observed differences in the distribution and performance of females over patches and between landscapes.

Key words Edge effects · Habitat patches · Home range · Landscape ecology · *Microtus pennsylvanicus*

Introduction

It is difficult to separate intrinsic differences in the performance of individuals from differences in the quality of habitats occupied (Bowers 1994). Many studies that demonstrate habitat differences in performance treat habitat variation at the between-habitat scale – with infer-

ences being made by comparing attributes of individuals and their environment averaged over some area (for small mammals this is typically a trapping grid). Such a coarse-grained approach assumes that the principal axis of habitat heterogeneity occurs at the level of grids. But it is the individual that chooses and occupies space, and it is the quality of the area occupied that, to some degree, determines whether an individual gives birth, dies or emigrates to another area. Discounting individualistic responses to small-scale habitat heterogeneity to focus on population averages is likely to produce weak tests of the importance of habitat variability and selection (Cockburn and Lidicker 1983; Lomnicki 1980).

Conducting detailed studies of individuals at large spatial scales is difficult. Averaging-out small-scale variability is one way of reducing the number of dimensions considered in studies of large-scale patterns (Wiens 1989). The larger the spatial extent considered the more likely it is that the responses of individuals will be treated as an average. Hence, landscape-scale studies have tended to focus on relationships between environmental heterogeneity (patchiness) and features of populations, communities and ecosystems rather than of individuals (Wiens et al. 1985, 1993). Wiens et al. (1993) argue that failure to include individualistic responses and multiple scales of resolution in landscape ecology have contributed towards a body of theory that is more descriptive than predictive.

If individuals really are the basic ecological unit (Stenseth 1985), and if there is a range of scales over which an organism might respond to habitat heterogeneity (O'Neill et al. 1986), then a detailed examination of how individuals use space offers a mechanistic way of predicting responses to different landscapes. In the case of small mammals, the standard measure of how individuals utilize space is the home range. Home ranges are operationally simple to define, and are one of the most commonly measured variables in animal ecology today. Variation in home range areas has been used to make inferences about food availability, habitat quality, breeding condition, and social organization (see Bowers et al. 1990 for review).

M.A. Bowers (✉) · K. Gregario · C.J. Brame · S.F. Matter
 J.L. Dooley Jr.
 Department of Environmental Sciences
 and Blandy Experimental Farm,
 University of Virginia, P.O. Box 175, Boyce,
 VA 22620, USA

Patterns of movement within and between home ranges allowed Van Horne (1982) to interpret landscape level patterns of survivorship, density, and reproduction in *Peromyscus maniculatus*. Home range area also provides a simple index of how an organism is scaled to particular features of its landscape: i.e., animals with large home ranges may be prohibited from occupying small habitat patches (Foster and Gaines 1991). That larger home ranges/territories of some birds are often found on the edges of isolated habitat patches and smaller ones in patch interiors (Krebs 1971; Wiens 1973) suggests that home range size may also vary at the within-patch scale. Explanations for this edge effect implicate home range defense: lower defense costs (fewer neighbors) and thus larger home ranges near patch edges than in more crowded patch interiors (see Stamps and Buechner 1985; Stamps et al. 1987). But as Diffendorfer et al. (1995) have shown, patterns of spatial use within patches are not separate from the usage of multiple patches by the same individual: i.e., if suitable habitat patches are smaller than home range areas, movement patterns and home range size expand so as to include multiple habitat patches.

Home ranges of small mammals, especially microtine rodents, are well-suited for detailed study of home range size variation at the landscape scale. Ims et al. (1993) studied spatial usage patterns of individual female *Microtus oeconomus* in continuous and fragmented habitat patches. Foster and Gains (1991) examined the response of *M. ochrogaster* populations (and that of two other species of small mammals) to habitat patches of different size, and Harper et al. (1993) studied home ranges of *M. pennsylvanicus* in habitat patches of the same size but of two shapes.

In this paper we examine spatial usage patterns of individual meadow voles (*M. pennsylvanicus*) using an experimental "microlandscape" approach (see also Foster and Gaines 1991; Robinson et al. 1992; Ims et al. 1993; Harper et al. 1993). We treat measures of individual performance and home range size as dependent variables and two experimentally created landscapes as treatments: a 20-ha unfragmented, continuous habitat landscape within which were 13 trapping grids of three sizes (1.0, 0.25, and 0.0625 ha); and an equal-sized fragmented landscape where all inter-grid areas were mowed, creating a system of 13 discrete habitat patches of three sizes. We tested three general hypotheses:

1. That home ranges on the edge of patches would be larger and more exclusive than those in patch interiors (see Stamps et al. 1987; Harper et al. 1993).
2. That as a result of high edge-to-interior ratios animals on small patches would have larger average home range size than those on medium or large patches.
3. That because of the edge effect noted above, average home ranges would be smaller in the continuous habitat landscape with no edge habitat than in the fragmented one with more edge.

In testing these hypotheses we consider a suite of variables in addition to home range size: i.e., the degree of

home range overlap, body size, persistence/residence times, and reproductive status. While other studies have used *Microtus* to test for patch edge/interior differences in home range size (Harper et al. 1993), and differences in spatial usage patterns over landscapes with different patch structure (Diffendorfer et al. 1995), our study treats a broader range of individualistic responses that might indicate overall habitat quality differences between edge and interior habitats. Our goal is to explore how individual performance varies according to home range position within and between patches, and then to project this response upwards in scale as a basis for interpreting patterns at the patch and landscape scales (see Van Horne 1983).

Field methods and design

Study site

We conducted our field study during 18 weeks, June through mid-October 1993, at the University of Virginia's Blandy Experimental Farm (BEF), Clarke County, Virginia (78°W, 39°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 (Bowers and Dooley 1993). In 1993 the field supported a mosaic of tall/dense stands (often >2.0 m) of thistle (*Carduus* spp.) between which were different mixtures of lower-growing herbs (i.e., *Daucus carota*, *Ambrosia*, and *Galium*) and grasses (*Festuca*, *Dactylis*, *Lolium*, and *Poa*).

Rodent community

The rodent community was comprised of two common species: white-footed mice (*Peromyscus leucopus*), and meadow voles (*Microtus pennsylvanicus*); house mice (*Mus musculus*), and deer mice (*Peromyscus maniculatus bairdii*) made up less than 1% of the resident individuals and are not considered further here. In 1993, *Microtus pennsylvanicus* accounted for more than 86% of the individuals and 84% of the captures. Because of the relatively low abundance of *Peromyscus*, especially in the fragmented part of the field, we restrict our analyses to *Microtus*.

Landscape design

We used mowing to create two types of landscapes: a fragmented landscape with 13 unmowed patches embedded in a mowed matrix; and an identically configured control landscape where traps were placed in grids rather than in habitat fragments and inter-grid areas were not mowed (Fig. 1). Mowing in the fragmented landscape was initiated in May 1993 and was repeated throughout the summer when vegetation reached 20 cm in height. Each landscape included four replicates of medium (0.25 ha), large (1.00 ha) and five small (0.0625 ha) patches/grids. Patches/grids were separated by mowed, "uninhabitable" areas (fragmented landscape) or unmowed vegetation (continuous landscape) of at least 50 m. Mowing reduced the amount of inhabitable area in the fragmented landscape by c. 50% and created c. 3 km of "edge habitat" that was absent in the continuous (control) landscape. 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 or that included different grids/patches (see Bowers and Dooley 1993; Dooley 1993). Consequently, both patches and grids represent largely separate entities.

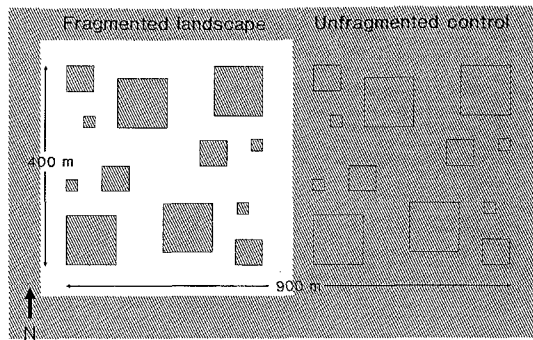


Fig. 1 Landscape design used in our field study. Inhabitable areas for small mammals are unmowed (*shaded*) and uninhabitable areas are mowed (*unshaded*). There were four replicates of three patch sizes (1.0, 0.25, and 0.0625 ha) positioned in four satellite groups within each landscape type – one that 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

Justification for the design of the patch “landscape” (i.e., the size, dispersion, shape, interpatch distances, and degree of replication) was based on a two-year study of rodent abundances and movement patterns in the field, details of which are given in Bowers and Dooley (1993), and Dooley (1993). 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 both rodent abundances and edge:interior ratios would vary markedly.

Rodent censuses

Small mammals inhabiting patches in the fragmented and grids in the continuous habitat landscape were censused by capture/recapture during the 18-week period from 1 June to 10 October 1993. Two folding Sherman live traps were placed at stations with 12.5 m spacing 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, sexual condition, and weight. Traps were locked in open position between trap sessions to allow free exploration and aeration.

We alternated censuses week-to-week between the two landscapes: traps were run 3 consecutive nights/week in one landscape and then shifted to the other the next week. In this paper we focus on spatial usage patterns; forthcoming papers will detail density differences.

Data analyses

We classified all captured animals as either transients or residents: transients were animals that were captured only in one week or animals captured on different patches/grids in different weeks; residents were animals captured on the same patch/grid over at least two different census periods (over at least three weeks). We used pelage and weight at first capture to categorize individuals as adults (generally >32 g) or sub-adults (<32 g).

We estimated home range size for residents using capture data and the convex-polygon or minimum-convex-polygon method (Jenrich and Turner 1969; Madison 1985). Home range size estimates made by this method, however, are extremely sensitive to capture number. How many captures then does one need to estimate home range size? This is not a trivial issue because requiring

a large number of captures would decrease our sample size while using too few captures would produce poor home range estimates. To answer this question we performed simple regression analyses of estimated home range size with animals captured a minimum of three to six times each. For animals with well-established home ranges, the home range estimate should increase with capture number up to a point and then level off. By performing a series of regressions where the minimum number of captures per individual was incrementally increased estimates of this capture threshold were possible.

Our hypotheses are based on the notion that there may be differences in the home ranges and general performance of individuals living in the interior and on the edge of patches. We used a simple metric to categorize position within patches: the shortest distance from traps within an individual’s home range to the edge of a patch. Animals captured at a trap on the edge of patches were scored as being on the edge; those captured entirely in patch/grid interiors and away from edges were scored as being in patch interiors.

We used ANOVA to test whether home range size of residents living on the edge of medium and large patches differed from those in patch interiors (hypothesis 1), whether home ranges were larger in the smaller than the larger habitat fragments (hypothesis 2), and whether home ranges were larger in the fragmented than the continuous habitat landscape (hypothesis 3). Separate analyses of home range size were performed for each sex by age category using logarithmically transformed home range estimates.

Comparing home ranges between landscapes (hypothesis 3), however, is not straightforward because the home ranges of “captured” individuals in fragments are totally confined to the census area, while those in the unfragmented landscape may include to varying degrees areas both on and off the trapping grid (see Otis et al. 1978). To eliminate individuals in the continuous habitat landscape whose home ranges included areas off grids (and who would have incomplete data to estimate home range size), we limited tests of landscape differences to those individuals captured in the interior of just large patches/grids (animals captured at edge stations or on medium or small patches/grids were dropped from the analyses). As a check on home range size estimates we also used ANOVA to test whether there were differences in the time periods over which home range estimates were made for the different patch sizes, and the total number of captures and stations over which home ranges were estimated.

Persistence (residency-time) distributions were constructed for adult male and female individuals living in the continuous habitat landscape, and separately for those on patch edges and patch interiors in the fragmented landscape. Persistence was expressed as the percent of resident animals remaining in a patch over subsequent weeks. A Kolmogorov-Smirnov two-sample test for large samples (Siegel 1956) was used to test for patch location and landscape differences in these distributions. We also used regression analyses to fit residency time distributions to exponential distributions and compared the “decay” exponents with *t*-tests.

Home range overlaps were tallied separately for resident animals in the four demographic groups and with respect to whether home ranges were on the interior or edge of patches. Overlap was measured categorically: either a home range was used exclusively by the resident or it was also used by other individuals (including other residents and transients). Overlap/no-overlap categorization was limited to those individuals who were present during the same time (trapping) period(s). Home range overlaps were summarized as counts of individuals with and without exclusive home ranges, living on patch interiors or edges, and were analyzed using contingency table analyses.

We also tested for differences in the reproductive performance and body weights (non-pregnant) of adult females between interior and edge habitats, among the different habitat fragment sizes, and between the two landscapes. The number of pregnant versus non-pregnant females for interior and edge habitats, for the three patch sizes, and over the two landscapes was tested using contingency table analyses. Body weights (logarithmically transformed) were tested using ANOVA.

Results

General

We captured 2,569 *Microtus* individuals over both 20-ha landscapes during the 18 weeks of trapping; 976 of these were categorized as residents and 1593 as transients. An average of 169 ± 56 (SE) resident *Microtus* were captured per week in the fragmented landscape and 216 ± 52 in the continuous habitat control. Resident individuals were captured an average of about four times each over an average period of 7–8 weeks.

Home range estimation

Estimates of home range size generally increased with the number of times an individual was captured up to an asymptote of c. four captures (Fig. 2). Home range areas were positively correlated ($P < 0.01$) with numbers of captures for individuals captured two or more times: adult females, $r = 0.35$, $n = 376$; adult males, $r = 0.47$, $n = 206$; sub-adult females, $r = 0.34$, $n = 171$; sub-adult males, $r = 0.33$, $n = 127$. Restricting the analysis to individuals captured at least three times showed a marked decrease in the magnitude of the correlations

(respectively, $r = 0.27$, $n = 236$; $r = 0.39$, $n = 110$; $r = 0.13$, $n = 101$; $r = 0.21$, $n = 60$). Finally, restricting the regression analyses to individuals captured a minimum of four times showed no significant relationship ($P > 0.05$) between home range size and number of captures for any of the four demographic groups: respectively, $r = 0.12$, $n = 157$; $r = 0.27$, $n = 58$; $r = 0.14$, $n = 69$; $r = 0.24$, $n = 30$. However, there was a trend for both adult and sub-adult male home ranges to increase with increasing number of captures beyond the four capture threshold (Fig. 2). That such a trend was not evident for females is consistent with Madison (1980) who found that female *M. pennsylvanicus* exhibited greater site tenacity and fewer shifts in home ranges than did males. Four captures appear to be the minimum number needed to estimate home range size with some degree of certainty, at least for the focal group of adult females (see also Fig. 2). All estimates of home range size are based on a minimum of four captures per individual (individuals with fewer captures were not included in the analyses).

Fig. 2 Estimated home range size (in m^2) expressed as a function of the minimum number of captures per individual, and for the four demographic groups of *Microtus*. Standard errors are also given

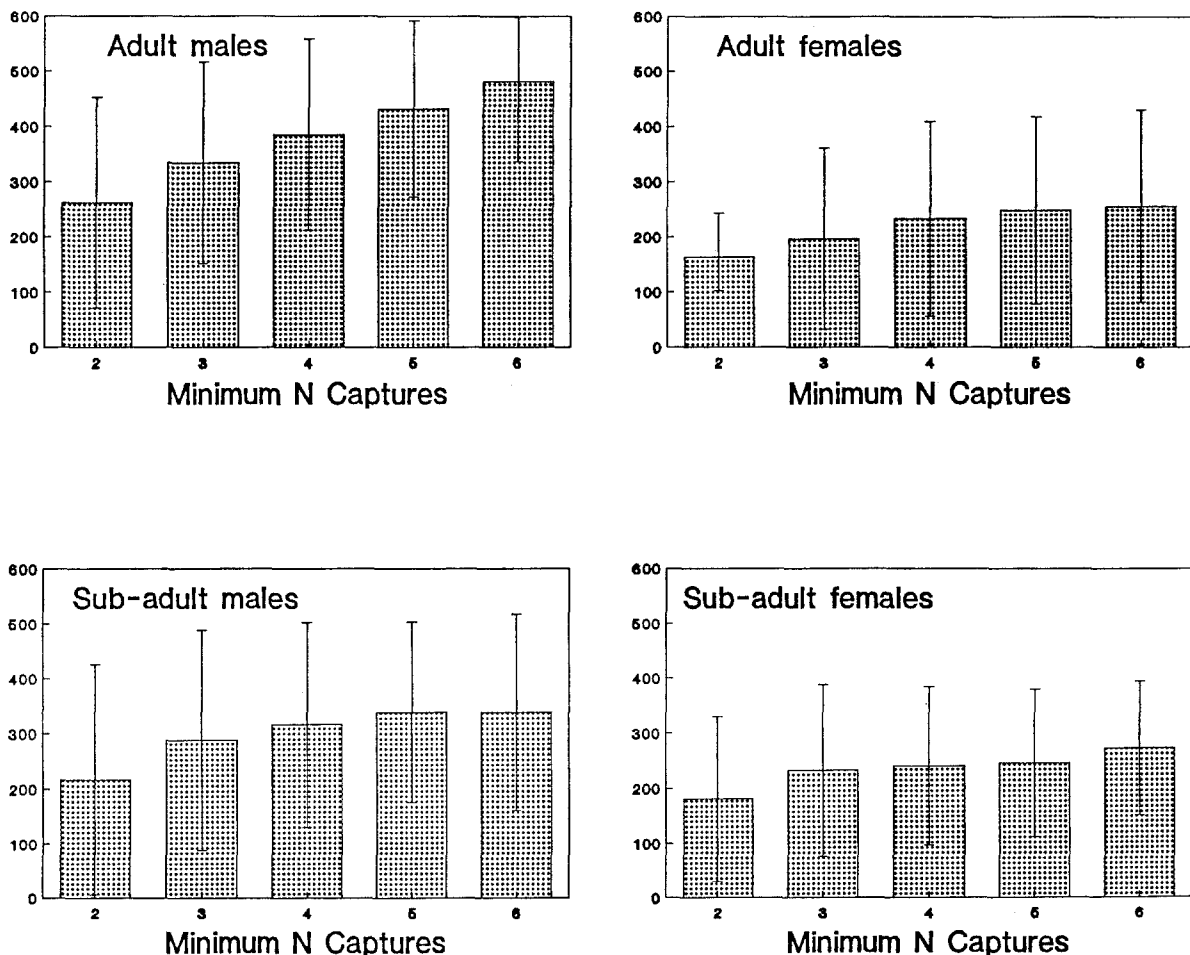


Table 1 Comparison of home range size, body mass, % individuals observed pregnant, and residence times for adult female resident *Microtus* on medium and large patches listed for edge and interior habitats (fragmented landscape only)

	<i>n</i>	Home range size m ² (+sd)	Body mass g (+SD)	% Pregnant	Residence wk (+SD)
Edge	43	252 (167)	47 (9)	63 (27/43)	13.7 (9)
Interior	40	183 (163)	43 (8)	50 (20/40)	10.1 (6)

Home range overlap

Concurrent use of resident home ranges by other resident and transient individuals was low. Over both landscapes and all patches/grids 81% of the home ranges were used exclusively. In the fragmented landscape, home ranges on patch edges tended to be more exclusive than those in patch interiors: 12 versus 28%, respectively, showed some overlap ($\chi^2 = 78.4$, $df = 1$, $P < 0.01$). Of the adult females on patch edges 23% overlapped with adult males compared to 38% in patch interiors. Overall, 9% of adult females with home ranges on patch edges shared their home ranges with other females while this figure was significantly greater (15%) in patch interiors ($\chi^2 = 6.32$, $P < 0.05$). Overlap was highest for adult males in patch interiors (55%). Transient individuals of all groups were captured in c. 4% of home ranges of adult female residents on patch edges and in 12% of those in patch interiors ($\chi^2 = 5.23$, $df = 1$, $P < 0.05$). For all comparisons, overlap tended to be greater for male residents than females and in patch interiors than on edges.

Test of patch position effects

Adult females residing on the edge of medium and large patches tended to have significantly larger home ranges than those in patch interiors ($F_{1,77} = 3.2$, $P = 0.07$; see Table 1). The general shape of female home ranges also varied according to proximity to patch edges. Specifically, there were negative correlations between the distance from patch edges and (1) the home range diameter (m) parallel to the nearest patch edge, and (2) the ratio of home range dimensions parallel-to-perpendicular the nearest patch edge (for adult females in large patches, respectively, $r = -0.45$, $n = 49$, $P < 0.01$; $r = -0.34$, $n = 49$, $P < 0.01$). Hence, home ranges near patch edges tended to be more linear with the the long dimension of an individual's home range running parallel to the edge while in patch interiors home ranges were more symmetrical. Adult and sub-adult males on the edge of patches, however, had home ranges that were not different in size or shape from those in the interior (both $P > 0.70$).

Adult females on edges also showed longer mean residency times ($F_{1,81} = 4.8$, $P = 0.03$), and had larger body sizes ($F_{1,81} = 3.65$, $P = 0.06$) than those in the interior of patches (Table 1). Moreover, a higher proportion of adult resident females living on patch edges were observed pregnant than those in patch interiors ($\chi^2 = 3.36$, $P = 0.07$). Sub-adult females and all males showed no difference (all $P > 0.30$) in body mass or residency time

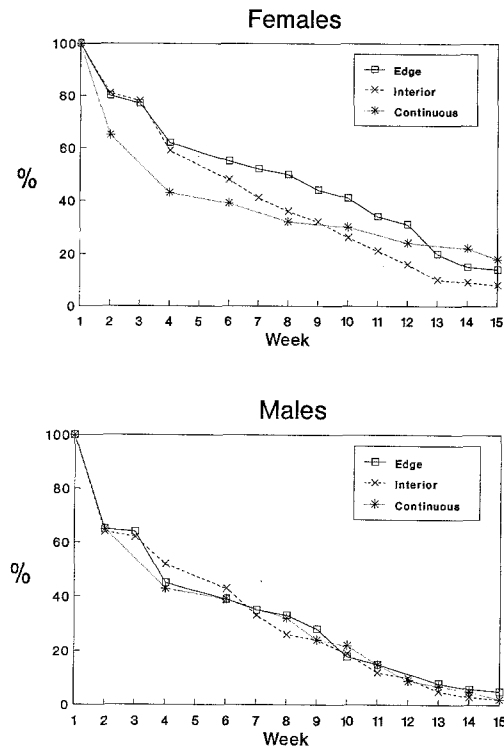


Fig. 3 Persistence "curves" for adult female (above) and male (below) *Microtus* listed separately for individuals in the continuous habitat landscape and for those on patch edges and interiors in the fragmented landscapes (medium and large patches only). Persistence is defined as a proportion of those individuals who remain in a home range over subsequent weeks (see text for more detail). Using regression analyses to estimate the exponential decrease in persistence over weeks, respectively as d , Y , and W , in the equation $Y = BW^d$, yielded the following estimates for d : females on patch edges, -0.65 (SE = 0.108); females in patch interiors, -0.93 (SE = 0.133); females in the continuous landscape, -0.58 (SE = 0.03); males on patch edges, -1.02 (SE = 0.16); males in patch interiors, -1.25 (SE = 0.23); and males in the continuous control, -1.14 (SE = 0.23)

with edge/interior position within patches. Females on patch edges also persisted on patches longer than those in patch interiors or for males in general (Fig. 3). Males on patch edges did not have different survivorship schedules than those in patch interiors ($P > 0.50$).

Contingency table analyses showed that transients were observed in greater than expected frequencies in patch interiors than on the edge. For large patches, 58% of the traps were within patch interiors but they captured 70% (90) of the adult male and 72% (92) of the adult female transients. The expected capture frequencies on patch edges was 42% compared to observed values of 30% for transient males and 28% for females (χ^2 values

Table 2 Comparison of home range size, body mass, % individuals observed pregnant, and residence times for adult female *Microtus* listed by landscape type and patch size (fragmented landscape only)

	<i>n</i>	Home range size m ² (±SD)	Body mass g (±SD)	% Pregnant	Residence wk (±SD)
Fragmented	83	219 (167)	45 (8)	54 (45/83)	12.0 (7.6)
Small	4	141 (108)	50 (11)	75 (3/4)	6.8 (7.1)
Medium	12	216 (122)	46 (6)	60 (7/12)	12.4 (13.0)
Large	67	224 (177)	45 (9)	52 (35/67)	12.2 (6.2)
Continuous	87 ^a	282 (153)	41 (6)	38 (33/87)	10.7 (7.1)

^a Including only individuals trapped at interior traps on large trapping grids

Table 3 Comparison of home range areas, number of captures, and weeks between first and last capture for *Microtus* in the fragmented and continuous landscapes. Comparisons include animals captured on just large and medium patches and whose home ranges included interior stations (not those on the edge). Standard deviations are given in parentheses

Demographic group	Landscape	<i>n</i>	Home range m ² (±SD)	<i>n</i> Captures (±SD)	<i>n</i> weeks weeks(±SD)
Adult male	fragmented	9	465 (236)	5.0 (1.33)	10.6 (10.8)
	continuous	8	367 (132)	4.6 (0.52)	10.5 (2.9)
Sub-adult male	fragmented	3	301 (65)	5.3 (1.53)	8.0 (5.3)
	continuous	7	306 (107)	5.0 (1.30)	8.6 (5.0)
Adult female	fragmented	39	188 (163)	5.7 (1.8)	10.3 (5.5)
	continuous	24	282 (153)	6.5 (2.4)	10.2 (5.8)
Sub-adult female	fragmented	7	113 (65)	4.6 (1.1)	8.7 (4.2)
	continuous	26	283 (157)	5.7 (2.6)	8.8 (5.5)

of 8.2 for males and 10.5 for females; both $P < 0.01$). By comparison, resident adults tended to be captured more frequently near the edges of patches than in interiors: 52 and 50% of females and males, respectively, were captured on patch edges even though only 42% of the traps were categorized as edge traps (χ^2 for female residents of 3.06, $P < 0.10$). The difference in the dispersion of transients and residents on patch edges versus interiors was highly significant ($\chi^2 = 27.3$, $df = 1$, $P \ll 0.01$)

Tests of patch size

There were no significant differences in home range size among habitat fragments of different size for any of the four demographic groups (Table 2). However, there was a slight tendency for adult males to have larger home ranges in the larger patches ($P = 0.37$). There were no differences in the number of times individuals were captured or the time interval between first and last capture for patches of different size ($P > 0.40$).

There was a trend for adult female residents on small patches to be of larger body size, and to reproduce more frequently in small than medium or large patches (Table 2). Persistence of adult females was lower on small than large patches (Table 2).

Tests at the landscape level

Adult and sub-adult female *Microtus* had significantly smaller home ranges in the fragmented landscape than in

the continuous habitat control (respectively, $F_{1,61} = 5.21$, $P = 0.02$, and $F_{1,31} = 7.62$, $P < 0.01$; Table 3). This difference can not be attributed to differences in the number of times females in the two landscapes were captured or the time-span between first and last capture (Table 3). By contrast, adult and sub-adult males appeared to have comparably sized home ranges sizes in the two landscape types (respectively, $F_{1,15} = 0.6$, $P = 0.45$ and $F_{1,8} = 0.01$, $P = 0.95$). However, tests of differences in male home ranges have low sample sizes; there is, in fact, a slight tendency for adult males to have larger home range areas in the fragmented landscape.

There were more adult females captured in the fragmented than the continuous landscape (267 versus 248) despite the fact that more than one-half of the fragmented landscape was mowed. The average body size of adult resident females was significantly greater ($F_{1,168} = 11.6$, $P < 0.01$) and a higher proportion were observed pregnant (54 versus 38%; $\chi^2 = 4.37$, $P = 0.04$) in the fragmented than the control landscape (Table 2). Adult female residents persisted for an average of 11.9 weeks (standard deviation ± 7.6) in the fragmented and 10.7 (± 7.1) weeks in the continuous habitat landscape.

Discussion

The prediction that home ranges would be larger and more exclusive on patch edges than in patch interiors was supported for female but not male voles. However, male voles, with more loosely defined and undefended home ranges (Madison 1980), would not be expected to

show the same response as female *Microtus* who have been shown to actively defend territories, especially against other females (Wolff 1985). Hence, our results appear to be consistent with the intruder pressure hypothesis of Stamps et al. (1987). Our results, however, document a more substantive response to patch edges than just that involving adjustments in home range size. Specifically, we found females inhabiting home ranges on patch edges to have greater body weights, higher persistence times, more exclusive home ranges, and to reproduce more frequently than those with home ranges in patch interiors or the continuous habitat landscape. We also found that home range shape varied according to proximity to patch edges and that a disproportionate number of residents were found near patch edges and a disproportionate number of transients in patch interiors.

We feel that many of these differences, especially the uneven distribution of large, reproductive females, is consistent with the notion that edge habitats may represent higher quality home range sites than interior habitats. Other studies have reported relationships between small-scale habitat heterogeneity and individual performance of voles, especially adult females (Lloyd 1970; Cockburn and Lidicker 1983; Wolff 1985; Sheridan and Tamarin 1988; Jones 1990). Our results project this individualistic pattern to the landscape scale.

Ostfeld et al. (1988) argued that differences in microhabitat quality could account for differences in both home range attributes and reproductive success of *M. pennsylvanicus* females. However, Ostfeld et al. (1988) did not discuss if the response of individuals to such variation might follow a lottery model of habitat occupancy or one of active habitat selection/relegation. The pattern of larger females occupying the higher quality edge habitats with smaller females in patch interiors implicates a model of despotic habitat selection and pre-emption: larger, more dominant female voles selecting edges and relegating smaller, subdominant and transient females to patch interiors. Ostfeld et al. (1988) also found that reproductively successful females had lower intra-sexual home range overlap than reproductively less successful ones and invoked a territory defense explanation. Not only is this explanation consistent with the edge-to-interior differences in body size, persistence times, and reproductive frequency, but it also provides a partial explanation for the observation that overlap was less for females on patch edges than in patch interiors. If dominant individuals tend to occupy patch edges rather than interiors, then one might expect transient individuals to be captured more often in patch interiors than along edges – a prediction that is consistent with our results.

The suggestion that patch edges are of higher quality and are preferred over interior habitats is counter to much of the recent literature on edge effects (Harris 1984; Yahner 1988). Bowers and Dooley (1993) found that seed removal by the rodent community (including *Microtus*) was lower on patch edges on bright moonlit nights than in patch interiors, and argued that the avoid-

ance of predation was the mechanism responsible – animals on edges on bright nights may be particularly susceptible to predators. Given that *Microtus* is more diurnal (or crepuscular) than nocturnal suggests that the responses measured by Bowers and Dooley (1993) may have been for more nocturnal species, especially *Peromyscus leucopus*. There is, in fact, evidence suggesting that *Microtus* may tolerate or even prefer patch edges. Harper et al. (1993) found no difference in the population densities of *M. pennsylvanicus* between artificially created habitat patches with different edge-to-interior ratios, and concluded that this species is edge tolerant. Getz (1985) argued that much of the biology of *M. pennsylvanicus* is oriented towards living in small, isolated and ephemeral habitat patches. Such habitats would be characterized by having large amounts of edge.

Diffendorfer et al. (1995), in a study somewhat similar to ours, reported that when habitat patches are smaller than the size of home ranges animals expanded their home ranges to include multiple patches. Further, they reported a net-movement of animals from highly fragmented areas comprised of many small patches towards less fragmented blocks of larger patches. But the study of Diffendorfer et al. (1995; see also Foster and Gaines 1991) used small patches that were about 20 times smaller than our small patches, medium-sized patches that were about twice as small as our medium patches, and large patches that were one-quarter the size of ours. The results of Diffendorfer et al. (1995) suggest that there is a minimum patch size that is acceptable for *Microtus*. Our study suggests that once that minimum size is reached, smaller patches with proportionately more edge may be preferred over larger ones.

In our study patch edges represented boundaries between unmowed habitats that were clearly inhabitable to *Microtus* and uninhabitable, mowed areas. Baker and Brooks (1982) have shown that predation on *M. pennsylvanicus* varied inversely with the amount of vegetation cover, and that *Microtus* actively selected sites with high amounts of cover. Thus, patch edges probably have a higher risk of predation than sites in patch interiors. But it is also clear for *Microtus* that effects of cover are largely separate from that of food (Krebs and DeLong 1965; Desy and Batzli 1989). Our results, in fact, seem to suggest that the quality of forage may be higher on and adjacent to patch edges than in patch interiors. There are two points to consider. First, companion studies to the one presented here (M.A. Bowers, unpublished work) have failed to detect any significant differences in vegetation structure or composition between edge/interior habitats. Second, it is clear from other studies (for review see Belsky 1986) that frequent mowing has the effect of increasing net productivity, plant growth rates, and palatability of vegetation for herbivores. This means that the early-growth vegetation around the periphery of patches may be more palatable and nutritious to *Microtus* than the older, unmowed plant material within patch boundaries. So while patch edges may be somewhat more risky to occupy, it may be that the availability of

highly palatable forage more than makes up for the risk. Given that home ranges along patch edges tended to be more linear than those in interior habitats, and that the longest home range axis typically ran parallel to that of patch edges, suggests a high affinity for patch edges. Thus, in our experimental system *M. pennsylvanicus* appears to be an edge-seeking species.

The edge effect we have documented for female voles is a response to habitat heterogeneity at a scale above that of the microhabitat and a scale below that of whole patches; it is more in line with what has been referred to as a macrohabitat response (see Bowers and Dooley 1993). We suggest that the response of individuals (especially adult females) to patch edges provides a mechanistic explanation for differences in population performance and structure at both the patch and landscape scales (respectively, hypothesis 2 and 3). This is consistent with the observation that female voles in smaller patches with higher ratios of edge habitat were of larger average body size and reproduced more frequently than those in large patches with lower amount of edge. By similar reasoning, the fragmented landscape with an additional 3 km of edge habitat appears to be of higher overall quality than the continuous landscape with no edge habitat. Hence, for *M. pennsylvanicus* in our experimental system a hierarchical approach to understanding landscape-level patterns seems to work.

Our results only partially supported the model of Stamps et al. (1987). While we did find home ranges of females to be larger on patch edges than in patch interiors in the fragmented landscape (in support of hypothesis 1), we also found that this difference also involved changes in home range shape. Home ranges were also larger, on average, in the continuous habitat landscape with no edge habitat compared to those in fragments, and we found no difference in home range size among patches with very different ratios of edge:interior habitats. The latter two results are not consistent with Stamps et al. (1987; see hypotheses 2 and 3).

It may be that a hypothesis based only on intruder pressure and home range defense and that does not account for differences in habitat quality is too simplistic to be of much predictive value in field tests. For example, while Stamps et al. (1987) predict that home ranges might be of larger size in the fragmented than those in continuous habitat landscape (because of lower intruder pressure in the former), the theory does not account for landscape differences in the quality of home ranges that may also be related to patch edges. Other studies have shown home range size in female *Microtus* to be more sensitive to habitat quality than to defense costs (Ostfeld and Klosterman 1986; Ims 1987). Ostfeld et al. (1988) found female voles that reproduced to have home ranges 2–3 time smaller than those that did not. Female voles which are able to satisfy their daily energetic needs in a smaller area may be freed from energetic expenditures of moving through and defending larger areas. Females in better habitats with small home ranges may then be able to expend more energy for reproduction. The relative

small degree of home range overlap we found suggests that home range size probably reflects local habitat quality more than the defense of sites from neighboring individuals (see also Ostfeld et al 1988). In any event, the opposing forces of intruder pressure and habitat quality may confound any edge/interior trend as simple as that predicted by Stamps et al. (1987).

One goal of our studies is to connect the small-scale individualistic responses of the sort we report here with that occurring at the population level and over longer time periods (see Wiens et al. 1993). After all, many of the issues in landscape ecology revolve around population responses and dynamics rather than behavior. It is well known, especially for small mammals, that behavioral interactions among conspecifics is related to demographic composition, spatial usage patterns, and population dynamics (Krebs 1970). It might be that small patches operate as sources for recruits and that larger, more continuous patches operate as sinks. Or it might be that the spatial usage patterns we report here have little consequence to the population. Analysis of longer-term data from our system should help answer these questions.

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