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Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects

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Abstract. Predator avoidance may involve response strategies of prey species that are time and space specific. Many studies have shown that foraging individuals avoid predators by altering microhabitat usage; alternatively, sites may be selected according to larger-scale features of the habitat mosaic. We measured seed removal by two small mammal species (*Peromyscus leucopus,* and *Microtus pennsylvanicus*) at 474 stations over an experimentally created landscape of 12 patches, and under conditions of relatively high (full moon) and low (new moon) predatory hazard. Our objective was to determine whether predator avoidance involved the selection of small-, medium-, or large-scale features of the landscape (i.e., at the scale of microhabitats, habitats, or habitat patches). We found rates of seed removal to vary more with features of whole patches than according to variation in structural microhabitats within patches. Specific responses included: under-utilization of patch edge habitats during full moon periods, and microhabitat effects that were only significant when considered in conjunction with larger-scale features of the landscape. Individuals residing on large patches altered use of microhabitats/habitats to a greater extent than those on smaller patches. Studies just focusing on patterns of microhabitat use will miss responses at the larger scales, and may underestimate the importance of predation to animal foraging behavior.

Key words: Foraging – Microhabitat – Habitat patches – Predation risk – Small mammals

Small mammals inhabiting a wide range of community types show consistent preference for microhabitats with high amounts of vegetation structure (Rosenzweig and Winakur 1969, Dueser and Shugart 1978; Price 1978; Kotler and Brown 1988). Recent work of Morris (1987, 1991), however, suggests that small-scale patterns of microhabitat usage may not be independent of the larger scale features of the habitat (and the selection of these habitats by small mammals). Risk of predation is clearly an important determinant of which microhabitats an individual uses (Kotler 1984; Bowers 1988, 1990). Dice (1945) observed that owls had difficulty detecting small prey under shrubs on cloudy nights – a result that has been experimentally corroborated by Kotler et al. (1988) and Longland and Price (1991). However, when predators employ a course-grained hunting strategy it is likely that predatory risk will vary more among than within habitat patches. This is one of several mechanisms that could create large-scale habitat associations like that of Morris (1987, 1991). To our knowledge no study has tested the extent to which foragers, under predatory hazard, alter small- versus large-scale patterns of habitat usage. If predatory risk is found to affect both the selection of microhabitats by foraging individuals, and the use of sites within and between habitat patches, then previous studies may have underestimated the importance of predation.

Our study was designed to detect the scale(s) at which rodents avoid predators. We used mowing to create an experimental landscape of 12 unmowed patches embedded in a 20 ha field of mowed (unsuitable) habitat. We used the seed removal technique of Thompson et al. (1991) and Bowers (1988, 1990) to quantify spatial usage patterns of *Microtus pennsylvanicus* and *Peromyscus leucopus* at three scales: among structural microhabitats, among habitat types (in the interior or on the edge of habitat patches), and among habitat patches of different size and shape. We reasoned that differences in rates of seed removal, when analyzed over moon phase (a factor shown to be related to predatory hazard for small mammals), could be used to infer whether predator avoidance involved small- or large-scale responses of the rodents.

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Scale of habitat use and hypotheses tested

Habitats are species- and scale-dependent. Some researchers distinguish microhabitat from macrohabitat selection (Morris 1987, 1991) depending on whether the use of space involves short-term selection of foraging sites, or longer-term selection at or near the scale of home ranges. While few studies have made the distinction between micro- and macro-habitat selection, it is clear that most studies of small mammal "habitats" (cf. Rosenzweig and Winakur 1974; Price 1978; Dueser and Shugart 1978) have used variables measured within very small areas (< 2 m). Hence, we have a much better understanding of microhabitat affinities of small mammals than associations involving larger-scale features of the habitat.

We studied spatial usage patterns at three spatial scales. First, microhabitats differed in vegetation composition/structure at the scale of 10^{0-1} m^2. Second, at the scale of 10^{1-2} m^2, habitats differed relative to position within patches and mowed areas (i.e., "edge" versus "interior" habitats). Finally, at the scale of 10^{2-5} m^2, the landscape was comprised of 12 habitat patches of different size/shape. It is important to note that these three elements of habitat heterogeneity are nested in a hierarchical, and statistically independent fashion: microhabitats are nested within habitats, and habitats are nested within habitat patches. This scheme of partitioning components of habitat heterogeneity allowed us to test a number of hypotheses:

1. Seed removal will be higher under low nocturnal illumination (new moon) than for full moon periods–a "moon" effect.
2. Seed removal rates will be higher for microhabitats with high vegetation cover than for more open sites, particularly during full moon periods–"microhabitat", and "microhabitat by moonlight" effects.
3. Patch edges will be under-utilized relative to interior sites, particularly on nights of high illumination–"habitat" and "habitat by moonlight" effects.
4. Patches with high interior:edge ratios will have higher rates of seed removal than smaller or more linear patches, particularly during full moon periods–"patch" effects.

All of these hypotheses are supported by published studies. It is well known that rodent activity is reduced during highly illuminated nights (Blair 1943; Lockard and Owings 1974; O'Farrell 1974; Kaufman and Kaufman 1982; Kotler 1984), and that during bright nights rodents prefer to forage in microhabitats with high vegetation cover (Price et al. 1984; Bowers 1988, 1990; Brown 1988; Travers et al. 1988). These responses are usually interpreted as the behavioral avoidance of predators by foraging rodents (Lima and Dill 1990). There is also evidence (mostly for birds) that prey species may forage predominately in patch interiors and away from the edges of patches (Gates and Gysel 1978; Grubb and Greenwald 1982; Wilcove 1985; Andren and Angelstam 1988; Temple and Cary 1988; Watts 1991) that may be especially attractive hunting areas for predators (Temple and Cary 1988). Geometry dictates that small or linearly shaped patches will have proportionately more edge than larger or more compact patches (Temple and Cary 1988) suggesting that predator avoidance could represent one criterion by which patches of different size/shape are selected. Predator avoidance strategies might include small scale adjustments in the use of foraging microhabitats (Hypothesis 2), and/or larger scale adjustments made at the level of patches (Hypotheses 3 and 4).

Methods

Study site

We conducted our study during June and July, 1991, at the University of Virginia's Blandy Experimental Farm (BEF), Clarke County, Virginia (ca. 78°00 W, 39°00 N). BEF is comprised of croplands, pasture, old-fields, the Orland E. White Arboretum, and assorted woodlots. Our study site was a 20 ha old-field bounded by U.S. highway 50, an adjacent field of similar vegetation structure, the Arboretum, and a small woodlot (Fig. 1). Prior to 1987 the field served as a pasture (with yearly mowings) for more than 20 years; from 1987 to the summer of 1990 the field lay fallow, but served as a site for several studies focusing on small mammals (Bowers and Dooley, unpublished data). In 1991 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 dicots (i.e., *Daucus carota, Ambrosia,* and *Galium*) and grasses (*Festuca, Dactylis, Lolium,* and *Poa*).

Rodent community

The rodent community was dominated by white-footed mice (*Peromyscus leucopus noveborcensis*), 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. *Microtus pennsylvanicus* is a mostly herbivorous, and highly fecund rodent that is associated with grassy meadow or swampy habitats (Hamilton and Whitaker 1979). During hot summer periods, *Microtus* has a nocturnal activity pattern. *Peromyscus leucopus* is typically found in forested habitats, but in the environs of BEF, often occurred at high densities in successional fields with thick vegetation cover (see Halama 1989). *Peromyscus* is mainly omnivorous in diet and is

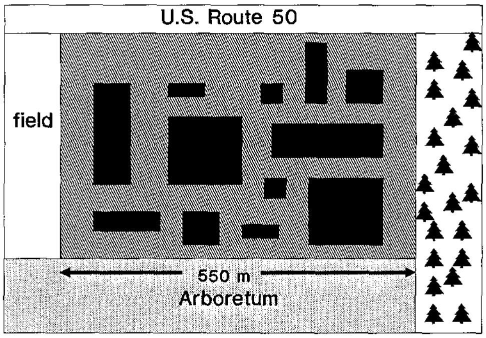

Fig. 1. Map showing the experimental patch landscape, and surrounding habitats at the Blandy Experimental Farm. Unmowed patches *(dark shading)* are surrounded by 50 m areas that were periodically mowed *(medium shading)*. East and west of the study field were, respectively, a 20 ha woodlot and an unused field of similar vegetation to that in patches; north and south of the field were US Route 50 and the Orland E. White Arboretum

nocturnal year-round. Both species readily come to traps baited with seeds and prefer habitats with extensive ground cover. Basic social structure and population dynamics have been well studied for both species (for reviews see King 1968; Krebs 1978; Tamarin 1985). Grant (1971) has shown *Microtus* to competitively dominate *Peromyscus* in field enclosures. But in our field both species showed similar preference for certain microhabitats (see below), and have coexisted in high abundance for at least three years (Dooley and Bowers, unpublished data). We have not found any evidence to suggest that these species compete.

Patch design

In July, 1990, we used mowing to create the array of 12 unmowed patches shown in Fig. 1; periodic mowings in 1990 and 1991 maintained the experimental landscape through January 1992. Our landscape design included three patch sizes (small, 0.0625 ha; medium, 0.25 ha; and large, 1.00 ha), and two shapes (square and rectangular: patches twice as long as wide). Patches of unmowed vegetation were separated by mowed, "uninhabitable" areas of at least 50 m. Mowing was performed when the vegetation approached 20 cm in height. Other studies have shown mowing effectively converted suitable small mammal habitats to unsuitable ones (see Birney et al. 1976; Swihart and Slade 1985; Foster and Gaines 1991).

The design of the patch "landscape" (i.e., the size, dispersion, shape, interpatch distances, and degree of replication) was based on published studies and several years of trapping in this field (see below).

Interpatch distances. A six-week baseline trapping period (i.e., before mowing) showed that less than 10 % of the inter-trap movements of *Peromyscus*, and $<5\%$ of those for *Microtus* were >50 m. Based on these figures, and the reasoning that animals would be less likely to move longer distances across unsuitable areas, we decided 50 m mowed areas would be adequate to create a system of largely independent patches. Trapping after mowing in 1991 showed that out of 751 intertrap movements for *Peromyscus* and 454 for *Microtus* less than 2% occurred between patches while 98% occurred within.

Patch sizes. Richter-Dyn and Goel (1972) suggested that 10–15 individuals is a threshold size below which extinction due to demographic stochasticity is likely. Based on preliminary trapping, we estimated that 10–20 rodents of each species could live in a patch 50 × 50 m (0.25 ha)–this is the size of exclosures used by Brown and Munger (1985), while the largest patch considered by Foster and Gaines (1991) was 0.5 ha. Considering 0.25 patches to be of medium size, we scaled small patches to be four times smaller (0.0625 ha) and large patches four times larger (1.0 ha).

Patch shape. Other studies suggest that patches with high ratios of perimeter to interior areas tend to have higher rates of emigration, lower densities, and greater density fluctuations than more compact patches (Forman and Godron 1981; Stamps et al. 1987a, 1987b). To assess the effects of patch shape we included in our design two patch shapes within each patch size category: square patches 25, 50, and 100 m on a side, and linear patches 12.5 × 50 m, 25 × 100 m, and 50 × 200 m.

Degree of replication. There were severe logistical limits to the number of patch replicates we could hope to sample in any detail. We decided to use four patch size replicates given that designs with fewer numbers often lack statistical power and those with more yield decreasing returns in power with an increase in effort. However, we also wanted to examine possible effects attributable to differences in patch shape. As a compromise, we decided to use four replicates of the three patch sizes with two square and two linear patches within each size category (Fig. 1).

Trapping design and seed removal experiments

Rodents were trapped and seed removal was monitored at 474 stations spaced at 12.5 m intervals over the 12 patches. Trapping was conducted over three consecutive nights every other week May – September, 1991. A single Sherman live trap was placed at each station. 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 left open between trap sessions to allow free exploration and aeration.

We conducted seed removal trials during non-trapping weeks over two new and two full moon periods in June and July, 1991, using the methods of Thompson et al. (1991) and Bowers (1990). Single millet seeds (*Panicum miliaceum* L.) were placed on 2 × 2 cm square plexiglas plates with a small depression to hold the seed. Seeds were placed at each of the 474 stations late in the evening, and were checked at first light the next morning. We recorded whether seeds were present or absent (i.e., removed). Trials where seeds were left out during the day consistently recorded removal rates of $<3\%$, suggesting that late or early foraging by seed-eating ants or birds was not a significant source of seed removal (but see Thompson et al. 1991). We replicated the seed removal experiment for two consecutive nights during each full and new moon period; weather allowed only one trial during the second new moon (in July). All trials were conducted on clear nights with no measurable precipitation or wind. Our measure of seed removal for each time period was whether seeds at a particular station had been removed zero, one or two times.

Microhabitat analysis

We measured structural microhabitats within a 6 m radius of each of the 474 stations between July – August, 1991, through ocular estimation of the percent cover of each plant species. The principal factor contributing to variation in structural microhabitats was local abundance of thistle (*Carduus* spp.): i.e., high cover, densely vegetated microhabitats with high thistle abundances versus more open low cover sites with other dicots such as *Galium, Ambrosia,* and low-growing *(Poa)* or bunch grasses *(Dactylis)*. Regression analyses performed on a similar set of data taken before mowing in 1990 showed that the number of captures of both *Microtus* and *Peromyscus* to be significantly correlated with coverage of thistle ($r=0.20$ and $r=0.22$, respectively, both $p<0.01$).

Data analyses

Seed removal data was analyzed by repeated-measures ANOVA (RMA) using program SPSS/PC+ (Norusis 1988), treating each of the stations as subjects. RMA included tests for within subject (repeated measures) factors including month (two levels: June and July), and moon phase (two levels: new and full). The dependent variable was the number of times seeds were removed at a station during each of the four time periods (logarithmically transformed to create a more uniform distribution of the response variable). To equalize the variance in seed removal over periods, we multiplied seed removal by two for the period with just one trial. Our analysis treated the three measures of habitat heterogeneity as between subject (fixed) factors: 1) coverage of thistle (*Carduus* spp.; i.e., higher or lower than the median value of 35%), 2) whether a station was on the edge or in the interior of patches, and 3) patch size/shape. Converting thistle measurements to a categorical variable allowed explicit tests of microhabitat effects with standard RMA procedures. We were particularly interested in comparing seed removal for stations on patch edges with those in patch interiors. But the smallest square patches had only one and the small linear patches contained no interior stations. Hence, we restricted the analysis here to include only the 436 stations (209 edge and 227 interior) in the four medium and four large patches.

An exploratory RMA showed no effect due to patch shape ($F_{1,357} = 0.01, p > 0.92$), or any interaction involving shape (all $p > 0.40$); all other between-subject factors and the small mammal density covariate had main or interactive effects with $p < 0.10$. As a result of these preliminary analyses we decided to drop the patch shape factor and concentrate on patch size.

One problem with using seed removal data as a direct measure of predator avoidance is that seed removal will vary according to both the number and the activity of foragers on patches. In fact, our study was designed to examine population-level responses to habitat patches of different size/shape (for a similar study see Foster and Gaines 1991). But in this paper we are more interested in foraging than numerical responses. Consequently, we decided to include density estimates of the minimum number of rodents alive (MNA; see Krebs 1966; Hilborn et al. 1976) in each patch for the four time periods (logarithmically transformed) as a covariate in the RMA; MNAs were entered first in the analyses, after which effects due to the other factors were tested. Because we could detect no differential seed removal effect due to rodent species, MNAs of the two species were combined. Companion papers will address the numerical/demographic responses (Dooley and Bowers, unpublished data).

Results

The average seed removal rate on medium and large patches was 29.1% (over all trials, months, and moon phases). A higher percent of seeds were removed under new than full moon periods (39% versus 19%), in patch interiors than on edges (36% versus 21%), and from medium than large patches (34% versus 26%).

RMA showed seed removal was significantly higher under new than full moon periods (hypothesis 1), and was higher in patch interiors than on edges (hypothesis 3; see Table 1 and Figs. 2 and 3). Our predictions that

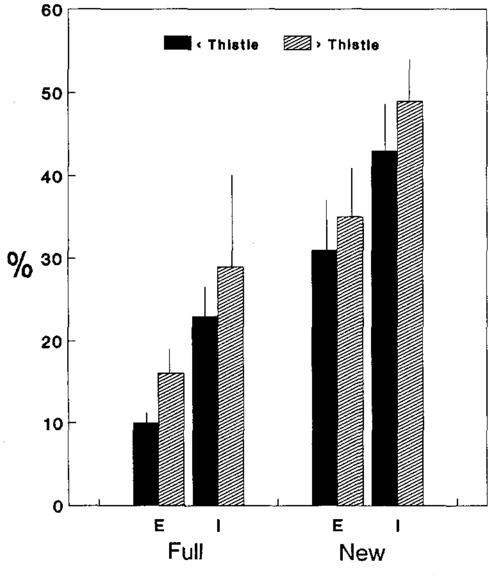

Fig. 2. Histogram showing the proportion of seeds removed for sites with greater- or lesser-than-median thistle coverage, for patch edge and interior habitats (as *E* and *I*), and for full and new moon periods. Standard errors are also given

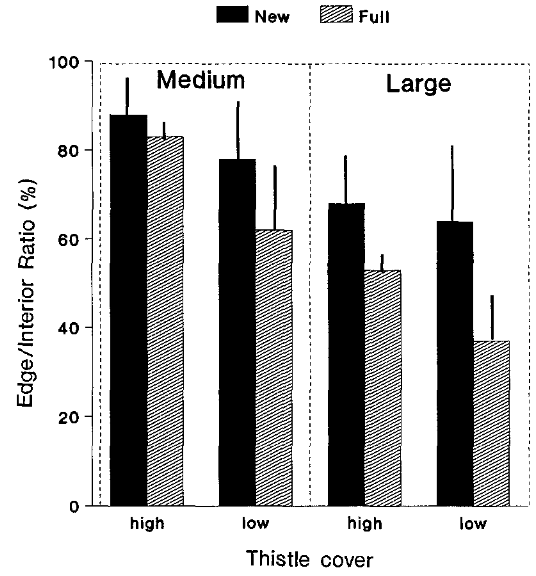

Fig. 3. Histogram comparing the proportion of seeds removed on patch edges relative to that removed in patch interiors (i.e., % removed on edges divided by the % removed for interior stations) for medium and large patches, for stations with high and low thistle coverage, and for new and full moon periods. Standard errors are also given

Table 1. Results of Repeated Measures ANOVA testing for between (top) and within (bottom) subject variation in rates of seed removal. Each of the 436 stations was a considered a subject, and seed removal over two new and two full moon the repeated measures factor. We tested for seed removal differences due to moon phase, microhabitat (thistle), habitat (edge vs. interior), and habitat-patch (patch size). Analyses were performed using MNA density estimates (both rodent species combined), entered first as a covariate, after which the other factors were tested. See text for more details

Source of Variation	SS	DF	MS	F	*P*
(Between station effects)					
Within cell	80.2	365	0.22		
Densities (MNA)	4.4	1	4.40	20.02	<0.00
Patch size	3.2	1	3.22	14.76	<0.00
Edge (vs. interior)	2.7	1	2.71	12.32	<0.00
Thistle	0.0	1	0.00	0.00	0.98
Size × edge	0.0	1	0.02	0.09	0.76
Size × thistle	0.3	1	0.25	1.12	0.29
Edge × thistle	0.1	1	0.07	0.32	0.57
Size × edge × thistle	0.0	1	0.01	0.02	0.97
(Within station effects involving moon)					
Within cell	66.3	365	0.18		
Densities (MNA)	0.1	1	0.08	0.44	0.51
Moon	1.12	1	1.12	6.16	0.01
Size × moon	0.00	1	0.00	0.01	0.93
Edge × moon	0.81	1	0.81	4.44	0.04
Thistle × moon	0.00	1	0.00	0.02	0.88
Size × edge × moon	1.66	1	1.66	9.12	0.03
Size × thistle × moon	0.02	1	0.02	0.09	0.77
Edge × thistle × moon	0.97	1	0.97	5.32	0.02
Size × edge × thistle × moon	1.68	1	1.86	10.27	0.01

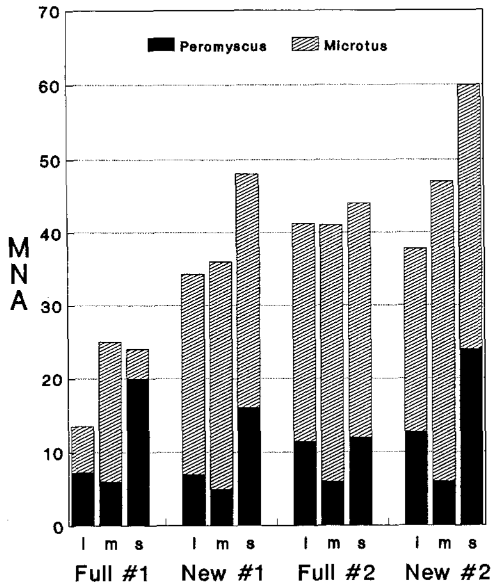

Fig. 4. Average density of *Microtus pennsylvanicus (crosshatching)* and *Peromyscus leucopus (solid bars)* for the three patch sizes, and over the four time periods when seed removal experiments were conducted: i.e., the sequence was full, new, full and new moon. Densities are the "minimum number alive" per 1.0 ha

seed removal would be higher for microhabitats with high vegetative cover (hypothesis 2), and higher for patches with higher interior:edge habitat ratios (hypothesis 4) were not supported in tests of main treatment effects (Table 1; but see below). There were, however, significant two, three, and four way interactions involving moon phase, microhabitat, habitat, and patch-level effects (Table 1). Rodent densities (Fig. 4) accounted for a significant portion of the between-site (i.e., station and patch) variation in seed removal but not variation in seeds removed at sites over time (Table 1). This was somewhat surprising given that rodent densities increased markedly over the two month study (Fig. 4).

Our predictions that moon phase might exaggerate differences in seed removal between edge and interior habitats (hypothesis 3), and between open and high cover microhabitats (hypothesis 2) were supported by the highly significant moon × edge, and moon × microhabitat × edge habitat interactions (Table 1; see also Fig. 2 and 3). Specifically, rates of seed removal for stations on patch edges were 60% higher during full moon periods for microhabitats with greater-than-median than less-than median thistle coverage; during new moon periods this difference was only 10%. Many other studies have shown that small mammals shift microhabitat use with moon phase (for reviews see Bowers 1990; Lima and Dill 1991), but in the present study, shifts towards high cover sites on bright nights were detectable only when location within habitat patches was considered. These results can not simply be explained by a disproportionate number of high thistle sites in interior or edge habitats. In fact, both interior and edge habitats had nearly equal ratios of stations with high and low thistle coverage (48%–52% for interiors versus 52% to 48% for edges, respectively).

There were two kinds of patch-level effects (see hypothesis 4). First, seed removal rates were consistently lower for large than medium size patches for all moon × edge contrasts (Fig. 3) despite the fact that prior to analyses the seed removal data was adjusted according to variation in local rodent densities (Table 1). Second, shifts in response to moon phase were more marked in large than medium sized patches as indicated by the strong three and four-way interactions involving moon, patch size, and habitat edge and/or microhabitat (see Table 1 and Fig. 3). These last two results indicate that predator avoidance may be affected by factors operating at the patch level, but not exactly in the manner we initially thought (see hypothesis 4). Specifically, moon-phase differences in seed removal between edge and interior habitats, and between high and low cover microhabitat was more marked in large than medium sized patches (Fig. 3).

Discussion

I. Habitat selection and predation hazard

Our results suggest that predator avoidance strategies of rodents involved the selection of larger-scale features of the landscape more than shifts in the use of structural microhabitats. Morris (1987, 1991) also found *Peromyscus* to select sites at the between-habitat scale rather than at the within-patch, microhabitat scale. And a number of authors have suggested that birds select breeding habitats on the basis of gross vegetation structure rather than foraging microhabitats (see Urban and Shugart 1986). James (1971) coined the term "niche gestalt" to describe habitat selection occurring at larger scales.

The avoidance of predators is a two-species rather than a one-species dynamic. The hunting strategy of the predator may set the scale at which its prey responds to risk (Holbrook and Schmitt 1988). In instances where the predator is more vagile than its prey, it is likely that the risk of predation may vary more according to larger-scale features of the habitat mosaic than among microhabitats. If predators of small mammals (at our site, foxes, raccoons, owls), behave like some other predators (see Alverson et al 1988; Harris 1988), the most risky areas might be along patch edges. It was, in fact, along patch edges that we detected the most marked shifts in foraging with moon phase. Further, we expect that predators will concentrate on areas where hunting success is highest (edges), and where prey densities are highest.

Our results suggest that animals in medium size patches may be particularly susceptible to predators for two reasons. First, the ability of prey in smaller patches to avoid predators may, in some manner, vary with local densities. In our study animals residing in large patches had larger home ranges and appeared to be more territorial than those in the smaller patches (Dooley and Bowers, unpublished data). This, we believe, is the main reason why large patches tended to support lower densities than the smaller patches. And it seems that with lower densities, and with each individual "controlling" more space, that the potential of using the available heterogeneity at the habitat or microhabitat scales may be higher than in medium patches where home ranges are smaller and densities higher. Second, it may be that there are qualitative differences between edge/interior habitats in medium compared to large patches. Specifically, interior sites in large patches, because of the geometry, probably had more of an interior "feel" than those in medium size patches–i.e., a station in the center of a medium size patch was no more than 25 m from a patch edge while in large patches an interior station could be 50 m from an edge. Hence, one could argue that the difference in quality of edge and interior habitats is greater in large than in medium sized patches. This reasoning (and our results) are consistent with Harris and Skoog (1980) who argued that the magnitude of edge effects will vary with the quality of adjacent habitats.

It is possible that factors other than predation risk (i.e., resource availability) change from patch interiors to edges. In fact, the traditional usage of "edge effect" referred to the high abundances and diversities of animals along habitat boundaries (i.e., "ecotones"; Alverson et al. 1988). Edge effects resulting from colonization/ shifts in performance of shade-intolerant plants with proximity to more open patch edges could create confounding effects of food availability and risk. Animals attempting to maximize fitness then may be faced with the problem of minimizing risk:gain ratios (Cerri and Fraser 1983; Gillaim and Fraser 1987). Edges that have high food abundance but also high risk have been called "ecological traps" (Harris 1988) for the obvious reason. Our data suggests that under predation pressure interior habitats will be over- and edge habitat under-exploited by foraging prey species. Even in the absence of microclimatic-induced shifts in food plant abundance (and we could not detect any differences in the composition of plants according to location within patches) we predict that edges will support more food resources than interiors as a result of the overuse of interior and the under use of edge habitats.

Ours is the first study to suggest that predatory risk for small mammals varies more at the patch level than at the within patch microhabitat scale–this is supported by the result that microhabitat effects were only significant when considered interactively with features of entire patches and with moon phase. Our conclusions are based on the assumption that risk of predation varies with moonlight intensity. Many other studies have shown moonlight to affect activity schedules of small mammals (Kotler 1984; Price et al. 1984; Kaufman and Kaufman 1982; Bowers 1988, 1990), and all have identified predatory risk as the cause. Several recent studies have, in fact, shown that the proficiency of predators to catch prey increases with nocturnal illumination and decreasing vegetative cover (Kotler et al. 1988; Longland and Price 1991).

Predation has been a potent evolutionary force in molding the traits of many prey species (Endler 1986). One need not invoke a separate set of behaviors to account for predator mediated microhabitat, habitat, or habitat patch selection. For example, the general avoidance of open sites under high illumination documented in many studies (for reviews see Kotler and Brown 1988; Bowers 1990; Lima and Dill 1990) could create strong affinities for cover at both small and larger scales. The exact type of response, however, may differ. For example, Bowers (1990) found that the exploitation of 1 g seed aggregates by *Dipodomys merriami* varied according to a microhabitat by moonlight interaction but removal of single seeds did not. For kangaroo rats predation hazard did not appear to change which microhabitats were visited, but rather the apportionment of time spent among them. Animals may, in fact, habitat select not by restricting the type of habitats used, but by altering the degree to which each is exploited (Rosenzweig 1974). That rodents in the present study consistently failed to remove seeds in certain habitats during bright nights suggests that predator avoidance can create an extreme form of habitat selection.

II. Landscape level effects

There is much interest in determining the extent to which landscape-scale features of the environment affect populations (cf. Forman and Godron 1986; Turner 1989; O'Neill 1989). One of the more obvious features of landscapes is the mosaic of habitat types (patches). A number of theoretical studies have examined population responses to the sizes, qualities, and dispersion of habitat patches (Stamps et al. 1987a, 1987b; Pulliam 1988; Pulliam and Danielson 1991; Karieva 1989). These studies demonstrate that the make-up of subpopulations can vary with patch-specific emigration:immigration ratios, differences in demographic performance, and, in some cases, interspecific competition. However, empirical corroboration of these responses are lacking, and most field studies of metapopulations have been more phenomenological than mechanistic (Simberloff 1988). There are, in fact, few field studies identifying particular mechanisms responsible for patch-to-patch differences in population structure/dynamics. Our study, along with several others focusing on avian populations (i.e., Gates and Gysel 1978; Andren and Angelstam 1988; Temple and Cary 1988; Watts 1991) identifies risk of predation as one possible mechanism.

We infer from our results that smaller patches may be of a lower quality than larger patches. Watts (1991) also reported that Savannah Sparrows altered use of both microhabitats and habitat patches with predatory risk. In both our study and Watts (1991) foraging behavior changed with conditions that might affect hunting proficiency–nocturnal illumination for rodents, and weather for birds. While Watts (1991) documented shifts in the use of habitats by the same set of birds, our results (because of the isolated nature of patches and lower vagilities of rodents) involve responses made by different subpopulations. Our design, in fact, allows us to extrapolate measures of individual foraging behavior upwards to examine patterns at the subpopulation level.

Specifically, To what degree are patch-to-patch differences in predator avoidance strategies related to local population structure/densities?

If smaller patches are of lower quality than larger patches (because of areal differences and/or because of the high proportion of edge habitats), why are rodent densities higher on the former than the latter? For *Microtus* and *Peromyscus,* density is probably a poor indicator of patch quality. Our analyses of population-level attributes show that larger patches have individuals with longer patch residence times than smaller patches, and a size/age make-up that is biased towards adults rather than juveniles (Dooley and Bowers, unpublished data). Anderson (1989) predicted that habitat patches of high quality may be occupied by dominant, territorial individuals that maintain relatively stable, but low density populations (Fretwell and Lucas 1970). By contrast, nonterritorial subdominants may actually occur at higher densities in lower quality "sink" habitats.

What then is the relationship between the ability/necessity of individuals to avoid predators and the structure of subpopulations. Further: Are predator escape strategies limited by social interactions within subpopulations, by the patch landscape mosaic, or by a combination of the two (as our study suggests)? One problem in determining cause and effect relationships is that simple changes in habitat geometry can affect a multitude of population level processes, and these are certainly more complex than can be predicted by the simple species-area, patch dynamic and demographic models that are rich in predictions but lacking in mechanism.

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References

Alverson WS, Waller DM, Solheim SL (1988) Forest too deer: edge effects in northern Wisconsin. Conser Biol 2:348–358

Anderson PK (1989) Dispersal in rodents: a resident fitness hypothesis. Spec Publ, Am Soc Mamm 9:1–141

Andren H, Angelstam P (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69:544–547

Birney EC, Grant WE, Baird DD (1976) Importance of vegetative cover to cycles of *Microtus* populations. Ecology 57:1043–1051

Blair WF (1943) Activities of the chihuahuan deermouse in relation to light intensity. J Wildl Manag 7:92–97

Bowers MA (1988) Seed removal experiments on desert rodents: the microhabitat by moonlight effect. J Mamm 69:201–204

Bowers MA (1990) Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. Ecology 71:2334–2344

Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobio 22:37–47

Brown JS (1989) Desert rodent community structure: a test of four mechanisms of coexistence. Ecol Monogr 59:1–20

Brown JH, Munger JC (1985) Experimental manipulation of a desert rodent community: food addition and species removal. Ecology 66:1545–1563

Cerri RD, Fraser DF (1983) Predation and risk in foraging minnows: balancing conflicting demands. Am Nat 121:552–561

Dice LR (1945) Minimum intensities of illumination under which owls can find prey on sight. Am Nat 79:385–416

Dueser RD, Shugart HH (1978) Microhabitats in a forest floor small mammal fauna. Ecology 60:108–118

Endler JA (1986) Natural selection in the wild. Princeton Univ. Press, Princeton, NJ

Foreman RTT, Godron M (1986) Landscape ecology. Wiley, New York

Foster J, Gaines MS (1991) The effects of a successional habitat mosaic on a small mammal community. Ecology 72:1358–1373

Fretwell SD, Lucas HL Jr (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. theoretical development. Act Biotheor 19:16–36

Gates JE, Gysel LW (1978) Avian nest dispersion and fledging outcome in field-forest edges. Ecology 59:871–883

Gilliam JF, Fraser DF (1987) Habitat selection when foraging under predation hazard: a model and test with stream-dwelling minnows. Ecology 68:1856–1862

Grant PR (1971) Experimental studies of competitive interaction in a two-species system. III. *Microtus* and *Peromyscus* species in enclosures. J Anim Ecol 40:323–350

Grubb TC Jr, Greenwald L (1982) Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. Anim Behav 30:637–640

Halama KJ (1989) Of mice and habitats: test for density dependent habitat selection. Unpublished M.S. Thesis. University of Virginia, Charlottesville, Virginia, USA

Hamilton WJ Jr, Whitaker JO Jr (1979) Mammals of the eastern United States. Cornell Univ Press, Ithaca, NY

Harris LD (1988) Edge effects and conservation of biotic diversity. Conserv Biol 2:330–332

Harris L, Skoog P (1980) Some wildlife habitat-forestry relations in the Southeastern Coastal Plain. Proceed Louisiana State Univ Forestry Sympos 29:103–119

Hilborn R, Redfield JA, Krebs CJ (1976) On the reliability of enumeration for mark and recapture census of voles. Can J Zool 62:2440–2444

Holbrook SJ, Schmitt RJ (1988) The combined effects of predation risk and food reward on patch selection. Ecology 69:125–134

James FC (1971) Ordinations of habitat relationships among breeding birds. Wilson Bull 83:215–236

Kareiva P (1989) Reviewing the dialogue between theory and experiments in population ecology. In: Roughgarden J, May RM, Levin SA (eds) Perspectives in ecological theory. Princeton Univ Press, Princeton, NJ

Kaufman DF, Kaufman GA (1982) Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat *(Dipodomys ordii).* J Mamm 63:309–312

King JA (1968) Biology of *Peromyscus* (Rodentia). Spec Publ 2, Am Soc Mammalogists

Kotler BP (1984) Risk of predation and the structure of desert rodent communities. Ecology 65:689–701

Kotler BP, Brown JS (1988) Environmental heterogeneity and the coexistence of desert rodents. Ann Rev Ecol Syst 19:281–307

Kotler BP, Brown JS, Smith RJ, Wirtz WO II (1988) The effects of morphology and body size on rates of owl predation of desert rodents. Oikos 53:145–152

Krebs CJ (1966) Demographic changes in fluctuating populations of *Microtus californicus.* Ecol Monogr 36:239–273

Krebs CJ (1978) Aggression, dispersal, and cyclic changes in populations of small rodents. In: Krames L, Pliner P, Alloway T (eds) Advances in communication and affect. Plenum Press, New York

Lima SL, Dill LM (1990) Behavioral decisions made under risk of predation: a review and prospectus. Can J Zool 68:619–640

Lockard RB, Owings DH (1974) Moon-related surface activity of bannertail *(Dipodomys spectabilis)* and Fresno *(D. nitratoides)* kangaroo rats. Anim Behav 22:262–273

Longland WS, Price MV (1991) Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? Ecology 72:2261–2273

Morris DW (1987) Ecological scale and habitat use. Ecology 68:362–369

Morris DW (1991) Fitness and patch selection by white-footed mice. Am Nat 138:702–716

Norusis MJ (1988) SPSS/PC+ advanced statistics V2.0. SPSS, Chicago, Illinois

O'Farrell M (1974) Seasonal activity patterns of rodents in a sagebrush community. J Mamm 55:217–233

O'Neill RV (1989) Perspectives in hierarchy and scale. In: Roughgarden J, Levin SA (eds) Perspectives in Ecological Theory. Princeton Univ Press, Princeton, N.J

Price MV (1978) The role of microhabitat in structuring desert rodent communities. Ecology 59:910–921

Price MV, Waser NM, Bass TA (1984) Effects of moonlight on microhabitat use by desert rodents. J Mamm 65:353–356

Pulliam HR (1988) Sources, sinks and population regulation. Am Nat 132:652–661

Pulliam HR, Danielson BJ (1991) Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am Nat 137:S50–S66

Richter-Dyn N, Goel NS (1972) On the extinction of a colonizing species. Theor Pop Biol 3:406–433

Rosenzweig ML (1974) On the evolution of habitat selection. In: Kamil AC, Sargent TD (eds) Foraging behavior: ecological, ethological and psychological approaches. Garland STPM, New York

Rosenzweig ML, Winakur J (1969) Population ecology of desert rodent communities: habitat and environmental complexity. Ecology 50:558–572

Simberloff D (1988) The contribution of population and community ecology to conservation science. Ann Rev Ecol System 19:473–511

Swihart RK, Slade NA (1985) Testing of independence of observations in animal movements. Ecology 66:1176–1184

Stamps JA, Buechner M, Krishman VV (1987a) The effects of edge permeability and habitat geometry on emigration from patches of habitat. Am Nat 129:533–552

Stamps JA, Buechner M, Krishman VV (1987b) The effects of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. Am Zool 27:307–325

Tamarin RH (1985) Biology of new world *Microtus*. Spec Publ 8, Am Soc Mamm

Temple SA, Cary JR (1988) Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conser Biol 2:340–347

Thompson DB, Brown JH, Spencer WD (1991) Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology 72: 852–863

Travers SE, Kaufman DW, Kaufman GA (1988) Differential use of experimental habitat patches by foraging *Peromyscus maniculatus* on dark and bright nights. J Mamm 69:869–871

Turner MG (1989) Landscape ecology: the effect of pattern on process. Ann Rev Ecol Syst 20:171–197

Urban DL, Shugart HH (1986) Avian demography in mosaic landscapes: modeling paradigm and preliminary results. In: Verner J, Morrison ML, Ralph CJ (eds) Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Univ Wisconsin Press, Madison

Watts BD (1991) Effects of predation risk on distribution within and between habitats in savannah sparrows. Ecology 72:1515–1519

Wilcove DS (1985) Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211–1214