

## Habitat Fragmentation and the Perceived and Actual Risk of Predation

Stephen F. Matter, John F. Zawacki, and Michael A. Bowers,  
Department of Environmental Sciences, University of Virginia,  
Charlottesville, VA 22903 and The Blandy Experimental Farm  
Boyce, VA 22620

### ABSTRACT

We used live-trapping and tethering trials to evaluate differences in both predatory risk assessment and actual predatory events for two small mammal species in fragmented and unfragmented (control) landscapes. We found no difference between the mean number of individuals captured in the fragmented or unfragmented landscapes for either species, however *Peromyscus leucopus* tended to be captured less frequently near patch edges in the fragmented treatment; *Microtus pennsylvanicus* did not exhibit this response. The total number of predatory events was low over both the fragmented and unfragmented landscapes. Two confirmed predation events, out of a total of 40 trials, occurred in the unfragmented landscape suggesting if any difference in actual predation risk exists it may be greater in continuous than in fragmented landscapes. The combination of these results indicates that edge avoidance may be an innate response to habitat structure rather than to the actual risk of predation.

### INTRODUCTION

Habitat fragmentation has been shown to lower species abundance/density, increase the probability of local extinction, and alter community structure (for reviews see Simberloff, 1988; Saunders et al., 1991). Several studies have also suggested that predation may be greater in fragmented than in continuous habitats. Andrén et al. (1985) reported that predation by corvid birds on artificial nests resembling those of woodland grouse tended to increase with increasing amount of fragmentation, and demonstrated that the proportion of nests preyed upon within woodlot fragments increased towards habitat edges (Andrén and Angelstam, 1988). Increasing woodlot fragmentation also resulted in increased corvid density (Andrén, 1992). However, because the preferred habitat of corvids, cropland, also increased with woodlot fragmentation it is not clear whether increasing densities were related to fragmentation *per se* or changes in habitat. Bowers and Dooley (1993) found seed removal by small mammals, particularly during full moon periods, to be higher in patch interiors than on patch edges, and interpreted this as a predator avoidance response.

From the perspective of a prey species, predation can be partitioned into two distinct components: the perception of predatory risk and actual predation. It is important to note that avoidance of areas perceived to be 'risky' may be an innate behavioral response and unrelated to the actual risk of predation or an individual's experience e.g. the general avoidance of open areas by small mammals (Lima and Dill, 1990). Separating these components of predation is important. Actual predation may be a rare event, however the impact of predation on an individual basis is quite severe. Hence

we may expect behavioral responses to be overly sensitive to regions of differing predatory risk.

Habitat fragmentation may affect both the perceived risk of predation and the actual rate of predation. Because fragmentation often results in the imposition of habitat edges, if a prey species perceives habitat edges or ecotones to be 'riskier' areas, these areas may be avoided and under-utilized, whereas habitat interiors may be viewed as safer and proportionally over-utilized (Bowers and Dooley, 1993). A variety of mechanisms have been proposed to account for greater predation rates in fragmented habitats. Success by 'edge predators' that forage on habitat peripheries may be increased by the introduction of habitat edges (Andrén and Angelstam, 1988). Fragmentation may also create localized patches containing prey species that can be more efficiently exploited by predators (Weins, 1976; Taylor, 1976a). Finally, habitat fragmentation may increase the diversity of a landscape thereby increasing the number of predatory strategies that can be supported, ultimately increasing the overall predation rate (Wolff, 1980; Keith, 1983; Andrén et al., 1985; Andrén, 1992).

The main objective of our research was to examine behavioral responses possibly related to predator avoidance in relation to the actual predatory risk for small mammals residing in fragmented and unfragmented landscapes. Based on previous work by Bowers and Dooley (1993), we hypothesized that in a fragmented landscape patch edges would be avoided and that predation rates would be greater than in a similar continuous landscape.

## METHODS

We conducted our study June through August 1993, at the University of Virginia's Blandy Experimental Farm (BEF) located in the Northern Shenandoah Valley, Clarke County, Virginia. The study site was a 20 ha old-field, bounded by a 50 ha mature oak-hickory woodlot, the Orland E. White arboretum, and a commercial alfalfa field. Prior to 1986 the site was used primarily as pasture, but has been unmanaged since. Subsequently, the field has come to be dominated by successional species such as *Carduus acanthoides*, *C. nutans*, *Celastrus scandens*, and *Rhus radicans* as well as several grasses eg. *Dactylis* sp., *Agrostis* sp., and *Festuca* sp. (for a complete vegetational description see Bowers, 1993).

## Study Species

The meadow vole (*Microtus pennsylvanicus*) and the white-footed mouse (*Peromyscus leucopus noveborcensis*) were the dominant small mammals. Although *P. leucopus* is generally considered a woodland species, at BEF it also inhabits early-successional old-fields (Halama, 1989; Dooley, 1993; Bowers and Dooley, 1993).

Mammalian predators observed at BEF include: red fox (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and feral cats (*Felis catus*). The northern short-tailed shrew (*Blarina brevicauda*) was occasionally captured during trapping and has been reported as a predator of juvenile *Microtus* (Getz et al. 1992). Avian predators include red-tailed hawks (*Buteo borealis*) and barn owls (*Strix pratincola*). Snakes and other predators capable of feeding on *Peromyscus* or *Microtus* are seldom observed at BEF, but may also be present.

### Experimental Design and Trapping Protocol

We established eight 50 x 50 meter patches/grids: four patches were in a fragmented treatment, isolated from other patches and surrounding vegetation by 25m wide mowed areas; and four trapping grids within unmanipulated, continuous vegetation which served as controls (Figure 1). The arrangement of patches/grids in the fragmented and unfragmented treatments was not identical due to logistic constraints. Twelve large folding Sherman live traps were used per patch/grid to quantify habitat use by small mammals. One trap was placed at each corner of each patch/grid, one on the middle of each side, and four traps, separated by 10 m, in the interior (each interior trap was 25 m from the nearest corner). This pattern provided four interior traps, four traps on edges, and four traps on the corners of each patch/grid. For patches, corner traps were surrounded by 25 % cover, and edge traps by 50 % cover. Corner and edge traps for grids and all interior traps were completely surrounded by unmanipulated vegetation. Vegetation around patches was initially mowed one month before trapping began, and subsequently when vegetation reached 12 cm in height.

Live trapping was conducted once per week from July 6 to August 3, 1993. Traps were baited with peanut butter approximately 2 hours before sunset and checked at dawn the following morning. Upon initial capture, individuals were tagged and toe-clipped for identification, and species, sex, age, reproductive condition, and weight were recorded. Between trapping sessions traps were locked open to allow free exploration.

To assess actual predation risk between the experimental landscapes, *Peromyscus* captured in a nearby woodlot were tethered using 20 cm of steel cord secured to the ground. To exclude avian predation and allow for identification of terrestrial predators, mice were also tethered in a similar manner within large Hav-a-heart traps. Each patch/grid had one tethering station on a randomly selected edge. Two patches/grids within each landscape had open tetherings while the other two patches/grids had avian exclusion tetherings. Five trials were run, totaling 40 tetherings. Mice were tethered in the evening prior to baiting and checked the following morning. Mice were scored as surviving, injured, preyed upon (evidence of remains), or missing (either escaped or no evidence of predation).

### Statistical Analyses

To evaluate differences in spatial usage patterns between landscapes, we examined the proportion of captures at each trap type (corner, side, or interior) using repeated measures analysis of variance (RMA). Trap location and landscape type were the between subjects factors while trapping date was the within- subjects effect. Data were expressed as the proportion of captures at each trap type, and were angularly transformed prior to analyses (Sokal and Rohlf, 1981). To test for differences in abundance between fragmented and unfragmented landscapes, the mean number of individuals captured per patch/grid was evaluated using Student's t-test. All tests were conducted separately for each species.

## RESULTS

Over seven trap sessions (672 trap nights), 75 *Peromyscus* and 92 *Microtus* individuals were captured a total of 136 and 110 times, respectively. No difference in the mean number of individuals captured over the seven trap periods in fragmented

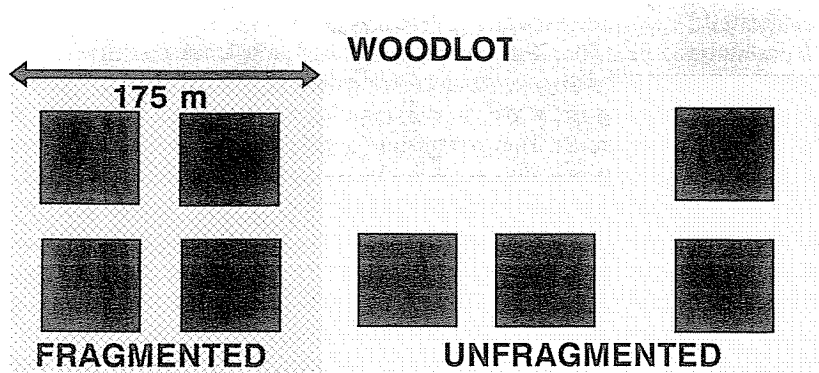


FIGURE 1. Experimental design and landscape configuration. Dotted areas indicate unmowed vegetation (unfragmented), while cross-hatched regions indicate mowed vegetation (fragmented). The grey area represents an oak-hickory woodland. Solid black squares symbolize trapping grids within the continuous region and patches within the fragmented region. Each patch/grid was 50 x 50 m, and separated from the nearest patch/grid by 25 m.

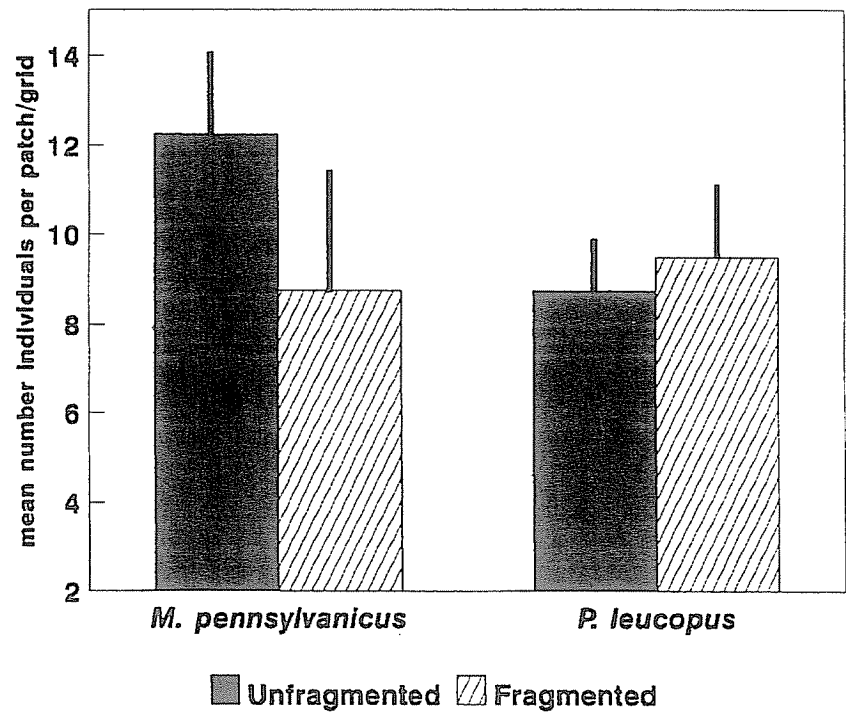


FIGURE 2. Mean number of individuals ( $\pm$  SE) trapped within patches in the fragment and control landscapes over the seven trap periods.

versus unfragmented patches was found for either *Microtus* ( $t=0.82$ ,  $df=6$ ,  $p=0.44$ ) or *Peromyscus* ( $t=-0.13$ ,  $df=6$ ,  $p=0.90$ ) (Figure 2).

TABLE 1. Analysis of variance table based on the mean proportion of traps occupied by *Peromyscus leucopus* (arcsine square root transformed). Main effects tested were fragmentation (frag) and trap position (corner, side, interior) (zone). Trapnight (nite) was the within subjects factor.

Source of Variation	SS	DF	MS	F	P
WITHIN CELLS	3.19	18	0.18		
CONSTANT	21.32	1	21.32	120.19	0.000
FRAG	0.03	1	0.03	0.19	0.669
ZONE	0.27	2	0.13	0.76	0.483
FRAG BY ZONE	1.26	2	0.63	3.54	0.050
Within-Subject Effect					
Source of Variation	SS	DF	MS	F	P
WITHIN CELLS	9.31	108	.09		
NITE	2.08	6	0.35	4.02	0.001
FRAG BY NITE	0.62	6	0.10	1.21	0.308
ZONE BY NITE	0.69	12	0.06	0.67	0.776
FRAG BY ZONE BY NITE	0.32	12	0.03	0.31	0.989
(Huynh-Feldt Epsilon = 1.00000)					

TABLE 2. Analysis of variance table based on the mean proportion oftraps occupied by *Microtus pennsylvanicus* (arcsine square root transformed). Main effects tested were fragmentation (frag) and trap position (corner, side, interior) (zone). Trapnight (nite) was the within subjects factor.

Source of Variation	SS	DF	MS	F	P
WITHIN CELLS	4.18	18	0.23		
CONSTANT	12.90	1	12.90	55.48	0.000
FRAG	0.13	1	0.13	0.56	0.463
ZONE	0.30	2	0.15	0.64	0.541
FRAG BY ZONE	0.54	2	0.27	1.15	0.339
Within-Subject Effects					
Source of Variation	SS	DF	MS	F	P
WITHIN CELLS	9.63	108	0.09		
NITE	3.64	6	0.61	6.81	0.000
FRAG BY NITE	0.49	6	0.08	0.92	0.486
ZONE BY NITE	0.60	12	0.05	0.56	0.869
FRAG BY ZONE BY NITE	0.65	12	0.05	0.60	0.835
(Huynh-Feldt Epsilon = 1.00000)					

Analyses of the proportion of captures revealed some effects of habitat edges. While the tests for the main-effects of fragmentation and trap location alone were not significant for either species there was a significant interaction term involving fragmentation and trap location for *Peromyscus* (Tables 1 and 2). The mean proportion of captures was highest in patch interiors, and lowest at corners in the fragmented

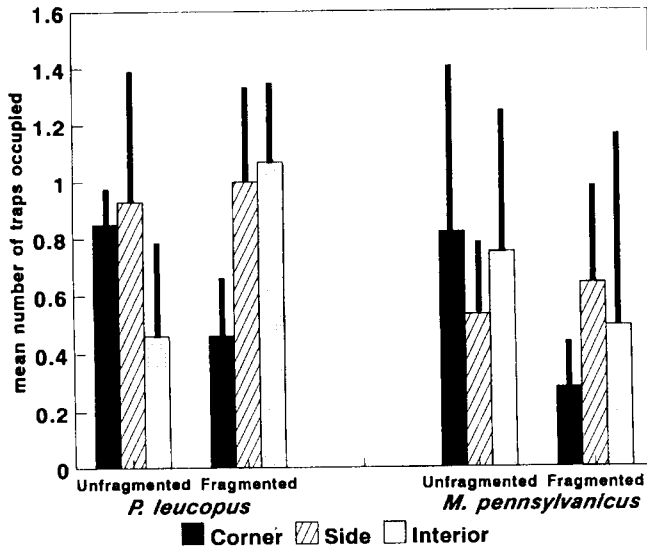


FIGURE 3. Results comparing the mean ( SE) number of traps occupied, either corner, side, or interior, in fragmented or unfragmented landscapes for *P. leucopus* and *M. pennsylvanicus*. Bars represent the mean across all trap sessions.

landscape, while in the continuous landscape captures were higher on sides and corners than for interiors (Figure 3). Analyses of *Microtus* captures showed no significant main or interaction effects, but the smallest proportion of captures was on corners of patches in the fragmented landscape. The within-subjects factor, trapping date, showed significant effects for both species resulting from an increasing number of captures throughout the study, but no significant interaction with any main effects factor.

Five nights of predatory trials (8 replicates per trial) resulted in one missing mouse, one wounded mouse, and two confirmed predatory events (one striped skunk was caught in a Hav-a-heart trap containing a tethered mouse, while one event was an open tethering and the predator could not be identified) all within the control landscape. All mice tethered in the fragmented landscape were unharmed.

### DISCUSSION

These results suggest that predation rates did not greatly differ between fragmented and continuous habitats, and if any trend actually exists predation rates may be greater in continuous than in fragmented landscapes. This result is contradictory to previous studies, where predation levels were greater in fragmented landscapes or at habitat edges (Andrén et al., 1985; Andrén and Angelstam, 1988; Andrén, 1992). Several factors may be operating in conjunction to produce the observed predation results. The lack of greater predation in the fragmented landscape may result from predators also avoiding open areas where they too may be at risk. Alternatively, predators may be responding to the distribution of prey. Habitat fragmentation produces a distribution of prey that is highly clumped. And this clumping of prey may be further exacerbated by edge avoidance behavior creating prey-poor areas within habitat patches. If

fragmentation produces a coarse 'grain' distribution of prey and predators are adapted to a uniform distribution of prey, then fragmentation may actually reduce rates of predation (Vine, 1971; Taylor, 1976b; Weins, 1976; Kareiva, 1987; Turchin and Kareiva, 1989).

Although actual predation rates were roughly equal in both landscapes, within the fragmented landscape, *Peromyscus* tended to avoid patch edges which is consistent with the notion that the perceived risk of predation is higher in the fragmented landscape (Bowers and Dooley, 1993). Given that fragmentation produced no difference in abundance between landscapes, but resulted in the avoidance of edges, implies that most activity of animals was concentrated in the interior regions of patches in the fragmented landscape. Thus, edge avoidance behavior may increase intra- and inter-specific interactions in fragmented habitats thereby eliciting changes in social and community structure. However, the mechanism of edge avoidance may be unrelated to the actual risk of predation.

It is difficult to explain why *Peromyscus* avoided edges while *Microtus* did not. Part of the explanation may be related to microhabitat preferences. *Peromyscus leucopus* is typically a woodland species, whose microhabitat contains a high degree of vertical stratification and whose movement is generally restricted to protected areas (Barnum et al., 1992). *Microtus pennsylvanicus* is typically found in grassy habitats (Klatt and Getz, 1987), and although Desy et al. (1990), found that increased vegetative cover decreases the risk of predation for *M. pennsylvanicus*, the difference between mowed vegetation and preferred cover for *Peromyscus* is probably much greater than for *Microtus*. A second possibility may be that *Microtus* is more tolerant of edges. This finding is in accordance with those of Harper et al. (1993) and Dooley (1993), who found that densities of *Microtus pennsylvanicus* were unaffected by habitat patch shape (a varying edge to interior ratio), which would be expected if edge avoidance were not a strong factor. A third possible factor relates to the use of space and home range position. Traps may not be equal in their accessibility to small mammals. Traps at corners of unfragmented patches may be encountered by more animals that do not have the opportunity to be trapped elsewhere, while in the fragmented patches the opposite pattern is true - corner traps are the least likely to be encountered. The magnitude of this effect will increase for species with larger home range sizes. The data presented here tend to support this notion, as activity areas of *Peromyscus* are approximately twice as large as *Microtus* (Dooley, 1993). Thus some of the 'edge avoidance' seen in the fragmented landscape may be more of a methodological problem than a biological reality. However, radio telemetric data indicated that *Peromyscus* routinely moved the 50m distance from edge to edge in both the fragmented and unfragmented landscapes, suggesting that this problem may be minimal (Zawacki, personal observation). Unfortunately similar data were not collected for *Microtus*. Innate individual behavioral responses resulting from fragmentation have the potential to influence populations, and such issues need to be addressed in any evaluation of the effects of habitat fragmentation.

#### ACKNOWLEDGEMENTS

We would like to thank J. Dooley, E. Connor, and G. Kirk for helpful comments on this manuscript. B. Arnold's knowledge of tractor repair was invaluable. The three authors contributed equally to the conception and execution of this research. The data

was analyzed and manuscript prepared by S.F.M. This research was funded in part by NSF grants DEB-9207722 and DIR-9322093 to M.A.B.

#### LITERATURE CITED

- Andrén, H. 1992. Corvid density and nest predation in relation to forest fragments. *Ecology*. 73:794-804.
- Andrén, H., P. Angelstam, E. Lindström, and P. Widén. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. *Oikos*. 45:273-277.
- Andrén, H., and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*. 69:544-547.
- Barnum, S. A., C. J. Manville, J. R. Tester, and W. J. Carmen. 1992. Path selection by *Peromyscus leucopus* in the presence and absence of vegetative cover. *Journal of Mammalogy*. 73:797-801.
- Bowers, M. A. and J. L. Dooley. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. *Oecologia*. 94:247-254.
- Bowers, M. A. 1993. Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. *Oikos*. 67:129-141.
- Desy, E. A., G. O. Batzli and J. Liu. 1990. Effects of food and predation on behavior of prairie voles: a field experiment. *Oikos* 58:159-168.
- Dooley, J. L. 1993. The influence of local patch structure on the demography of two grassland rodents. Ph.D. Dissertation. University of Virginia, Charlottesville, VA.
- Getz, L. L., C. M. Larson, and K. A. Lindstrom. 1992. *Blarina brevicauda* as a predator on nestling voles. *Journal of Mammalogy*. 73:591-596.
- Halama, K. 1989. Of mice and habitats. M.S. Thesis. University of Virginia, Charlottesville, VA.
- Harper, S. J., E. K. Bollinger, and G. W. Barrett. 1993. Effects of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). *Journal of Mammalogy*. 74:1045-1055.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*. 68:619-640.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* 321:388-391.
- Keith, L. B. 1983. Role of food in hare population cycles. *Oikos*. 40:385-396.
- Klatt, B. J. and L. L. Getz. 1987. Vegetation characteristics of *Microtus ochrogaster* and *M. pennsylvanicus* habitats in east-central Illinois. *Journal of Mammalogy*. 68:569-577.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Biological Conservation*. 5:18-32.
- Simberloff, D. 1988. The contribution of population and community ecology to conservation science. *Annual Review of Ecology and Systematics*. 19:473-511.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman and company, New York. 859p.
- Taylor, J. 1976a. The advantage of spacing-out. *Journal of Theoretical Biology*. 58:485-490.
- Taylor, R. 1976b. Value of clumping prey and the evolutionary response of ambush predators. *The American Naturalist*. 110:13-29.
- Turchin, P. and P. Kareiva. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology*. 70:1008-1016.



- Vine, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. *Journal of Theoretical Biology*. 30:405-22.
- Weins, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics*. 7:81-120.
- Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of the snowshoe hare. *Ecological Monographs*. 50:111-130.

**VIRGINIA JOURNAL OF SCIENCE**