Disturbance and habitat use: is edge more important than area?

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In their efforts to maximize fitness while reducing the probability of dying, animals must decide which patches to forage in, when to forage, and how long to forage in each patch. Each decision will be modified by habitat and habitat disturbance. We evaluate the effects of habitat disturbance on foraging behaviour by imagining an initially homogeneous environment that is altered to create patches of different sizes. Disturbance increases predation risk, or otherwise alters patch profitability. Foragers can respond by changing their pattern of foraging, or by reducing their activity. We develop predictions for each scenario. We then test the predictions with data on the abundance and foraging activity of meadow voles (*Microtus pennsylvanicus*) in and around four sizes of circular disturbed patches. We created the patches by mowing vegetation in an abandoned hay field in northern Ontario, Canada. The treatments had no effect on vole density, and there was no consistent relationship between vole activity and distance from the edge of disturbed patches. Incidental predation of sunflower seeds, our measure of vole foraging behaviour, declined linearly with increasing patch circumference (edge). Seed consumption by meadow voles, and predation by voles on lower food levels, correlates with the length of edge habitat rather than with the area disturbed. Adaptive behaviour can thereby explain edge effects that, under current priorities emphasizing area, would appear at odds with conservation ecology.

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Introduction

When individuals of a species forage optimally, the distribution of animals in any given area should reflect the relative abundances and qualities of feeding patches. Differences in patch quality will alter profitability, and thus the allocation of foraging effort. When some patches are richer than others, optimally foraging individuals that maximize energy gain should allocate their foraging effort to those patches that are more profitable than the average patch in the environment (Charnov 1976, Brown 1988).

Theory and observed foraging patterns in the field demonstrate, however, that patch use is not always based solely on resource availability. Foragers often tradeoff food for safety (Andersson 1981, Lima and Dill 1990, Kotler et al. 1991, Kotler 1992, 1997, Moody et al. 1996, Grand and Dill 1997, Arcis and Desor 2003). When a patch becomes more dangerous, the cost of foraging increases and animals spend less of their time foraging (Kotler et al. 1991). But animals that balance risk and reward will forage in dangerous patches that are rich in resources. For example, in small aviary enclosures, Allenby's gerbil (*Gerbillus andersoni allenbyi*) forages equally in safe patches under shrubs and in risky patches in the open, but only when the open patches contain eight times more food than those under shrubs (Kotler and Blaustein 1995). In large field enclosures, the differences in food abundance required to equalize habitat use are much less (Abramsky et al. 2002a, 2002b). Nevertheless, when the 'risky' habitat is made

less dangerous by building refuges, the gerbils increase their foraging (Abramsky et al. 1990).

The balance between risk and reward likely depends not only on differences in danger and the amount of food, but also on the area and spatial context of risky patches in the habitat. An understanding of the tradeoffs animals make is especially necessary in landscapes where habitat disturbance can quickly create novel patches of different sizes in a previously homogeneous matrix. Assuming that predators optimize their foraging based on patch size, it should be possible to calculate, from first principles, the expected relationship between patch area and predation risk to prey. More generally, we should be able to predict how foragers will respond to any habitat disturbance that creates new patches of variable size. We begin our study by developing simple predictions on how the area of disturbed patches should influence predation risk, and thus the activity of fine-grained foragers (MacArthur and Levins 1964). We then outline and interpret experiments that manipulated the size of patches to test the predictions in the field.

Predictions

We imagine disturbances that reduce habitat quality by increasing predation risk to foragers, but that can also modify reward by altering resources and their abundance. Disturbances are small and are created suddenly in a landscape composed of a single homogeneous habitat (matrix). In its new state the habitat now contains disturbed patches of various sizes that are smaller than, or equal to, the home range of a single foraging animal. The animal can thus approach a disturbed patch from any direction and exploit as much or as little of the patch as it wants.

Individual animals living in the habitat will, if behaving optimally, reassess their foraging strategies to reflect changes in fitness potential caused by the disturbance. We visualize three types of responses to the disturbance by foragers. 1) Foragers exploit the disturbed patch optimally without altering their overall activity level. 2) Foragers avoid (or are attracted to) the disturbed site. 3) The disturbance causes foragers to alter their overall activity. We wish to know whether these responses depend on patch area or its edge.

The relative effects of area versus edge are easily tested by an experiment that creates circular disturbances of different sizes (radii) in an otherwise occupied habitat. Effects of area will scale as the square of the disturbed patch's radius whereas effects associated with edge (perimeter) will scale linearly with radius. Effects of distance from undisturbed habitat (e.g. safety) will not depend on patch size (radius).

To predict the influence of area on patch use we imagine that the forager exploits successive annuli as it moves from the edge into the disturbed patch. The assumption does not require the animal to forage in a circular rotation, only that it moves into the patch from different directions on different foraging occasions. The area of each equally-wide annulus decelerates with the square of its distance from the centre of the patch. Forager activity within the patch will thus scale with the square of the radius of the disturbance. The exact relationship between use and radius will depend on whether risk and reward are constant or whether they vary throughout the patch (see Moenting 2004 for explicit equations). But if an animal's assessment of risk and reward is determined only by how far it is from the edge (distance from safety), then knowing the radius of the patch will not help us predict the forager's activity.

If disturbance increases predation risk such that foragers avoid the area around disturbed patches, rather than exploiting them, then habitat use will decelerate away from the edge with each successive annulus outside of the patch. But, since the circular patches vary in size, different patches will be associated with annuli of different sizes. Predation risk will decelerate with distance from the centre of the patch. So, in this instance, animal activity outside of the patch will depend on patch radius. Again, this will not be the case if predation risk depends only on distance from the edge because the risk will be similar for patches of different size.

Finally, if foragers reduce their overall activity in the landscape in response to the area disturbed, their average activity will decelerate with increased patch radius. But if animals reduce their activity according to the length of edge created by the disturbance, activity will decline linearly with patch radius. The opposite would occur if animals increase their activity.

Our working hypothesis in our study system is that disturbances increase predation risk. Yet it is clear that resources will also be influenced and that many types of disturbance might even improve habitat quality. It is for this reason that we couched our predictions in terms of circular patches varying in size. Effects related to patch size versus edge will also apply to disturbances that alter such characteristics as resource availability or foraging efficiency. The signs of coefficients will depend on whether the disturbance creates a net benefit or net loss in habitat quality.

Our predictions imply that predation risk varies with the size of patches, the distance from safety, and the amount of edge habitat. But our tests are based on foraging and animal activity rather than the direct assessment of risk. We thereby assume that an individual's food consumption and activity in or around a disturbed patch will be inversely proportional to the total predation risk caused by the disturbance. The functional relationship between activity and risk will vary among species and habitats but will nevertheless reflect the scale of predation risk. Thus, if risk increases

with patch area, animal activity will decline with the size of the risky patch. And if risk depends on the distance from the edge, or its length, so too will activity.

Study species

We tested our predictions on patch use by meadow voles (*Microtus pennsylvanicus*; Ord 1815) occupying an abandoned hay field. The meadow vole, a widespread, herbivorous rodent that lives in a variety of open habitats (Batzli 1985, Zakrzewski 1985), is appropriate for our tests because it has been used previously as a model system for studies of habitat fragmentation (Schweiger et al. 2000), habitat disturbance (Pusenius and Schmidt 2002), and the connection between habitat use and population dynamics (Lin and Batzli 2001).

Microtus density increases with plant cover (Eadie 1953, Lobue and Darnell 1959), and vole populations decline dramatically when cover is reduced (e.g. by grazing cattle; Birney et al. 1976, or by mowing; Pusenius and Ostfeld 2002). Cover has an overwhelming influence on foraging behaviour of meadow voles (Pusenius and Schmidt 2002), primarily because it reduces predation risk (Baker and Brooks 1982).

Study site and field methods

We created disturbed patches within a recently abandoned hay field near Thunder Bay, Ontario (48° 17′ 30″ N, 89° 38′ 10″′ W) during the months of May to August, 2003. The field (approximately 10 ha in area) was dominated by birdsfoot trefoil (*Lotus corniculatus*). Other prominent plants included dandelion (*Taraxacum* spp.), and various sedge species (*Carex* spp.) with wild strawberry (*Fragaria virginiana*) interspersed throughout the field. Wild rose (*Rosa acicularis*), and goldenrod (*Solidago* spp.) occurred in scattered patches. The field was planted with red pine (*Pinus resinosa*) seedlings at approximately 3 m intervals. At the time of the study, the pine seedlings were less than 0.5 m tall. Meadow vole runways, latrines, and cuttings were common throughout the field.

Field design

We subdivided the field into four sub-units (minimum distance between sub-units was 50 m). We employed a stratified design within each unit by establishing four 30 × 30 m square study plots separated by 40 m. Live-trap stations were located in a regular grid on the study plots at 10 m intervals. We superimposed onto every plot, a 20 × 20 m 'activity' grid consisting of 121 sampling points, each 2 m apart. Each grid was centred on a plot (Fig. 1). We measured vole activity by presence
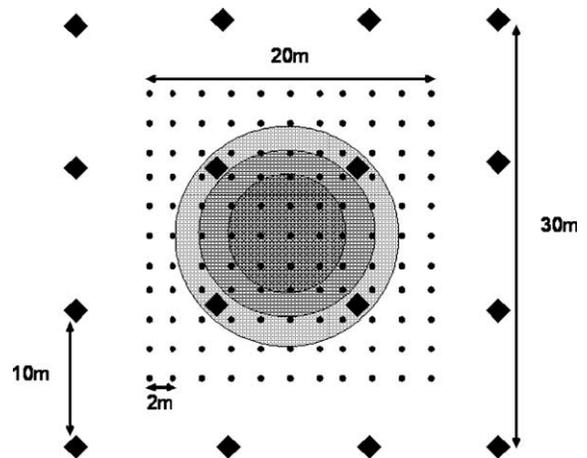
Fig. 1. Schematic illustration of a treatment plot. Circles correspond to 'risky' patches of mowed vegetation used to accentuate predation risk. Each plot contained only one of these treatment sizes. Dots represent the 121 stations of the 20 × 20 m 'activity' grid (2 m spacing). Diamonds represent the 30 × 30 m live-trapping grid (10 m spacing).

or absence of tracks in tracking tubes and by the incidental predation of seeds (Pusenius and Schmidt 2002). We estimated vole density by live-trapping.

We began collecting 'control' data in May before we disturbed the habitat to create circular patches. In July, we mowed circular risky patches with a clothesline trimmer. We assigned patches of 0 m (control), 4 m, 6 m, or 8 m radius randomly to the plots within each sub-unit (Fig. 1). We cut all vegetation (except red pine seedlings) to a height of approximately 5 cm, thus creating clear differences between the old-field matrix and disturbed patches. We mowed again three weeks later to maintain the treatment. Otherwise, the height of the mown shoots would have approached the height of those in the matrix. A third mowing was unnecessary because further plant growth was negligible. We finished field work in August 2003 and tested the theory by comparing pre-mowing (control) data with post-mowing (treatment) data.

Density estimates

We live-trapped meadow voles to document the presence of animals on all study plots, to verify that only voles were present, and to reveal any changes in vole density over the field season that might complicate our measurement of activity. Animals were live-trapped at approximately three-week intervals (beginning 19 May and ending 19 August, 2003) using Tomahawk and Sherman small-mammal live traps protected from sun and rain by aluminum covers. Each live-trap grid contained 16 trapping stations (Fig. 1). We baited each trap with oats, peanut butter, and a potato wedge, and insulated them with cotton mattress stuffing. We checked the traps

at twilight and at dawn for two days. Dirty traps were collected, washed with detergent, sanitized with a bleach solution and dried before being reset. We measured the body and tail length of each vole captured, and weighed, sexed, and marked it using a uniquely numbered ear tag.

We used the number of different animals captured on each plot during the trapping sessions before and after mowing to determine any effects of habitat disturbance on relative vole density. Mark–recapture techniques for voles can be sensitive to capture probabilities of individuals (especially if the probabilities are lower than 0.5, Hilborn et al. 1976). However, the relative biases among estimates are generally consistent across a wide range of differences in trappability (Efford 1992). Capture probabilities of the population from which we sampled are unlikely to vary among our plots because all were within the same 10 ha field. Any bias in actual density estimates should be similar among plots.

Activity estimates

We used two measures of activity to test the predictions from the three different possible responses by rodents. First, we examined patterns of food removal by recording consumption of single sunflower seeds (*Helianthus annus*) placed in a systematic grid (Pusenius and Schmidt 2002). Second, we used the presence or absence of vole tracks in tracking-tubes (Davidson and Morris 2001).

We placed an individual black sunflower seed at every stake-wire flag marking each 2×2 m intersection of the activity plot (Fig. 1). Seeds were placed in small depressions at the base of each stake so that we could identify those that were consumed by voles. Other potential seed predators included birds and other small mammal species, but we found little evidence that these animals exploited the seeds. The placement of seeds in depressions minimized their possible discovery by birds, we captured only one non-vole rodent (a single chipmunk, *Tamias minimus*), and masked shrews (*Sorex cinereus*) caught in our traps did not consume seeds. We checked for seed presence or absence after three nights and removed all remaining seeds and hulls at that time.

We placed plastic tracking-tubes (4 cm diameter, 30 cm long) within one m of each of the 121 points in the activity grid. Each tube contained a 277×53 mm strip of white paper with a carbon-mineral-oil ink patch painted on a piece of plastic shelf-liner in the centre (van Apeldoorn et al. 1993, Davidson and Morris 2001). Tubes were removed from the field, and tracked tubes recorded, after four nights.

We calculated the Euclidean distance from the centre of each plot to each tracking and seed-placement sample point (19 different distance values). We standardized the data by calculating the proportion of all seeds consumed

and the proportion of all tubes with tracks over the 16 experimental plots. These proportions, calculated separately prior to and post-disturbance, allowed us to correct for any changes in preference for seeds by the voles as the season progressed (Batzli 1985, Heroldova 2002). We multiplied the proportion by the number of grid points at each distance to generate the expected number of seeds consumed (or tubes tracked) at that distance if activity was distributed equally across all distances throughout all the plots. Then, for each plot, we calculated the spatial pattern of seed consumption by subtracting the expected number at each distance from the observed number of seeds consumed. These standardized 'corrections' of animal activity compensated for unequal sampling effort with distance caused by the overlay of a rectangular grid on a circular plot. The standardized scores allowed us to test for both distance and area effects predicted by models assuming that the animals either exploited or avoided the disturbed patches. We also calculated the difference between expected and observed numbers of seeds consumed (and tubes tracked) for entire plots. These data were used to test the predictions where animals simply reduce their overall activity.

Statistical design

We tested for changes in vole density over the course of the experiment with a repeated measures analysis of variance (ANOVA; SPSS version 12). The radius of the circular risky patch was the among-subjects fixed factor, disturbance (before and after mowing plots) was the within-subjects factor.

We tested for differences in activity prior to habitat disturbance by using a univariate ANOVA with radius of the future circular risky patches as a fixed factor. We used univariate repeated measures ANOVA, following the guidelines of Potvin et al. (1990), to evaluate the influence of disturbance on our estimates of tracking-tube activity and standardized seed consumption. Again, disturbance was the within-subjects factor, and distance and patch radius were fixed factors in the analysis. We used a priori polynomial contrasts of the distance and radius factors to test whether risk was constant, or varied with distance, in the disturbed patch. Effects of area (radius²) will be revealed by quadratic terms whereas effects of edge will include only linear relationships with radius (equations in Moenting 2004).

We completed our analyses by evaluating the 'reduced activity' model with a polynomial regression of standardized seed consumption (after disturbance) against patch radius. Again, a quadratic relationship will represent the effect of patch area, and a linear relationship will emerge if activity scales with the amount of edge. We calculated Akaike's information criterion for

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small sample sizes (AIC_C) and Akaike differences (Burnham and Anderson 2002) to determine the best of the competing models.

Results

Meadow voles dominated the small mammal community

We caught a total of 196 individual voles, 95 of which were recaptured at least once. There were few mammalian competitors inhabiting the field. We captured only one least chipmunk (*Tamias minimus*), one Arctic shrew (*Sorex arcticus*), and recorded eight captures of masked shrews (*Sorex cinereus*). There was no significant difference in vole abundance among the patch sizes (among-subjects fixed factor 'radius'; $F_{3,12} = 1.97$, $P = 0.17$). The 'disturbance by radius interaction' was not significant ($F_{3,12} = 1.26$, $P = 0.33$) and vole numbers did not change significantly after habitat disturbance ($F_{1,12} = 1.18$, $P = 0.30$; Fig. 2). It thus appears that the fine-scale disturbances assumed by our models had no significant effect on vole dynamics.

Vole activity was similar on all plots before habitat disturbance

Though activity varied substantially from one plot to the next, there was no significant difference among plots in standardized seed consumption before habitat disturbance ($F_{3,11} = 0.35$, $P = 0.79$). Similarly, there was no significant difference among plots in the standardized number of tracked tubes before disturbance ($F_{3,12} = 0.94$, $P = 0.45$). These results confirm our assumption that the pre-disturbance pattern of vole activity was similar throughout the study area.
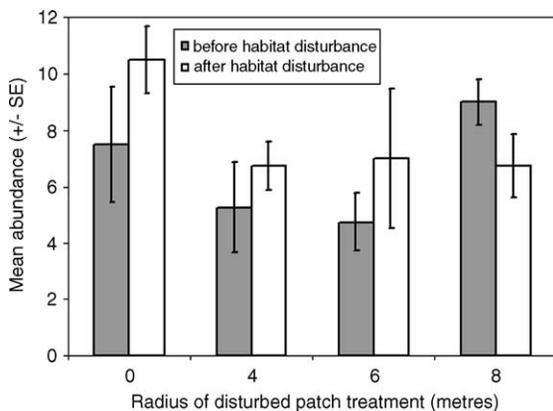
Fig. 2. Mean population density of voles ($\pm$ SE, N = 4) did not change significantly after habitat disturbance. Closed bars represent vole abundance before disturbance. Open bars represent vole density following disturbance.

Habitat disturbance and patch radius explained variation in vole activity

Voles consumed 288 seeds before habitat disturbance (15 experimental plots sampled once each), and they consumed 458 seeds after disturbance (16 plots). The expected number of seeds consumed per plot before disturbance was 19.2 versus 28.6 after. Thus, voles ate more seeds after disturbance than before ($F_{1,209} = 8.94$, $P = 0.003$, Table 1). There was also a significant interaction between disturbance and radius on the standardized number of seeds consumed ($F_{3,209} = 44.32$, $P < 0.001$, Table 1). The interaction explains why seed consumption increased even though vole activity within the disturbed patches declined to near zero. Seed consumption following disturbance increased in the control and 4 m radius patch treatments, but declined in the 6 m radius and 8 m radius treatments where many more of the sampling points were located in the disturbed area, and where voles reduced their activity (Fig. 1, 5).

Seed consumption among disturbance treatments did not vary significantly with distance from the centre of the mowed patches even though voles rarely entered the patches ($F_{18,209} = 0.40$, $P = 0.99$, Table 1). Seed consumption varied inversely with the radius of the mowed patch (and thus with the length of the edge, $F_{3,209} = 15.32$, $P < 0.001$, linear contrast, $P < 0.001$, Table 1). The inverse relationship was caused primarily by reduced foraging outside of the disturbed patches along with low seed consumption inside all the patches (Fig. 3A). Nevertheless, voles reduced their consumption of seeds in direct proportion to the length of edge of the disturbed habitat.

On 16 plots sampled once each for tracks, voles entered 403 tubes before and 337 tubes after habitat disturbance. Meadow voles did not enter tracking tubes within the circular patches after mowing (Fig. 3B), and there was no pattern in the number of tracked tubes with distance ($F_{3,228} = 1.09$, $P = 0.37$, Table 2). Fewer tubes contained tracks in the 4 m radius and 8 m radius treatments than in the controls and 6 m radius treatments ($F_{3,228} = 33.67$, $P < 0.001$, Fig. 4). The differences were not caused by mowing (21% of tubes were tracked per plot before disturbance, versus 17% after, $F_{1,228} = 0.002$, $P = 0.96$), but reflect, instead, the low tracking rates within the 4 m and 8 m radius treatments throughout the summer (Fig. 4). Only the 8 m radius plots had fewer tubes tracked after the creation of risky patches than before (Fig. 4). The reduction in the number of tubes tracked on the 8 m plots caused a significant interaction between disturbance and radius (treatment size, $F_{3,228} = 3.62$, $P = 0.01$, Table 2).

There was a clear disconnect between the patterns of seed consumption versus tracks in the 6 m radius plots (Fig. 3). Seed consumption declined at about the same rate in these plots as it did in smaller and larger

Table 1. Summary of the repeated measures ANOVA on seeds consumed by meadow voles (*M. pennsylvanicus*). Vole foraging did not vary with distance from the centre of disturbed patches. The disturbance by radius interaction remained significant even when the distance factor was removed from the analysis.

Source	Df	MS	F	P
Within-subject factors				
Disturbance (d)	1	9.907	8.936	**0.003**
d $\times$ distance (s)	18	0.951	0.858	0.630
d $\times$ radius (r)	3	49.140	44.324	**<0.001**
d $\times$ s $\times$ r	54	0.849	0.766	0.876
Error	209	1.109		
Among-subject factors				
Intercept	1	5.085	1.993	0.160
Distance	18	1.024	0.401	0.987
Radius	3	39.095	15.319	**<0.001**
s $\times$ r	54	1.135	0.445	1.000
Error	209	2.552		

Polynomial contrasts with radius	estimate	lower bound 95% confidence interval	upper bound 95% confidence interval	P
Linear	−0.884	−1.142	−0.627	**<0.001**
Quadratic	−0.016	−0.282	0.249	0.903

disturbances (Fig. 3A, 5), but activity revealed by tracks did not. As noted above, animals avoided tubes in the disturbed sites, regardless of patch size. And there was no effect of disturbance on the proportion of tracked tubes. It would appear, therefore, that vole use of tracking tubes reflects idiosyncratic and perhaps spurious differences among treatments that do not correlate with foraging activity.

Some readers might wonder whether an analysis based on proportions of seeds consumed and tubes tracked would yield similar results to our standardized analysis. We repeated all of the ANOVAs using the proportions of seeds consumed and tubes tracked (arcsine square-root transformed data). The only difference in the results for seed consumption was a significant intercept (i.e. voles ate seeds). For the tracking tube results, the intercept was significant, and significant disturbance and interaction terms reflected the absence of tracks in mowed areas of plots with different radii. Most importantly, the radius main effect remained highly significant, and there was no effect of distance in either analysis.

Vole foraging for seeds declined linearly with increasing perimeter of disturbed patches

We used standardized seed consumption for entire plots to reassess the inverse relationship between seed consumption and the area of disturbed patches. We extracted the post-disturbance data and analysed treatment size (radius) by polynomial regression. Standardized seed consumption declined significantly with patch radius in both the linear and quadratic regressions (linear, F $=10.85$, P $=0.005$, adjusted $R^2 = 0.40$; Table 3,

Fig. 5; quadratic, F $=5.04$, P $=0.024$, adjusted $R^2 = 0.35$; Table 3). We used Akaike's information criterion to assess which of the reduced activity models provided the best fit with the data (Burnham and Anderson 2002). The linear (perimeter) model had the lowest AIC_C difference ($\Delta_{min} = 0$). The quadratic (area) model had considerably less support ($\Delta_1 = 4.15$, Table 3). The linear model was significant, but the variances in seed consumption were heterogeneous. We corrected this problem by repeating the analysis with a heteroscedasticity-consistent covariate matrix for small sample sizes (HC3, Long and Ervin 2000, using the SPSS syntax of Hayes 2003). The linear regression remained significant (t $= -2.27$, P $=0.039$).

Discussion

Meadow voles reduced their foraging around disturbed patches of old-field habitat in apparent response to increased predation risk. Foraging did not vary with distance from the edge of disturbed patches, nor did it vary with the area of the disturbance. Rather, meadow voles tended not to enter disturbed patches, and altered their seed consumption outside of the patches (Fig. 3). If voles were merely not using the disturbed patches, their foraging would scale with the area of the disturbance. But this effect was overwhelmed by the dramatic linear reduction in mean seed consumption (in the original habitat) with increased radius of disturbance (Fig. 5). The linear negative relationship with radius demonstrates that vole activity depended on the perimeter of the patches.
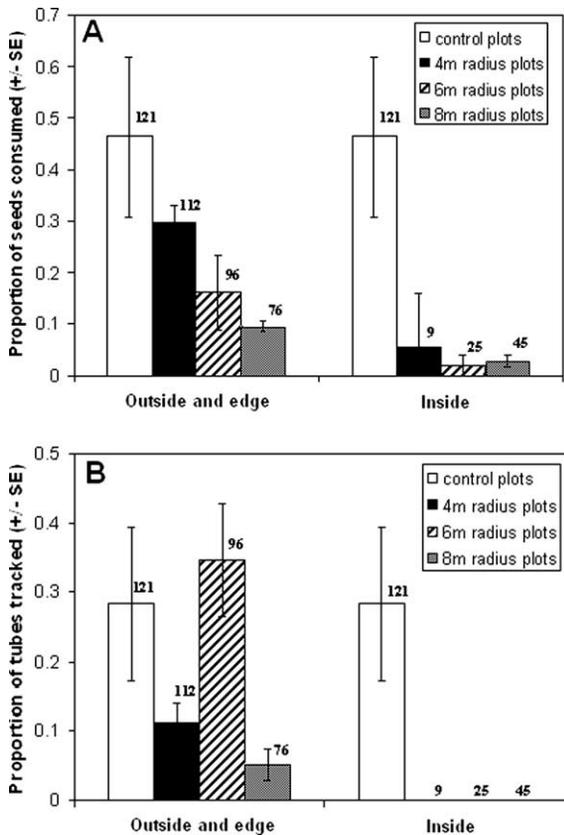
Fig. 3. (A) The mean proportion of seeds consumed ($\pm$ SE, N = 4) by meadow voles declined linearly outside of disturbed patches but was low and more-or-less constant inside (post-disturbance data only). (B) No tubes contained vole tracks inside the disturbed patches ($\pm$ SE, N = 4). Numbers correspond to the availability of seeds or tracking tubes on each plot in control (open bars), 4 m (solid bars), 6-m (coarse hatching), and 8 m radius patches (stippling) respectively.

The absence of a 'distance from disturbance effect' on vole seed consumption and activity might surprise many readers. One possible interpretation is that vole activity declined in the matrix over the summer. Such an effect could (without our control data) yield the illusion that voles reduced their activity in direct response to disturbance. But this explanation is rejected by our track data on control plots that clearly illustrate similar activity in matrix habitat before and after disturbance (Fig. 4). The absence of the distance effect reflects, instead, the fine-grained scale of our experiments. If we had assessed activity at larger distances from the disturbed patches we would inevitably have encountered some distance where activity increased to the levels found in undisturbed controls.

We do not know how voles would react to less disturbed patches or whether the 'edge effect' we have documented would still predominate when voles exploit less risky areas. It seems likely, as disturbed patches become less dangerous or more profitable, that voles might change their strategy and alter their foraging with distance or area. If they do so, we would seem to possess a set of theories, and protocols, to detect the altered strategy.

Why does meadow vole foraging activity scale with patch perimeter?

Herbivorous rodents (e.g. the root vole, *M. oeconomus*), have limited perceptual range (Lima and Zollner 1996, Mech and Zollner 2002). Unable to determine the area of risky patches, voles may simply use their frequency of encounter with edge as a measure of risk. How should they respond? If the edge represents increased risk, and if the voles can detect it easily, then they should reduce their activity as they approach the risky patch (a distance effect). But if voles forage more or less randomly, then their encounter with edge will also be random. A longer edge yields a higher encounter probability that increases the risk over the entire habitat exploited by a vole. The marginal value of safety will be increased, so animals should exploit their environment less (Brown 1988). Though we lack data on quitting-harvest rates that could provide a definitive test of this prediction (Brown 1988), the data on vole seed consumption are unequivocal: proportionately fewer seeds were consumed from plots with longer patch perimeters than from those with shorter perimeters, and the decline was linear. Vole numbers were more-or-less constant across treatments and through time. Thus, the voles reduced their per-capita foraging in direct proportion to the length of edge habitat.

Some readers might wonder whether voles lack the ability to assess rapid changes in risk (or other indicators of habitat quality) along the cut lines of our disturbed patches. Gerbils, for example, show incredible ability to rapidly alter behaviour in direct response to both short and long-term predation risk (Abramsky et al. 2002b, 2004). Voles do the same. They avoid disturbances with low cover. But voles also reduce their foraging outside of the disturbed areas. It is certainly possible that the voles are incapable of assessing short-distance changes in habitat quality. But it is also possible that spatial patterns of seed consumption by voles reflect increased edge-dependent effects in undisturbed habitat. Open patches in old-field habitats are likely to attract predators, and thereby inflate predation risks along the perimeter of those disturbed patches. Edge-dependent microclimatic effects might also reduce habitat quality.

What are the lessons for landscape and conservation ecology?

Though landscape ecologists frequently measure 'edge', the effect of 'area' dominates the literature on habitat

Table 2. Summary of the repeated measures ANOVA on tubes tracked by meadow voles (*M. pennsylvanicus*). The creation of risky patches does not explain variation in tubes tracked.

Source	Df	MS	F	P
Within-subject factors				
Disturbance (d)	1	0.003	0.002	0.962
d × distance (s)	18	1.688	1.086	0.368
d × radius (r)	3	5.627	3.619	**0.014**
d × s × r	54	1.793	1.153	0.237
Error	228	1.555		
Among-subject factors				
Intercept	1	0.000	0.000	0.997
Distance	18	0.852	0.473	0.967
Radius	3	60.704	33.675	**<0.001**
s × r	54	2.069	1.148	0.244
Error	228	1.803		

Polynomial contrast with radius	estimate	lower bound 95% confidence interval	upper bound 95% confidence interval	P
Linear	−0.518	−0.732	−0.303	**<0.001**
Quadratic	−0.066	−0.280	0.149	0.546

fragmentation. And 'edge effects' are seldom differentiated from those related to fragment size or shape (Robinson et al. 1992, Bender et al. 1998, Manson and Stiles 1998, Debinski and Holt 2000, Schweiger et al. 2000, Andreassen and Ims 2001). Yet in one of the relatively few fragmentation studies that assessed edge rigorously, rove beetle (Staphilinidae) densities were lowest in treatments with the most edge (but not the least amount of habitat, Golden and Crist 2000). And

Fig. 4. Comparison of the mean number of tubes containing vole tracks on plots before and after mowing circular patches in an abandoned hay field in northern Ontario, Canada (±SE, N = 4). Values are standardized as the difference between expected (assuming all tubes tracked equally) and observed results. Dashed bars represent pre-disturbance data, whereas the post-disturbance data are represented with solid bars.

now we see a behavioural response in meadow voles that may force ecologists to rethink whether eventual reductions in population size are caused by loss of original 'matrix', or are mediated through the length of edge habitat. Carefully designed experiments, such as those outlined here, will be necessary to explore the full implications of area versus edge in habitat-fragmentation research. It is nevertheless crucial to note that different patterns, such as those that depend on distance, may emerge under lower regimes of disturbance than habitat "loss" caused by mowing.

It is important to reflect, as well, on the community consequences of edge versus area effects revealed by our vole experiments. Meadow voles have the demonstrated ability to influence the invasion of plants in old fields (Ostfeld and Canham 1993, Nickel et al. 2003). But the establishment and persistence of plant species is tied directly to the spatial pattern of vole foraging (Pusenius et al. 2000, Pusenius and Schmidt 2002). Voles facing predation risk reduce their foraging and thereby create enemy-free space for their prey (plants). In our study, an extreme case of enemy-free space occurs within the disturbed patches. Very few seeds were consumed by the voles in disturbed patches regardless of patch size (Fig. 3A). Outside the patches, vole seed consumption declined in direct proportion to the length of edge. The emerging pattern is a gradient in enemy-free space for plants that increases linearly with the length of edge habitat. Thus, evasion of disturbed patches by foragers can have consequences that 'cascade' along trophic connections, and thereby alter ecological communities in both time and space (Manson et al. 1999, Lortie et al. 2000, Pusenius and Schmidt 2002, Pusenius and Ostfeld 2002, Schmitz et al. 2004). An intriguing conservation

Table 3. Comparison of linear and quadratic models of the mean seeds consumed (Y) by voles with increasing radius (X) of risky patches in an abandoned hay field in northern Ontario, Canada (N = 16).

	Linear regression	Quadratic regression
Equation	$Y = 27.05 - 6.05X$	$Y = 27.05 - 6.05X - 0.001X^2$
F	$F_{1,14} = 10.58$	$F_{2,13} = 5.04$
Adj. R^2	0.40	0.35
P	0.005	0.024
AIC_C difference	$\Delta_{min} = 0.00$	$\Delta_1 = 4.15$

implication is that establishment of plant species in fragmented landscapes might, when those plants are consumed by herbivores, be most effective under management strategies that maximize the perimeter to area ratio (contrary to the usual advice to minimize edge, Fraver 1994).

The pattern of vole foraging in disturbed habitats highlights the importance of behaviour to our understanding of population, community, and landscape ecology. Adaptive behaviours affect the dynamics of populations, the structure of communities, and patterns of distribution in landscapes. Behaviourally-mediated trophic interactions with plant communities may alter the landscape itself (Ostfeld et al. 1999), and thereby feed back onto evolution of the vole niche (Odling-Smee et al. 2003). Our ability to use those behaviours to better understand populations and communities, and to apply that understanding, depends on clear logic, appropriate protocols, and definitive experiments. We hope that other ecologists will also use behaviour and its associated
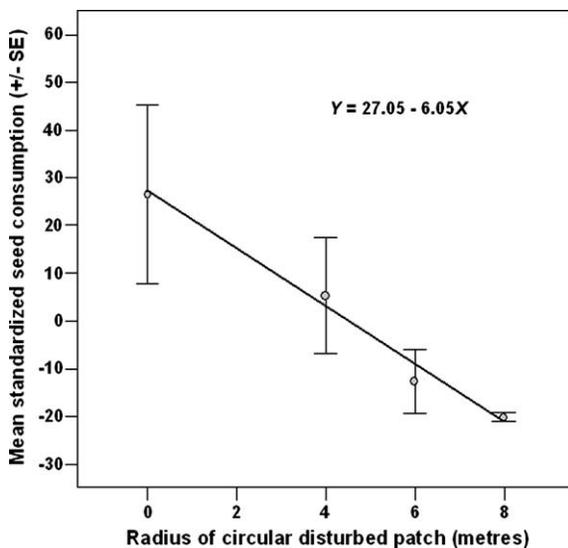
Fig. 5. Mean seeds consumed by meadow voles per plot after habitat disturbance ($\pm$SE) scaled with the length of edge. Seed consumption declined linearly as the radius of a risky patch increased (seeds consumed $= 27.05 - 6.05 \times$ radius, P $= 0.005$, adjusted $R^2 = 0.40$, N $= 16$). Values are standardized as the difference between the observed and expected results (assuming that all seeds were equally likely to be eaten).

optimisation research program (Mitchell and Valone 1990) to help explore how adaptive foragers respond to habitat disturbance.

References

Abramsky, Z., Alfia, H., Schachak, M. et al. 1990. Predation by rodents and the distribution and abundance of the snail *Trochoidea seetzenii* in the Central Negev Desert of Israel. – Oikos 59: 225–234.

Abramsky, Z., Rosenzweig, M. L. and Subach, A. 2002a. Measuring the benefit of habitat selection. – Behav. Ecol. 13: 497–502.

Abramsky, Z., Rosenzweig, M. L. and Subach, A. 2002b. The cost of apprehensive foraging. – Ecology 83: 1330–1340.

Abramsky, Z., Rosenzweig, M. L., Belmaker, J. et al. 2004. The impact of long-term continuous risk of predation on two species of gerbils. – Can. J. Zool. 82: 464–474.

Andersson, M. 1981. Central place foraging in the whinchat, *Saxicola rubetra*. – Ecology 62: 538–544.

Andreassen, H. P. and Ims, R. A. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. – Ecology 82: 2911–2926.

Arcis, V. and Desor, D. 2003. Influence of environment structure and food availability on the foraging behaviour of the laboratory rat. – Behav. Proc. 60: 191–198.

Baker, J. A. and Brooks, R. J. 1982. Impact of raptor predation on a declining vole population. – J. Mammal. 63: 297–300.

Batzli, G. O. 1985. Nutrition. – In: Tamarin, R. H. (ed.), Biology of New World *Microtus*. – Am. Soc. Mammal., Spec. Publ. 8: 779–806.

Bender, D. J, Contreras, T. A. and Fahrig, L. 1998. Habitat loss and population decline: a meta–analysis of the patch size effect. – Ecology 79: 517–533.

Birney, E. C., Grant, W. E. and Baird, D. D. 1976. Importance of vegetative cover to cycles of *Microtus* populations. – Ecology 57: 1043–1051.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – Behav. Ecol Sociobiol. 22: 37–47.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed). – Springer-Verlag.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – Theor. Popul. Biol. 9: 129–136.

Davidson, D. L. and Morris, D. W. 2001. Density-dependent foraging effort of deer mice (*Peromyscus maniculatus*). – Funct. Ecol. 15: 575–583.

Debinski, D. M. and Holt, R. D. 2000. A survey and overview of habitat fragmentation experiments. – Conserv. Biol. 14: 342–355.

Eadie, W. R. 1953. Response of *Microtus* to vegetative cover. – J. Mammal. 34: 263–264.

Efford, M. 1992. Comment-revised estimates of the bias in the 'minimum number alive' estimator. – Can. J. Zool. 70: 628–631.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke river basin, North-Carolina. – Conserv. Biol. 8: 822–832.

Golden, D. M. and Crist, T. O. 2000. Experimental effects of habitat fragmentation on rove beetles and ants: patch area or edge? – Oikos 90: 525–538.

Grand, T. C. and Dill, L. M. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. – Behav. Ecol. 8: 437–447.

Hayes, A. F. 2003. (School of Communication, Ohio State University, Columbus OH. hayes.338@osu.edu). Heteroscedasticity-consistent standard error estimates for the linear regression model: SPSS AND SAS implementation [monograph on the Internet]. Columbus: Ohio State University; c2003 [cited 2004 Sept. 20]. Available from: http://www.jcomm.ohio-state.edu/ahayes

Heroldova, M. 2002. Food selection of *Microtus agrestis* in air-pollution affected clearings in the Beskydy Mts. Czech Republic. – Folia Zool. Suppl. 1: 83–91.

Hilborn, R., Redfield, J. A. and Krebs, C. J. 1976. On the reliability of enumeration for mark and recapture census of voles. – Can. J. Zool. 54: 1019–1024.

Kotler, B. P. 1992. Behavioral resource depression and decaying perceived risk of predation in two species of coexisting gerbils. – Behav. Ecol. Sociobiol. 30: 239–244.

Kotler, B. P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. – Oikos 78: 274–282.

Kotler, B. P. and Blaustein, L. 1995. Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? – Oikos 74: 251–258.

Kotler, B. P., Brown, J. S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. – Ecology 72: 2249–2260.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

Lima, S. L. and Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. – Trends Ecol. Evol. 11: 131–135.

Lin, Y. K. and Batzli, G. O. 2001. The influence of habitat quality on dispersal, demography, and population dynamics of voles. – Ecol. Mongr. 71: 245–275.

LoBue, J. and Darnell, R. M. 1959. Effect of habitat disturbance on a small mammal population. – J. Mammal. 40: 425–437.

Long, J. S. and Ervin, L. H. 2000. Using heteroscedasticity consistent standard errors in the linear regression model. – Am. Stat. 54: 217–224.

Lortie, C. J., Ganey, D. T. and Kotler, B. P. 2000. The effects of gerbil foraging on the natural seedbank and consequences on the annual plant community. – Oikos 90: 399–407.

MacArthur, R. H. and Levins, R. 1964. Competition, habitat selection and character displacement in a patchy environment. – Proc. Natl Acad. Sci. USA 51: 1207–1210.

Manson, R. H. and Stiles, E. W. 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. – Oikos 82: 37–50.

Manson, R. H., Ostfeld, R. S. and Canham, C. D. 1999. Responses of a small mammal community to heterogeneity along forest-old-field edges. – Landscape Ecol. 14: 355–367.

Mech, S. G. and Zollner, P. A. 2002. Using body size to predict perceptual range. – Oikos 98: 47–52.

Mitchell, W. A. and Valone, T. J. 1990. The optimization research program: studying adaptations by their function. – Q. Rev. Biol. 65: 43–52.

Moenting, A. E. 2004. Habitat change and the scale of predation risk. MSc thesis. – Lakehead Univ., Thunder Bay, ON, Canada.

Moody, A. L., Houston, A. I. and McNamara, J. M. 1996. Ideal free distribution under predation risk. – Behav. Ecol. Sociobiol. 38: 131–143.

Nickel, A. M., Danielson, B. J. and Moloney, K. A. 2003. Wooded habitat edges as refugia from microtine herbivory in tallgrass prairies. – Oikos 100: 525–533.

Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. 2003. Niche construction: the neglected process in evolution. – Princeton Univ. Press.

Ostfeld, R. S. and Canham, C. D. 1993. Effects of meadow vole population density on tree seedling survival in old fields. – Ecology 74: 179–1801.

Ostfeld, R. S., Manson, R. H. and Canham, C. D. 1999. Interactions between meadow voles and white-footed mice at forest-oldfield edges: competition and net effects on tree invasion of oldfields. – In: Barrett, G. W. and Peles, J. D. (eds), Landscape ecology of small mammals. – Springer Verlag, pp. 229–247.

Potvin, C., Lechowicz, M. J. and Tardiff, S. 1990. The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. – Ecology 71: 1389–1400.

Pusenius, J. and Schmidt, K. A. 2002. The effects of habitat manipulation on population distribution and foraging behavior in meadow voles. – Oikos 98: 251–262.

Pusenius, J. and Ostfeld, R. S. 2002. Mammalian predator scent, vegetation cover, and tree seedling predation by meadow voles. – Ecography 25: 481–487.

Pusenius, J., Ostfeld, R. S. and Keesing, F. 2000. Patch selection and tree seedling predation by resident vs immigrant meadow voles. – Ecology 81: 2951–2956.

Robinson, G. R., Holt, R. D., Gaines, R. S. et al. 1992. Diverse and contrasting effects of habitat fragmentation. – Science 257: 524–526.

Schweiger, E. W., Diffendorfer, J. E., Holt, R. D. et al. 2000. The interaction of habitat fragmentation, plant, and small mammal succession in an old field. – Ecol. Mongr. 70: 383–400.

Schmitz, O. J., Krivan, V. and Ovadia, O. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. – Ecol. Lett. 7: 153–163.

van Apeldoorn, R., el Daem, M., Hawley, K. et al. 1993. Footprints of small mammals: a field method of sampling data for different species. – Mammalia 57: 407–422.

Zakrzewski, R. J. 1985. The fossil record – In: Tamarin, R. H. (ed.), Biology of New World *Microtus*. Am. Soc. Mammal. Spec. Publ. 8: 1–37.