Habitat change and the scale of predation risk

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Abstract

In their efforts to maximise fitness while reducing the probability of dying, animals must trade off food for safety. The trade-off is likely to depend on habitat and habitat change. I imagine an environment with both safe and risky (manipulated) patches in which foragers can respond by altering their pattern of foraging, by avoidance, or by reduced activity. Analytical models predict that if foragers exploit risky patches, predation risk will either increase with distance from safety, or with the area foraged. But if foragers avoid risky patches, predation risk will either decelerate or decline sigmoidally with area away from the risky patch. The reduction in foraging activity will either scale with the area of the risky patch or with the length of its edge. I tested the models in an abandoned hay field in northern Ontario, Canada, by measuring the foraging activity (incidental predation of sunflower seeds) and abundance of meadow voles (*Microtus pennsylvanicus*) around four sizes of circular risky patches (0-m, 4-m, 6-m, 8-m radius) created by mowing vegetation. Vole abundance and activity was measured before and after habitat manipulation. There was no treatment effect on vole density, and no consistent relationship between vole activity and distance from the edge of risky patches. Incidental predation on sunflower seeds declined linearly with increasing patch circumference (edge). Thus, the habitat dependent patterns in foraging activity of meadow voles, and their predation on lower food levels, correlates with the length of edge habitat. Foragers that reduce their activity around risky patches create enemy-free space for their prey. Adaptive foraging to optimise between food and safety thus has far-reaching consequences that 'cascade' to lower trophic levels. The spatial scale of the cascade depends on how intermediate consumers alter their foraging behaviour.

Introduction

When individuals of a species forage optimally, the distribution of animals in any given area should reflect the relative abundances, qualities, sizes, and configuration of feeding patches. When patches are small, animal distribution is best understood in the context of individual foraging behaviour (see Lima and Dill 1990 for a review, Kotler *et al.* 1991, Kotler 1992). Differences in the quality or size of patches will alter their profitability, and thus the allocation of foraging effort. When some patches are richer than others, for example, optimally foraging individuals that maximise 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 energy return. Foragers often trade-off food for safety (e.g. Sih 1980, Andersson 1981, Grubb and Greenwald 1982, Cerri and Fraser 1983, Werner *et al.* 1983, Lima 1985, Anderson 1986, Gilliam and Fraser 1987, Holbrook and Schmitt 1988, Abrahams and Dill 1989, Nonacs and Dill 1990, Kotler *et al.* 1991, Moody *et al.* 1996, Grand and Dill 1997, Kotler 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). Kotler and Blaustein (1995) found that Allenby's gerbil (*Gerbillus allenbyi*), required eight times more food in open habitat than under shrubs to offset differences in foraging cost caused by predation risk. Similarly, Abramsky *et al.* (1990) built refuges in a 'risky' habitat and observed a significant increase in foraging.

Assuming that predators optimise 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. I begin the search for those relationships by developing simple theories that predict how the area of risky patches should influence foraging risks to fine-grained foragers (MacArthur and Levins 1964). The models predict patterns of forager activity expected inside and outside different sizes of risky patch. I then outline experiments that manipulated the size of risky patches to test the theory in the field. My study of foraging behaviour by meadow voles allowed me to assess whether predation risk varied with the size or perimeter of my patches and whether it varied with distance from safety. Contrary to predictions based on distance and area, voles reduced their foraging effort in direct proportion to the length of edge between risky patches and safe matrix. I conclude with a discussion of the significance of these results to patterns of animal distribution, edge effects, enemy-free space, and community structure.

Theory

Imagine that a homogeneous habitat is modified suddenly. In its new state, the safe matrix contains risky patches of various sizes that are smaller than, or on the same order as, the home range of an animal. Individuals living in the habitat will, if behaving optimally, reassess their foraging strategies to reflect changes in fitness potential they perceive in the two patch types.

Models where foragers exploit risky patches

Consider, first, a fine-grained forager that can use both habitats but must decide how much time to spend in each. If the animal forages randomly, the proportion of time spent in the risky patch should match the proportion of habitat composed of risky patches:

$$T_R/T = A_R/(A_R + A_S) \qquad (1)$$

where T_R is the time in risky patches, T is the total time spent foraging ($T = T_R + T_S$) and, A_i is the area of safe ($_S$) and risky ($_R$) patches respectively. The time spent in each patch is proportional to patch area.

Whereas the encounter of risky patches can be assumed random for fine-grained foragers, the exploitation of the patches may violate this 'patch-match' rule (Eqn. 1) if predation risk accumulates with time spent in the risky patch. As foragers move deeper into the risky patch, and farther from the safe refuge of the matrix, the risk of predation should increase. Assuming a fitness trade-off between food and safety (e.g. Kotler *et al.* 1991), the food energy required to lure the animal into the risky area should also increase with distance (e.g. Todd and Cowie 1990, Brown *et al.* 1992, Hughes and Ward 1993). Imagine that such a forager travels directly into a risky patch to distance d_x in discrete movements of x. Constant x corresponds to the trivial movement distance (e.g. gait) of the organism at constant speed s. If the animal exits to safety by the same route, the total time spent at risk to predation in the patch will increase twofold for every unit distance traveled into the patch.

Exposure time (T_E), then, will increase in a simple linear fashion with distance, d_x ($0 \leq d_x \leq r$), from the edge of the safe matrix such that,

$$T_E = 2sd_x \tag{2}$$

where s represents the speed of travel. The accumulated predation risk encountered by such an individual at any distance from safety will be a function of exposure time and its predation risk as d_x increases. Therefore,

$$\Delta P = (T_E)(R) \tag{3}$$

where ΔP equals the accumulated predation risk while in the patch, and $R = f(d)$ represents instantaneous predation risk at distance d_x. Using Taylor's theorem, R can be expressed as a polynomial in d, that is, $R = a$; $R = a + bd$; $R = a + bd + hd^2$, and so on. Assuming first that R is a constant (every area in the risky patch is equally dangerous), and substituting equation (2) into (3) (Fig. 1A),

$$\Delta P = 2sad_x. \tag{4}$$

Thus, assuming one has a reasonable metric of ΔP, its relationship with distance can be estimated by linear regression.

Next, imagine that instantaneous predation risk increases with distance so that R is linear in d_x. The accumulated predation risk, ΔP, will fit the increasing quadratic equation (Fig. 1B):

$$\Delta P = 2sad_x + 2sb(d_x)^2 \tag{5}$$

If an animal does not exit the risky patch by the same route, the expression ($T_E = g[sd_x]$) will be somewhat more complicated but can still be solved by regression. Higher order functions for R will yield higher order positive relationships for ΔP.

Time spent in the patch could, for a fine-grained forager, increase with the patch area exploited. Mathematically, the problem of determining the risk to the forager from this perspective is most easily addressed with circular patches. Imagine a fine-grained forager that is able to approach a circular risky patch from any direction. The cumulative area an animal can exploit over its trivial movement distance, x, can be estimated by receding annuli inside the patch's perimeter. The area of any given annulus of width x at distance d_x is thus the decelerating function

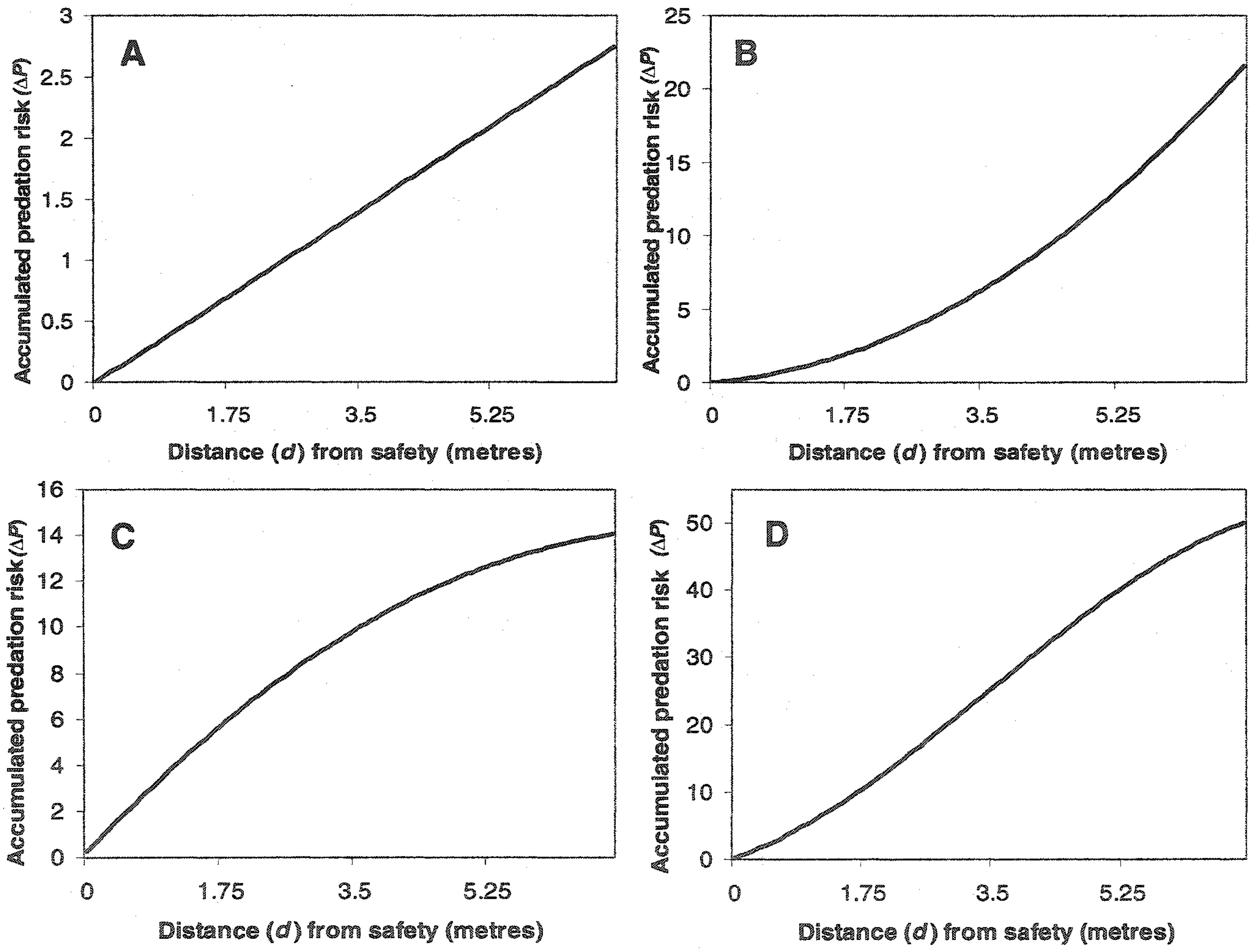
$$A_{\mathrm{n}} = \pi(r - d_x + x)^2 - [\pi(r - d_x)^2] \tag{6}$$

where A_{n} is the area of the annulus, and r is the radius of the risky patch. One way to model this scenario is to sum the total predation risk across all exploited annuli of width x.

Figure 1: Four potential relationships between accumulated predation risk and distance from safety for a fine-grained forager. (A) Exposure time increases linearly with distance from safety but instantaneous predation risk does not ($\Delta P = 2sad$), (B) both instantaneous predation risk and exposure time increase linearly with distance ($\Delta P = a2sd + b2sd^2$), (C) exposure time increases linearly with the total annulus area exploited and instantaneous predation risk is a constant ($\Delta P = \sum_{i=1}^{j} \alpha\pi\,[(2axr + ax^2) + (2ax)d_{xi}]$), (D) exposure time is proportional to the area exploited and instantaneous predation risk increases linearly with distance from safety

($\Delta P = \sum_{i=1}^{j} \alpha\pi\,[(2axr + ax^2) + (2bxr - 2ax + bx^2)d_{xi} - (2bx)(d_{xi})^2]$).

Parameter values as follows: $\alpha = 0.7$, $a = 0.1$, $b = 0.1$, $r = 8$, $s = 2$, $x = 0.07$.

A
B
C
D
Accumulated predation risk (ΔP)
Distance (d) from safety (metres)
0
1.75
3.5
5.25
0
0.5
1
1.5
2
2.5
3
0
5
10
15
20
25
0
2
4
6
8
10
12
14
16
0
10
20
30
40
50

As a fine-grained forager travels deeper into a patch, the time of exposure to predation will increase in proportion to the total size of all annuli it exploits. So,

$$T_E = \sum_{i=1}^{j} \alpha A_{\mathrm{n}} = \sum_{i=1}^{j} \alpha\pi(2xr - 2r(d_{xi})x + x^2) \tag{7}$$

where α is a scaling constant to convert area into exposure time. Substituting equation (7) into equation (3), the accumulated predation risk at d_x can be approximated by

$$\Delta P = \sum_{i=1}^{j} \alpha\pi(2xr - 2r(d_{xi})x + x^2)(R).$$

If R is constant (a), predation risk can be modeled by (Fig. 1C)

$$\Delta P = \sum_{i=1}^{j} \alpha\pi[(2axr + ax^2) + (2ax)d_{xi}]. \tag{8}$$

Finally, if R is linear in d, the best solution will be (Fig. 1D)

$$\Delta P = \sum_{i=1}^{j} \alpha\pi[Q + Ed_{xi} - F(d_{xi})^2] \tag{9}$$

where Q, E, and F represent the constant and scalars in equation (9) respectively ($[2axr + ax^2]$,$[2bxr - 2ax + bx^2]$, and $[2bx]$). Please note that, as in any 'integral', the final cumulative solution for ΔP will be one order higher than equations (8) and (9). In Eqn. (9), for example, the area of the annulus decreases with the square of distance. So when risk increases linearly, the accumulated predation risk yields a cubic function (when $i > 1$).

Note, as well, the difference between models that assume exposure time is related to distance and those that assume exposure time is related to area. Distance models have the same form regardless of patch area (Eqns. 4 and 5) whereas area models vary with patch sizes (Eqns. 8 and 9 include the circle's radius). By using circular risky patches of different size, I can test whether total predation risk depends on distance or area, and whether the instantaneous risk of predation increases with distance or area.

Models where foragers avoid risky patches

Habitat change can produce patches so risky that individuals will not use them. If the edge of a patch is very abrupt, animals may view the edge as a habitat boundary and avoid it completely (e.g. Manson *et al.* 1999, Nickel *et al.* 2003).

I can model patch avoidance by imagining that there is some average background level of predation risk (A) in the safe habitat at distance K from the centre of the circular risky patch. As individuals move from K toward the patch's perimeter, the instantaneous predation risk (R) can remain constant or increase with distance D_x from K ($0 \leq D_x \leq [K\text{-}r]$; Fig. 2). As an animal is foraging, the risk should increase as it approaches the patch edge in the same way it increases with area foraged if it exploits the risky patch (Eqns. 8 and 9). Thus, if R is equal to constant A, then

$$\Delta P = \sum_{i=1}^{j} \gamma\pi(2AKx + Ax^2 - 2AxD_{xi}), \tag{10}$$

which is the same form as Eqn. (8). Or, if R is linear in D, then the accumulated predation risk should increase toward the risky patch sigmoidally in the same form as Eqn. (9)

$$\Delta P = \sum_{i=1}^{j} \gamma\pi[G + H(D_{xi}) - I(D_{xi})^2] \tag{11}$$

where G, H, and I represent the constant and scalars respectively ($[2AxK + Ax^2]$, $[2BxK - 2Ax + Bx^2]$, and $[2Bx]$).

I do not know the value of K, and thus I cannot measure D_x. But I do know that ΔP reaches its maximum value (ΔP_{max}) at the edge of the risky patch. Thus, if we define d'_x as the distance moving outward from the patch's perimeter (Fig. 2) and then substitute (K - r - d') for D_x, the decline in total predation risk moving away from the risky patch (when $R = A$) is given by (Fig. 3)

$$\Delta P' = \Delta P_{max} - \sum_{i=1}^{j} \gamma\pi[(2Axr + Ax^2) + (2Ax)d'_{xi}]. \qquad (12)$$

Whereas if R varies linearly with distance, then total decline in predation risk is (Fig. 3),

$$\Delta P' = \Delta P_{max} - \sum_{i=1}^{j} \gamma\pi[J + Ld'_{xi} - N(d'_{xi})^2]. \qquad (13)$$

where J, L, and N correspond respectively to the constant and scalars in Eqn (13) ([$2Axr + Ax^2 + 2BxKr - 2Bxr^2 + BKx^2 - Brx^2$], [$2Ax + 2BKx - 4Bxr - Bx^2$], and [$2Bx$]). By creating circular risky patches, and monitoring their use, I can determine whether animals' avoidance of risky patches is based on a constant risk of predation outside the patch (Eqn. 12) or a declining risk (Eqn. 13). By creating patches of different sizes, I can detect whether accumulated predation risk depends on the area disturbed (the patch radius is included in both equations).

Figure 2: Schematic illustration of the model used to evaluate accumulated predation risk ($\Delta P'$) of a foraging individual that uses the matrix but avoids a circular risky patch (shading). K represents the distance where predation risk equals the background level of risk, and D_x ($0 \leq D_x \leq (K - r)$) is the distance exploited by the forager. Distance outward from the edge of the circular risky patch (bold circle) is represented by d'_x.

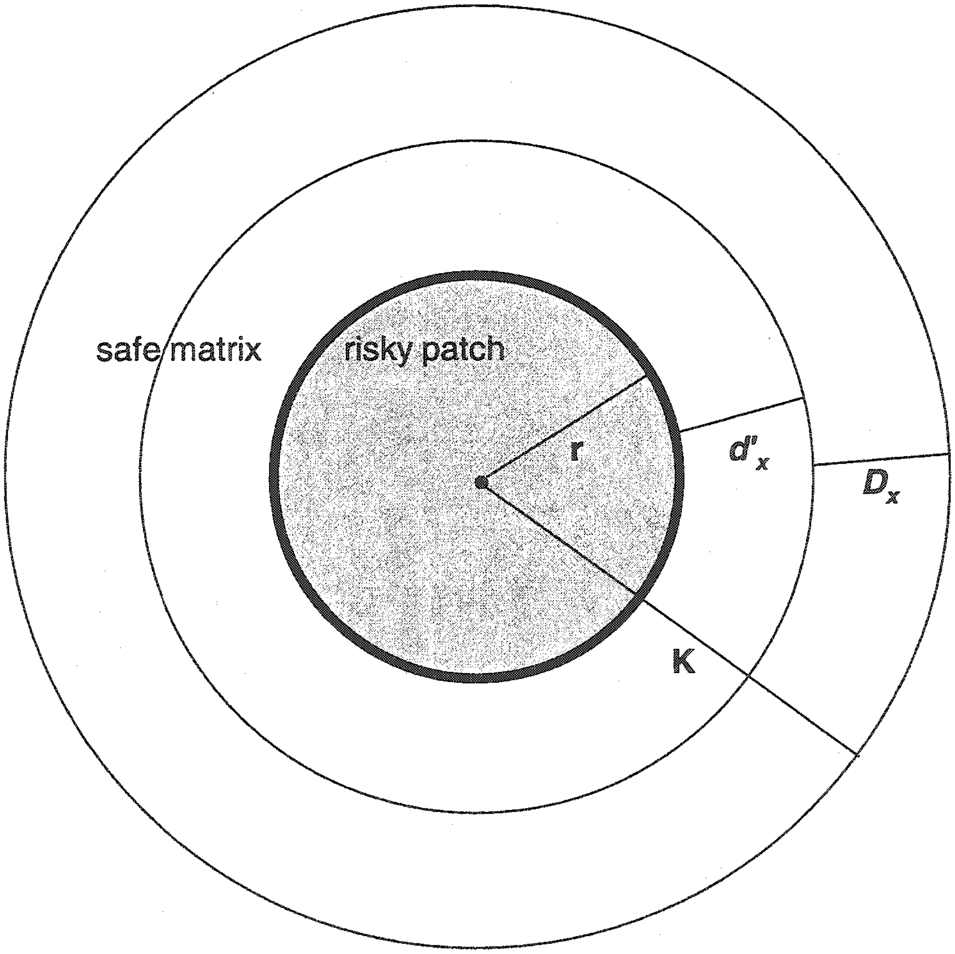
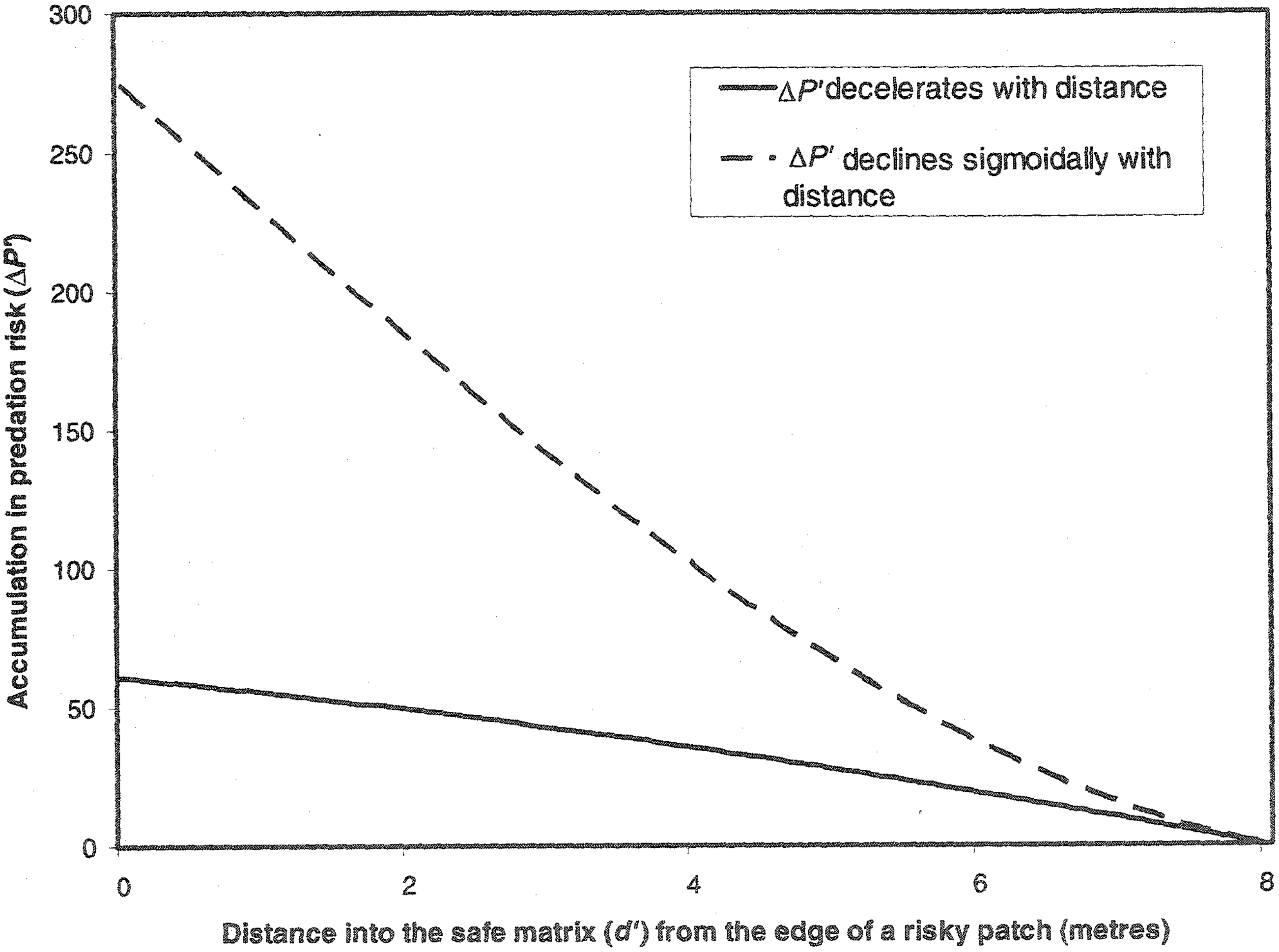

safe matrix
risky patch
r
d'x
Dx
K

Figure 3: Simulations of accumulated predation risk where foragers avoid risky patches. The decelerating solid line depicts how accumulated predation risk decreases away from the risky patch if instantaneous risk is constant in the safe matrix ($R = A$; $\Delta P' = \Delta P_{max} - \sum_{i=1}^{j} \gamma\pi[(2Axr + Ax^2) + (2Ax)(d')_{xi}]$). The alternative model predicts that accumulated predation risk will decline sigmoidally toward zero as instantaneous predation risk increases with distance toward the risky patch $R = A + BD_x$;

$$\Delta P' = \Delta P_{max} - \sum_{i=1}^{j} \gamma\pi[(2Axr + 2Ax^2 + 2BxKr - 2Bxr^2 + 2BKx^2 - Brx^2)$$

$$+ (2Ax + 2BKx - 4Bxr - Bx^2)d'_{xi} - (2Bx)(d'_{xi})^2])$$. Parameter values as follows:

$\gamma = 0.5, A = 0.1, B = 0.1, x = 0.08, r = 8, K = 16$.


ΔP'decelerates with distance
ΔP' declines sigmoidally with distance
Accumulation in predation risk (ΔP')
Distance into the safe matrix (d') from the edge of a risky patch (metres)
0
50
100
150
200
250
300
0
2
4
6
8

Models of reduced forager activity

Foragers faced with dramatic but small-scale disturbance patches in their habitat may alter their activity in various ways. Animals may, (1) alter their exploitation of a risky patch with distance from the disturbance, (2) shift their foraging away from the patch, or leave the vicinity of the disturbance, (3) not use the altered habitat, (4) reduce their foraging and engage in other fitness enhancing activities (Charnov *et al.* 1976, Brown 1988), and (5) employ some combination of these strategies.

I can model reduced foraging activity in a similar way that I modeled accumulated predation risk. Consider first a 'null model' corresponding to options 1 to 3 where average activity declines in direct proportion to the area of disturbed habitat. Then,

$$C = M - \sigma A \qquad (14)$$

where C represents average activity, A represents the area of the disturbed patch, σ is a scaling constant, and M is the baseline activity in undisturbed habitat. Then, assuming circular patches of disturbance,

$$\mathrm{C} = M - \sigma(\pi r^2) \qquad (15)$$

where r is the radius of the patch (Fig. 4).

Alternatively, foragers may reduce their activity in proportion to the amount of 'edge' habitat. Animals that cannot afford to use the risky patch may not perceive its entire size and may therefore judge risk by the amount of edge they encounter (e.g. animals do not avoid the disturbed habitat, but the indirect influence of predators from risky patches increases the cost of foraging [options 4 and 5]). Again assuming a circular patch of disturbed habitat,

$$C = M - \rho(2\pi r) \qquad (16)$$

where ρ is a scaling constant (Fig. 4).

Note, in the area model, that animal activity will scale with the square of the radius of a circular patch. With the edge model, activity scales linearly with the radius.

Model summary and predictions

Assuming that change in foraging activity is the complement of the change in predation risk, then:

(1) If foragers exploit circular risky patches,

    if they are at equal risk everywhere in the disturbed patch,

        and if exposure time depends on distance from safety,

            (a) then forager activity will decrease linearly with distance into the patch

                (Eqn. 4, $\Delta P = 2sad_x$).

...   and if exposure time depends on the area foraged,

            (b) then forager activity will decelerate with distance into the patch

                (and vary with patch radius, Eqn. 8,

$$\Delta P = \sum_{i=1}^{j} \alpha\pi[(2axr + ax^2) + (2ax)d_{xi}]).$$

    but if their risk increases with distance from safety,

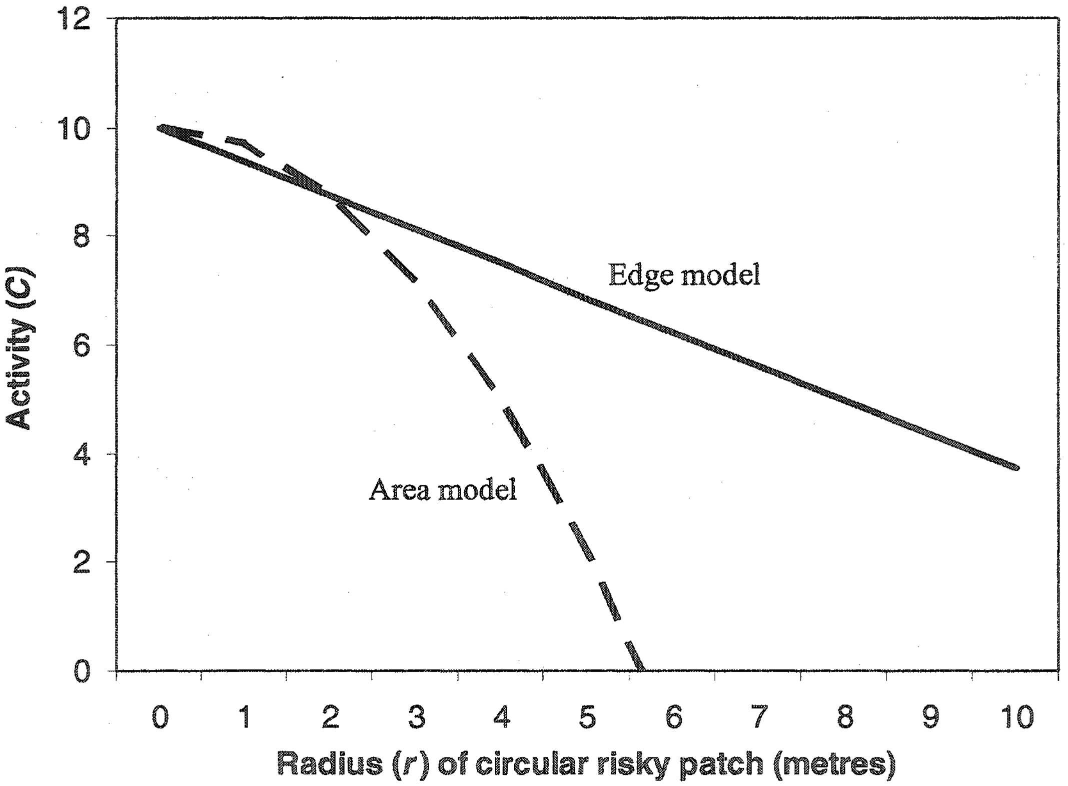
        and their exposure time increases with distance from safety,

            (c) then forager activity will decrease exponentially with distance into the

                patch (but be independent of patch radius,

                Eqn. 5, $\Delta P = 2sad_x + 2sbd_x$)

Figure 4: Comparison of two models demonstrating reduced activity with increasing radius of a circular risky patch. The 'null' area model (dashed line) is curved downward ($C = M - \sigma[\pi r^2]$). The alternative 'edge model' (solid line) is linear ($C = M - \rho[2\pi r]$). Parameter values as follows: $M = 10$, $\sigma = 0.1$, $\rho = 0.1$.


12
10
8
6
4
2
0
Activity (C)
0
1
2
3
4
5
6
7
8
9
10
Radius (r) of circular risky patch (metres)
Edge model
Area model

... and if exposure time depends on area foraged,

(d) then forager activity will decline sigmoidally with distance into the risky patch (Eqn. 9, $\Delta P = \sum_{i=1}^{j} \alpha\pi[Q + Ed_{xi} - F(d_{xi})^2]$).

(2) If foragers avoid circular risky patches,

if exposure time depends on area foraged,

and if foragers are at equal risk everywhere in the safe matrix,

(a) then forager activity will accelerate with distance into the safe matrix from the patch edge toward a mean background rate of activity (Eqn. 12, $\Delta P' = \Delta P_{max} - \sum_{i=1}^{j} \gamma\pi[(2Axr + Ax^2) + (2Ax)d'_{xi}]$).

... and if instantaneous predation risk increases linearly toward the risky patch,

(b) then activity will increase sigmoidally with distance away from the patch (Eqn. 13, $\Delta P' = \Delta P_{max} - \sum_{i=1}^{j} \gamma\pi[J + Ld'_{xi} - N(d'_{xi})^2]$).

(3) If foraging activity is reduced

in direct proportion to the area of the circular risky patch,

(a) then activity will decline exponentially with radius of the risky patch (Eqn. 15, $C = M - \sigma[\pi r^2]$).

in direct proportion to length of edge of the circular risky patch,

(b) then activity will decline linearly with the radius of risky patches (Eqn. 16, $C = M - \rho[2\pi r]$).

Study species

I tested the theoretical 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, Appendix 1), has been used previously as a model system for studies of habitat fragmentation (e.g. Schweiger *et al.* 2000), habitat use and population dynamics (e.g. Lin and Batzli 2001).

Microtus density increases with plant cover (e.g. 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).

Patch use by meadow voles has far-reaching implications, not just to vole density and distribution, but also to the community structure of their prey. Enemy-free space for plants, measured by the incidental consumption of oat seeds placed in a regular grid, was greater in mowed patches than in adjacent unmowed areas (Pusenius and Schmidt 2002). Meadow voles reduce the establishment of the plant and tree species they consume, and thus play an important role in the composition of the entire community (Ostfeld and Canham 1993, Pusenius *et al.* 2000).

Study site and field methods

An assistant and I created risky patches within a recently abandoned hay field near Thunder Bay, Ontario (48° 17' 30" N, 89° 38' 10" W) during 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 three-m intervals. At the time of the study, the pine seedlings were less than 0.5 m tall. Appendix 2 includes a more detailed site description as well as a list of common plants, potential vole predators, and photos.

Field design

I subdivided the field into four locations (minimum distance between locations ≥ 50 m, Fig. 5A). I employed a stratified design within each location by establishing four 30 m x 30 m square study plots separated by 40 m. Live-trap stations were located in a regular grid at 10-m intervals. I superimposed a 20 m x 20 m 'activity' grid consisting of 121 sampling points, each 2 m apart, onto the study plots. Each grid was centred on a plot. I measured vole activity by presence or absence of tracks in tracking tubes and by the incidental predation of seeds (e.g. Pusenius and Schmidt 2002; Fig. 5B). I estimated vole density by live-trapping.

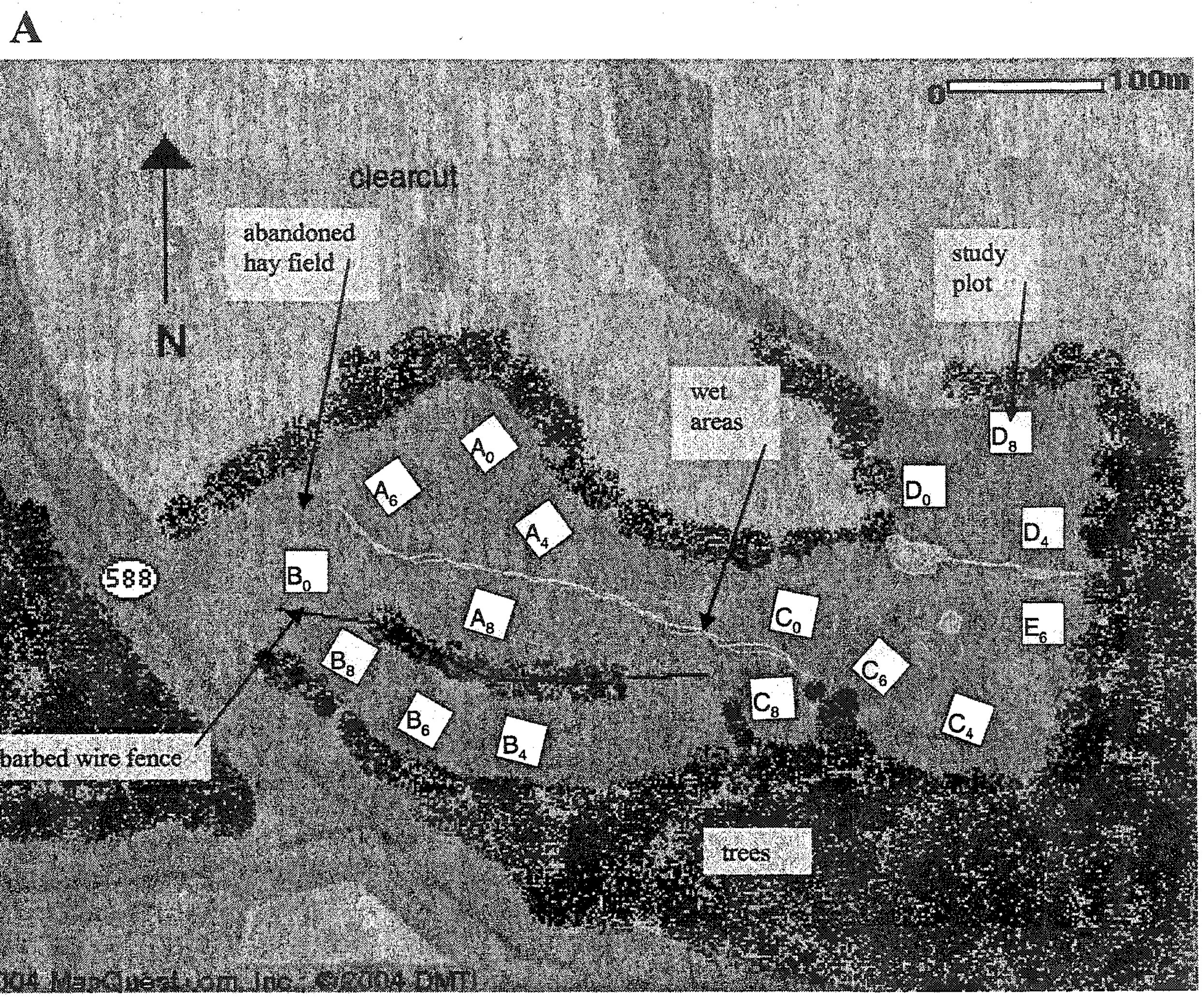
I began collecting 'control' data in May before habitat manipulation (Appendix 3). I mowed circular risky patches with a clothesline trimmer in July. I assigned patches of 0-m (control), 4-m, 6-m, or 8-m radius randomly to the plots within each location (Fig. 5A). I cut all vegetation (except red pine seedlings) to a height of approximately 5 cm, thus creating clear differences between covered matrix (safe) and risky patches. I mowed again three weeks later. I tested the theory by comparing pre-mowing (control) data with post-mowing (treatment) data. I finished data collection in August, 2003 (Appendix 3).

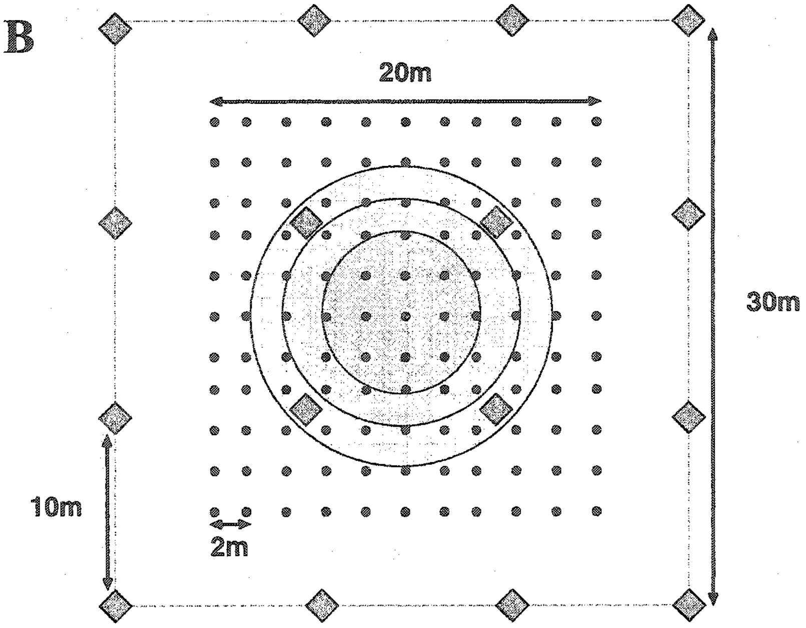
Density estimates

I 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 measures of activity. Animals were live-trapped at approximately three-week intervals (beginning May 19 and ending August 19, 2003; Appendix 3) 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 5B). I baited each trap with oats, peanut butter, a potato wedge, and cotton mattress stuffing. I checked the traps at twilight and at dawn for two days. Dirty traps were collected, washed with detergent, sanitised with a bleach solution and dried before being reset. I measured the body and tail length of each vole captured, and weighed, sexed, and marked it using a uniquely numbered ear tag (Lakehead University Animal Care Committee Protocol no. 2002-02).

I used the number of different animals captured on each plot during the trapping sessions before and after habitat manipulation to determine any effects of habitat manipulation 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 (e.g. Efford 1992). Capture probabilities of the population from which I sampled are unlikely to vary among the plots because all were within the same 10 ha field. Any bias in actual density estimates should be similar among plots.

Figure 5: (A) Approximate size and location of the sampling plots in an abandoned hay field near Thunder Bay, Ontario. The squares within the field represent the placement of the four 30 m x 30 m treatment plots nested within each of four replicate locations (labeled A, B, C, and D). The subscripted numbers at each plot represent the radius of the circular risky patches I created. (B) 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 m x 20 m 'activity' grid (2 m spacing). Diamonds represent the 30 m x 30 m live-trapping grid (10 m spacing).


A
0
100m
clearcut
N
abandoned hay field
study plot
wet areas
588
A_0
A_6
A_4
A_8
B_0
B_8
B_6
B_4
C_0
C_6
C_8
C_4
D_8
D_0
D_4
E_6
barbed wire fence
trees
©2004 MapQuest.com, Inc.; ©2004 DMTI


B
20m
30m
10m
2m

Activity estimates

I tested the alternative models empirically in the field using two measurements of activity. First, I examined patterns of food removal by recording consumption of single sunflower seeds (*Helianthus annus*) placed in a systematic grid (Pusenius and Schmidt 2002). Second, I used the presence or absence of vole tracks in tracking-tubes (Davidson and Morris 2001).

I placed an individual black sunflower seed at every stake-wire flag marking each 2 m x 2 m intersection of the activity plot. Seeds were placed in small depressions at the base of the stake-wire flags so that I could identify those that were consumed by voles. Other potential seed predators included birds and shrews (*Sorex* spp.), but I found little evidence that these animals exploited the seeds. The placement of seeds in depressions minimised their possible discovery by birds, and shrews caught in our traps did not consume seeds. I checked for seed presence or absence after three nights and removed all remaining seeds and hulls at that time.

I 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 mm x 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.

Enemy-Free Space

I used the seed consumption and tracking tube data to quantify differences in the amount of enemy-free space (plants are 'free' of their vole herbivores; sensu Pusenius and Schmidt 2002) for plants among plots caused by the different manipulation sizes. I calculated the

Euclidean distance from the centre of each plot to each tracking and seed-placement sample point (19 different distance values). I standardised the data by calculating the proportion of all seeds consumed or of all tubes with tracks over the 16 experimental plots. These proportions, calculated separately prior to and post-manipulation, allowed me to correct for any changes in preference for seeds by the voles as the season progressed (Batzli 1985, Heroldova 2002). For each plot, I 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, I calculated the spatial pattern of seed consumption by subtracting the expected number from the observed number of seeds consumed. These 'corrections' compensated for unequal sampling effort with distance as well as the very low activity of voles within the risky patches (see results, below). I also calculated the difference between expected and observed numbers of seeds consumed (and tubes tracked) for entire plots. These data were used to compare activity across the treatment sizes, and to test the reduced-activity model.

Statistical design

Density

I 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, manipulation (before and after manipulating plots) was the within-subjects factor.

Activity

I tested for differences in activity prior to habitat manipulation by using a univariate ANOVA with radius of the future circular risky patches as a fixed factor. I used univariate repeated measures ANOVA, following the guidelines of Potvin *et al.* (1990), to evaluate the influence of manipulation on my estimates of tracking-tube activity and seed consumption. Again, manipulation was the within-subjects factor, and distance and patch radius were fixed factors in the analysis. I used *a priori* polynomial contrasts of the distance and radius factors to test for the linear, quadratic, and cubic predictions of the predation-risk and activity models.

I completed my analyses with a polynomial regression of seed consumption after manipulation against patch radius to evaluate the 'reduced activity' model. I calculated Akaike's Information Criterion for 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

I caught a total of 196 individual voles, 95 of which were recaptured at least once (see Appendix 1 for vole census data). There were few mammalian competitors inhabiting the field. I captured only one least chipmunk (*Tamias minimus*), one Arctic shrew (*Sorex arcticus*), and recorded eight captures of masked shrews (*Sorex cinerus*). 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 'manipulation by radius interaction' was not significant ($F_{3,12} = 1.26$, $P = 0.33$) and vole numbers did not change significantly after habitat manipulation ($F_{1,12} = 1.18$, $P = 0.30$; Fig. 6).

Vole activity was similar on all plots before habitat manipulation

Though activity varied substantially from one plot to the next, there was no significant difference among plots in seed consumption before habitat manipulation ($F_{3,11} = 0.35$, $P = 0.79$; Fig. 7A). Similarly, there was no significant difference among plots in the number of tracked tubes before habitat manipulation ($F_{3,12} = 0.94$, $P = 0.45$; Fig. 7B).

Habitat manipulation and patch radius explained variation in vole activity

Seed consumption

Voles consumed 288 seeds before habitat manipulation (15 experimental plots sampled once each) and they consumed 458 seeds after manipulation (16 plots). The expected number of seeds consumed per plot before manipulation was 19.2 versus 28.6 after manipulation. Thus, voles ate more seeds after manipulation than before (Table 1, $F_{1,209} = 8.94$, $P = 0.003$, Table 2). There was also a significant interaction between manipulation and radius ($F_{3,209} = 44.32$, $P < 0.001$, Table 2). The interaction occurred because seed consumption increased for the control and 4-m radius patch treatments, but declined in the 6-m radius, and 8-m radius treatments after manipulation (Table 1).

Seed consumption did not vary significantly with distance among treatments even though voles rarely entered the risky patches ($F_{18,209} = 0.40$, $P = 0.99$, Fig. 8, Table 2). This result is inconsistent with the models where voles exploit or avoid the risky patches. Seed consumption varied inversely with the radius of the mowed patch ($F_{3,209} = 15.32$, $P < 0.001$, linear contrast, $P < 0.001$, Table 2). The inverse relationship was caused primarily by reduced foraging outside of the risky patches (Fig. 9A).

Figure 6: Mean population density of voles (±SE, N = 4) did not change significantly after habitat manipulation. Closed bars represent vole abundance before manipulation. Open bars represent vole density following manipulation.

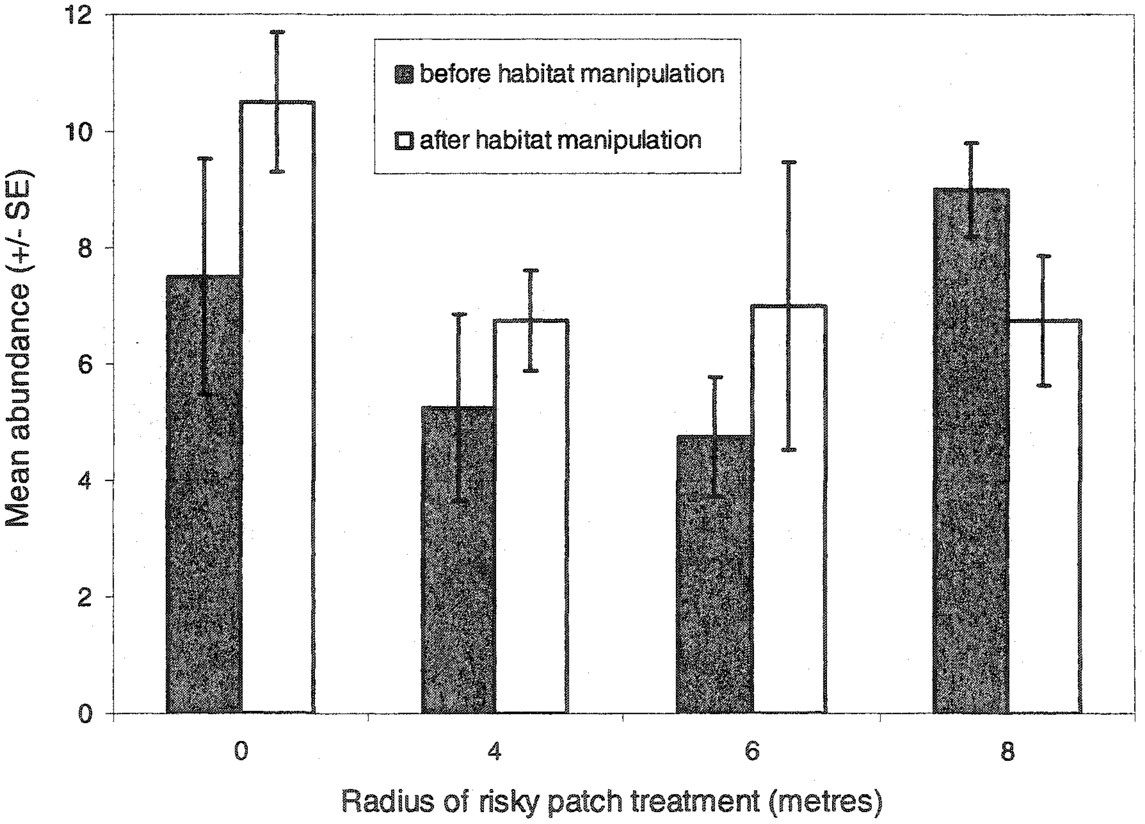
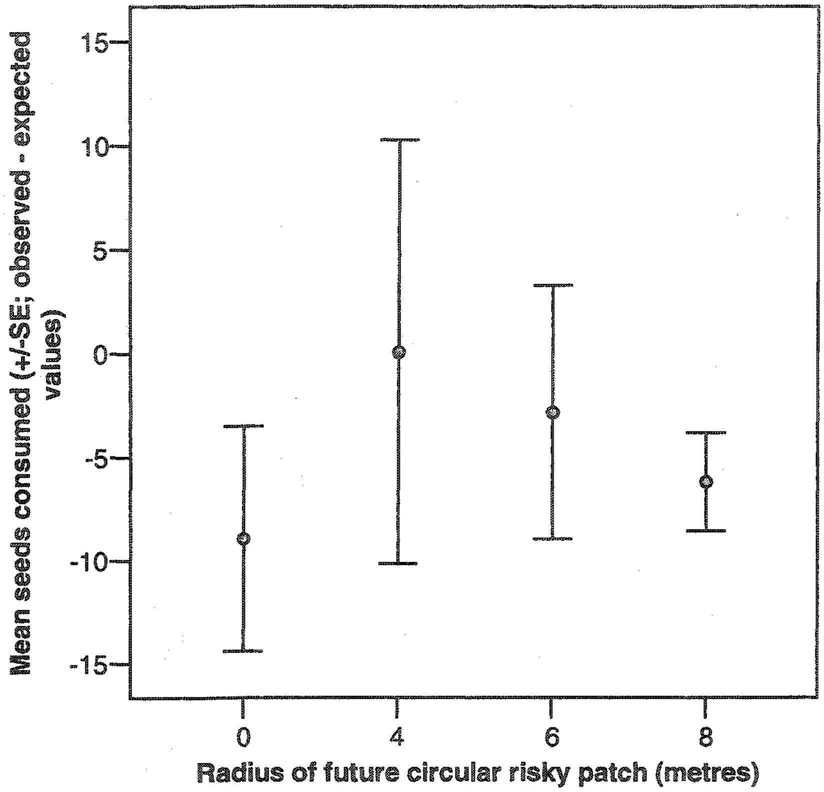

12
10
8
6
4
2
0
Mean abundance (+/- SE)
before habitat manipulation
after habitat manipulation
0
4
6
8
Radius of risky patch treatment (metres)

Figure 7: Comparison of two measures of activity prior to habitat manipulation. There was no significant difference in (A) mean seed consumption (±SE, N = 4), or (B) mean tubes tracked (±SE, N = 4) among future treatment sizes. Values correspond to the difference between observed and expected results. A value of zero indicates that the number of seeds consumed (or tubes tracked) was equal to that expected from the entire (pre-manipulation) data set. Negative values occur when the number of seeds consumed (or tubes tracked) was less than expected.

A


Mean seeds consumed (+/-SE; observed - expected values)
15
10
5
0
-5
-10
-15
0
4
6
8
Radius of future circular risky patch (metres)

B

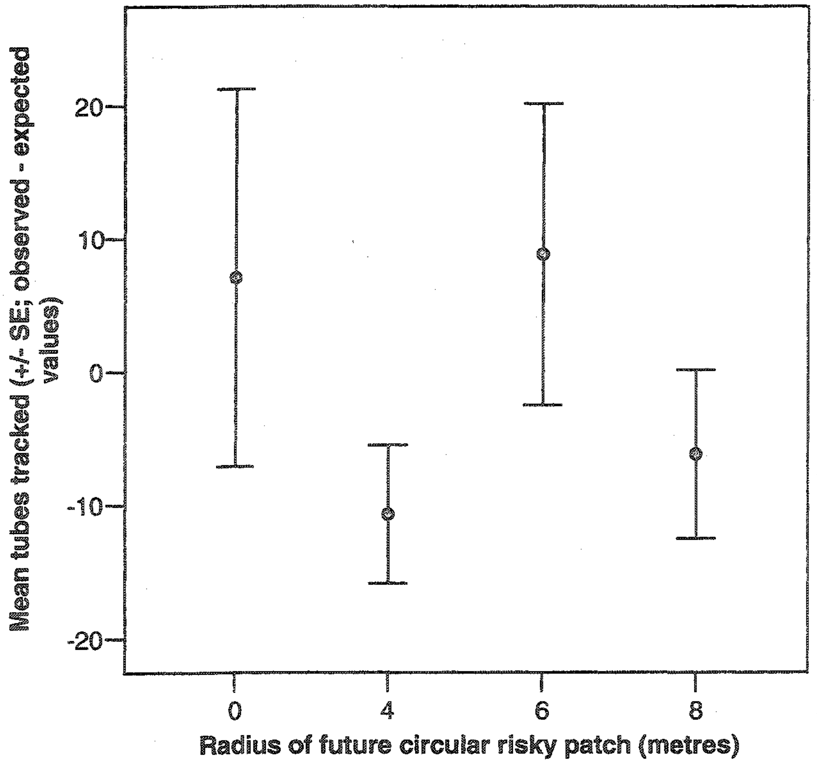

Mean tubes tracked (+/- SE; observed - expected values)
20
10
0
-10
-20
0
4
6
8
Radius of future circular risky patch (metres)

Table 1: Mean (observed - expected values, and standard errors) seeds consumed by voles, and mean number of tubes with vole tracks, (N = 4) in an abandoned hay field in northern Ontario, Canada. Habitat manipulation was accomplished by mowing circular risky patches of vegetation.

		seeds consumed		tubes tracked	
radius of patch	**pre- or post-manipulation**	**mean**	**SE**	**mean**	**SE**
0 m	pre-	-8.95	6.575	7.06	9.962
	post-	26.62	12.112	12.69	7.828
4 m	pre-	0.05	6.575	-10.69	9.962
	post-	5.37	12.112	-8.56	7.828
6 m	pre-	-2.87	7.592	8.81	9.962
	post-	-9.96	13.985	12.19	7.828
8 m	pre-	-6.20	6.575	-6.19	9.962
	post-	-20.13	12.112	-16.81	7.828

Table 2: Summary of the repeated measures ANOVA on seeds consumed by meadow voles (*M. pennsylvanicus*). Vole foraging did not vary with distance from the edge of the risky patch. The manipulation by radius interaction remained significant when the distance factor was removed from the analysis.

Source	*df*	*MS*	*F*	*P*
Within-subject factors				
manipulation (m)	1	9.907	8.936	**0.003**
m by distance (d)	18	0.951	0.858	0.630
m by radius (r)	3	49.140	44.324	**<0.001**
m by d by 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**
d by 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

Figure 8: Mean seeds consumed (±SE, N = 4) at each distance from the centre of each plot after habitat manipulation. There was no pattern in seed consumption with distance for any of the treatments. Negative values occur when the number of seeds consumed was less than the expected values at that distance. Control (unmowed) plots are represented by circles, 4-m radius plots by triangles, 6-m radius plots by crosses, and 8-m radius plots by squares.

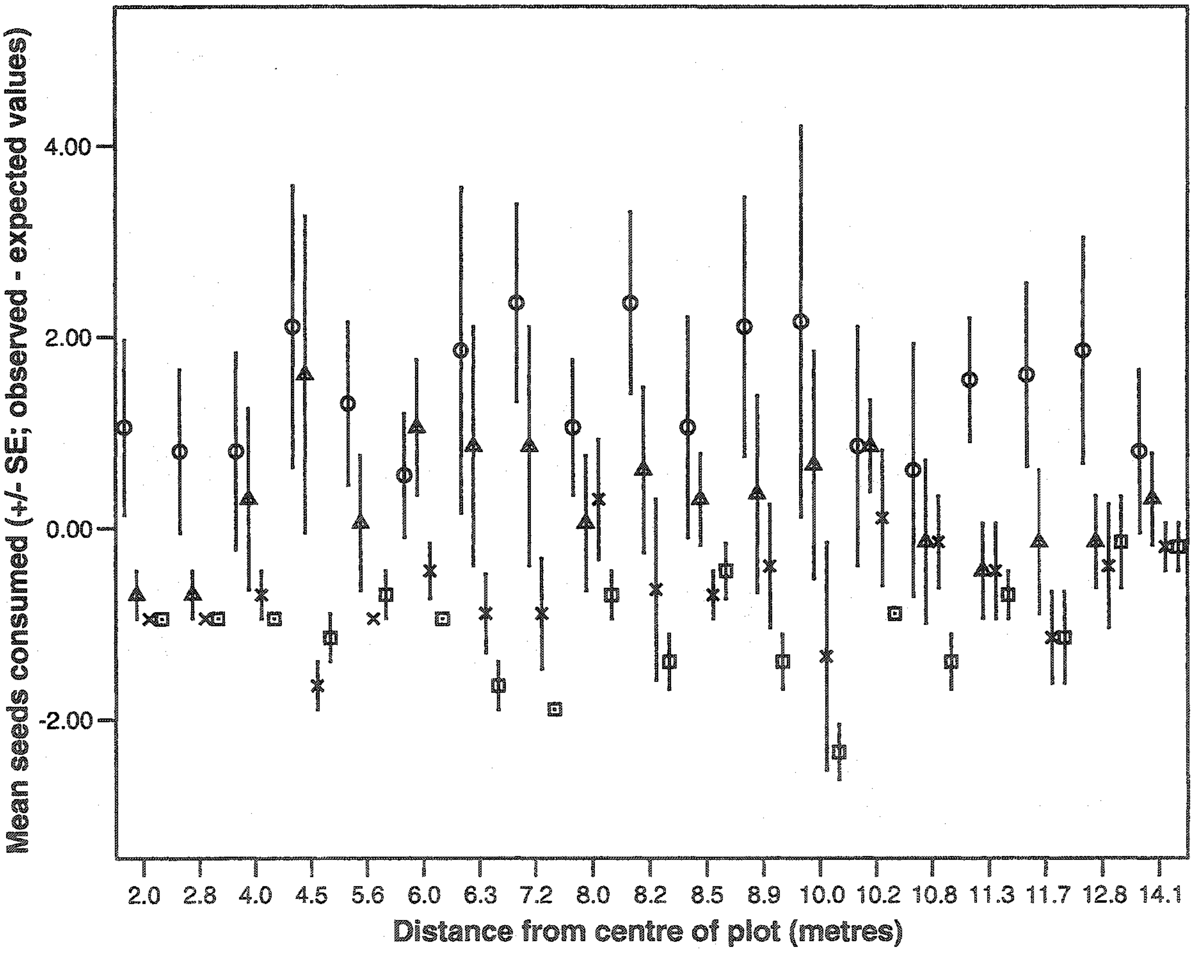
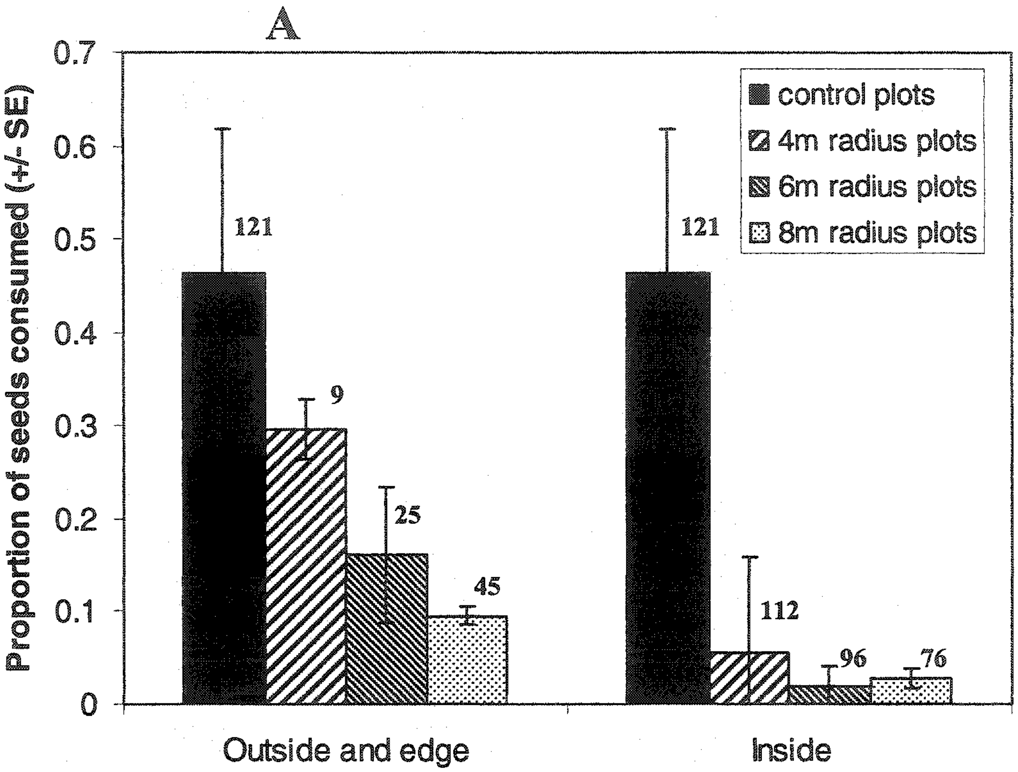

Mean seeds consumed (+/- SE; observed - expected values)
4.00
2.00
0.00
-2.00
2.0
2.8
4.0
4.5
5.6
6.0
6.3
7.2
8.0
8.2
8.5
8.9
10.0
10.2
10.8
11.3
11.7
12.8
14.1
Distance from centre of plot (metres)

Figure 9: (A) The mean proportion of seeds consumed (±SE, N = 4) by meadow voles declined linearly outside of risky patches but was low and more-or-less constant inside (post-manipulation data only). (B) No tubes contained vole tracks inside the risky patches (±SE, N = 4). Numbers correspond to the total availability of seeds or tracking tubes in control (solid bars), 4-m (coarse hatching), 6-m (fine hatching), and 8-m radius patches (stippling) respectively.


A
Proportion of seeds consumed (+/- SE)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
■ control plots
▨ 4m radius plots
▧ 6m radius plots
▩ 8m radius plots
121
9
25
45
121
112
96
76
Outside and edge
Inside

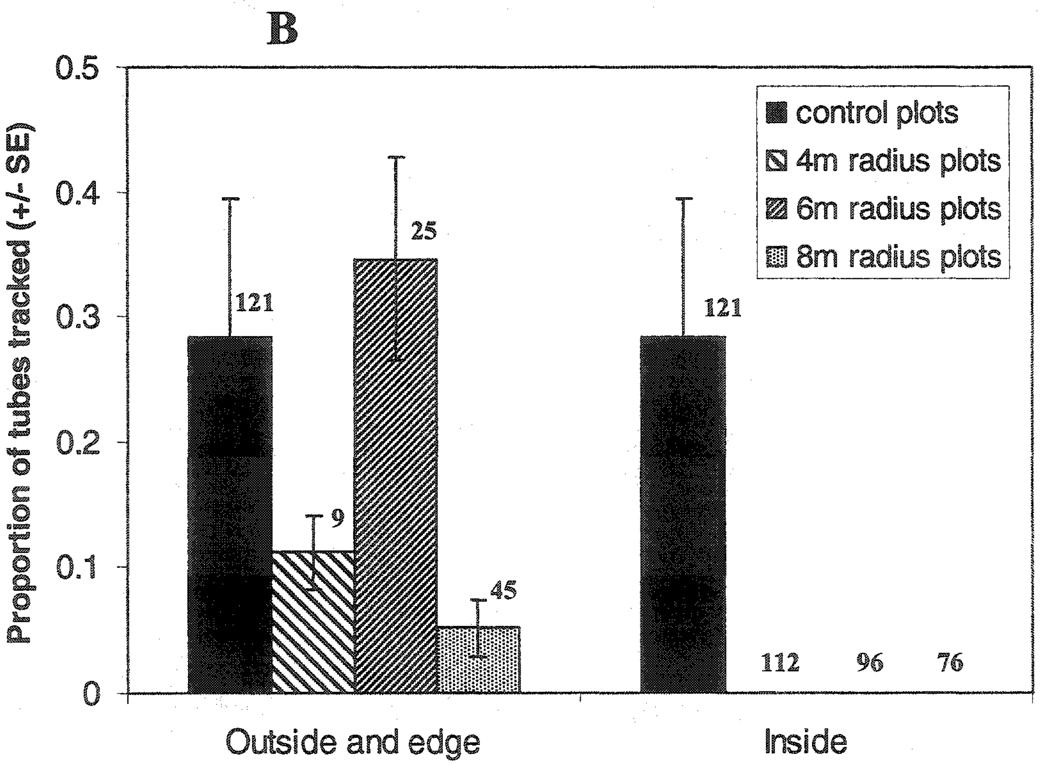

B
Proportion of tubes tracked (+/- SE)
0.5
0.4
0.3
0.2
0.1
0
■ control plots
▧ 4m radius plots
▨ 6m radius plots
▩ 8m radius plots
121
9
25
45
121
112
96
76
Outside and edge
Inside

Table 3: 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				
manipulation (m)	1	0.003	0.002	0.962
m by distance (d)	18	1.688	1.086	0.368
m by radius (r)	3	5.627	3.619	**0.014**
m by d by 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**
d by r	54	2.069	1.148	0.244
error	228	1.803		

Polynomial contrasts 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

Tracking tubes

On 16 plots sampled once each for activity, voles entered 403 tubes before and 337 tubes after habitat manipulation. Meadow voles did not enter tracking tubes within the circular risky patches (Fig. 9B), and there was no pattern in the number of tracked tubes with distance ($F_{3,228}$ = 1.09, $P = 0.37$, Table 3). Fewer tubes contained tracks in the 4-m radius and 8-m radius treatment sizes than in the controls and 6-m radius treatments ($F_{3,228}$ = 33.67, $P < 0.001$, Fig. 10). The differences were not caused by the manipulation (21% of tubes were tracked per plot before manipulation, 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. 10). However, only the 8-m radius plots had fewer tubes tracked after the creation of risky patches than before (Table 1, Fig. 10). The reduction in the number of tubes tracked on the 8-m plots caused a significant interaction between manipulation and radius (treatment size, $F_{3,228}$ = 3.62, $P = 0.01$, Table 1, Table 3).

Caveats

Some readers might wonder whether an analysis based on proportions would yield similar results (despite the limitations of proportions in parametric analyses). I 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 (voles ate seeds). For the tracking tube results, the intercept was significant, and significant manipulation 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 risky patches

I used the difference between observed and expected seeds consumed (for entire plots) to reassess the inverse relationship between seed consumption and treatment size. I extracted the post-manipulation data and analysed treatment size (radius) by polynomial regression. Seed consumption declined significantly with radius of the risky patch in both the linear and quadratic regressions (linear, $F = 10.85$, $P = 0.005$, adjusted $R^2 = 0.40$; Table 4, Fig. 11; quadratic, $F = 5.04$, $P = 0.024$, adjusted $R^2 = 0.35$; Table 4). I 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 model had the lowest AIC_C difference ($\Delta_{min} = 0$). The quadratic model had considerably less support ($\Delta_i = 4.15$, Table 4). The linear model was significant, but the variances in seed consumption were heterogeneous. I 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 ($t = -2.27$, $P = 0.039$).

Figure 10: 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 standardised as the difference between expected (assuming all tubes tracked equally) and observed results. Dashed bars represent pre-manipulation data, whereas the post-manipulation data is represented with solid bars.

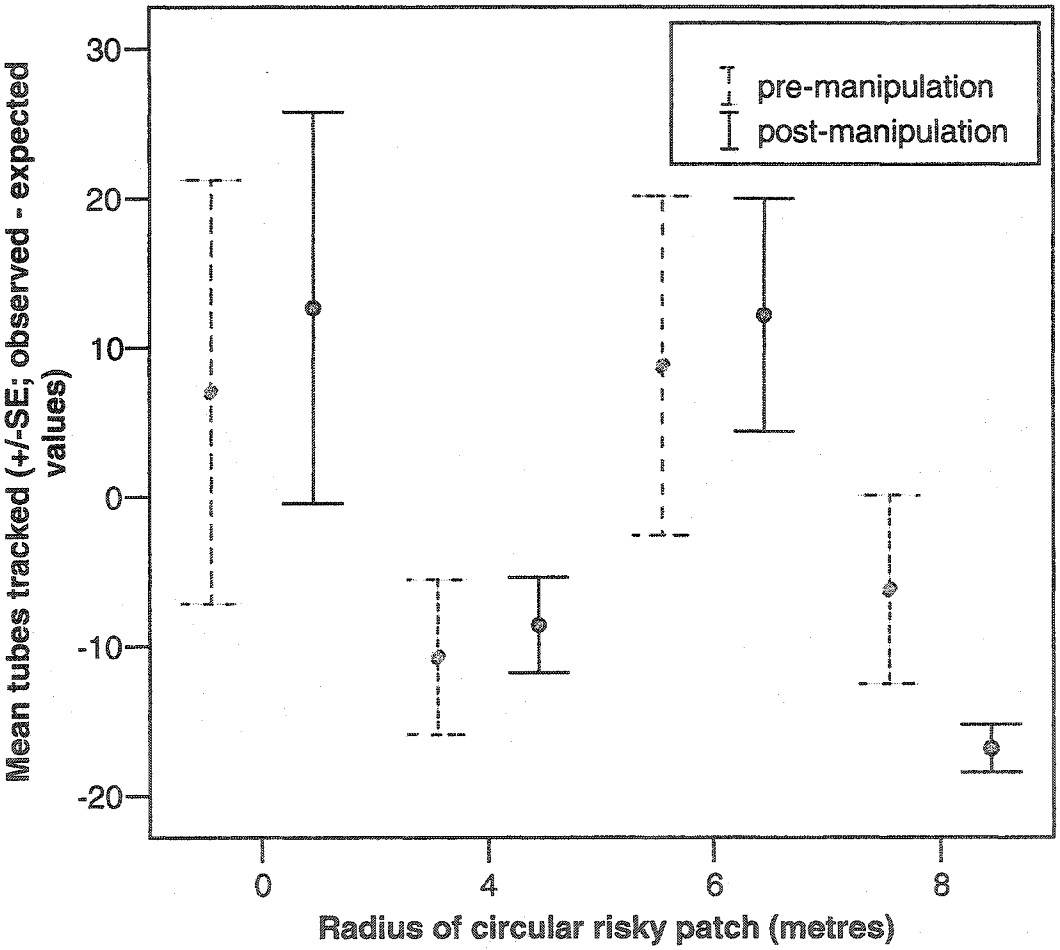

pre-manipulation
post-manipulation
Mean tubes tracked (+/-SE; observed - expected values)
30
20
10
0
-10
-20
0
4
6
8
Radius of circular risky patch (metres)

Figure 11: Mean seeds consumed per plot after habitat manipulation (±SE) scales with edge. Foraging activity declined linearly as the radius of a risky patch increased (seeds consumed = 27.05 - 6.05 x radius, $P = 0.005$, adjusted $R^2 = 0.40$, N = 16). Values are standardised as the difference between the observed and expected results (assuming that all seeds were equally likely to be eaten).

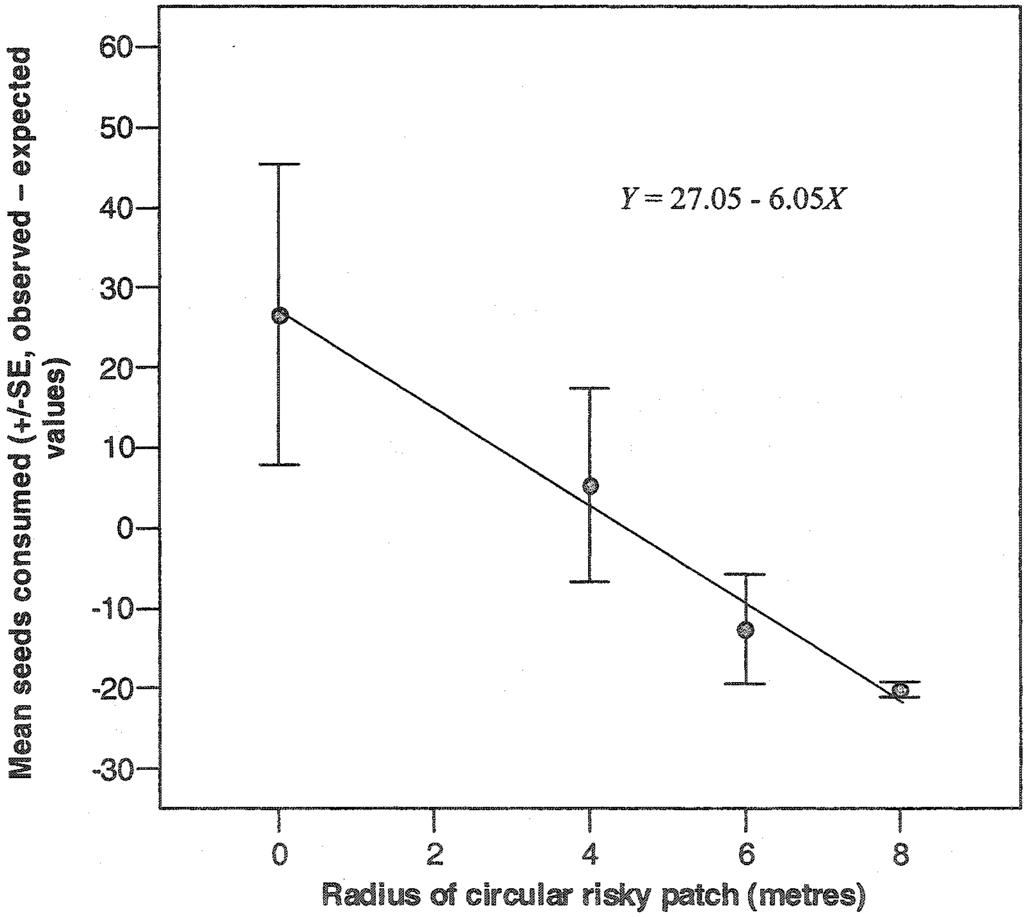

Y = 27.05 - 6.05X
Mean seeds consumed (+/-SE, observed – expected values)
60
50
40
30
20
10
0
-10
-20
-30
0
2
4
6
8
Radius of circular risky patch (metres)

Table 4: 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	$\Delta_{min} = 0.00$	$\Delta_1 = 4.15$

Discussion

Meadow voles reduced their foraging around disturbed patches of field habitat in apparent response to increased predation risk. Foraging did not vary with distance from the edge of the risky patches, nor did it vary with the area of the disturbance. Rather, meadow voles tended not to enter risky patches, and altered their foraging activity outside disturbed habitats (Fig. 9). If voles were merely not using the risky patches, their foraging would scale with the area of the disturbance, but this effect was overwhelmed by the dramatic changes in mean foraging activity in safe habitat across patch sizes (Fig. 11). The net outcome is that vole foraging depends on the perimeter of these patches. The absence of a distance effect reflects the scale of our experiments. At some larger distance away from the patch, activity necessarily increases to the levels found in undisturbed plots.

At this point I do not know how voles would react to less disturbed patches or whether the 'edge effect' I have documented would still predominate when voles exploit less risky areas. It seems likely, as disturbed patches become less dangerous, that voles might change their strategy and alter their foraging with distance-related measures of safety. If they do so, we would seem to possess a set of theories, and protocols, to detect the changed strategy.

Why does meadow vole foraging activity scale with patch perimeter?

Meadow voles, like other herbivorous rodents of similar size (e.g. the root vole, *M. oeconomus*) may have limited perceptual range (Lima and Zollner 1996, Mech and Zollner 2002). Being unable to determine the area of the risky patch, they may simply use an estimate of the length of edge they encounter 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, and 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 and quit foraging at a higher harvest rate (Brown 1988). Though I lack data on quitting-harvest rates, the data on vole activity 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.

What are the implications of enemy-free space resulting from habitat disturbance?

Voles can influence the invasion of plants significantly (e.g. 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 this study, an extreme case of enemy-free space occurs within the risky patches. Very few seeds were consumed by the voles in risky patches regardless of patch size (Fig. 9A). Outside the patches, vole activity was related directly to the length of edge of risky patches. The emerging pattern is a gradient in enemy-free space for plants that increases linearly with the length of edge habitat. Thus, evasion of predation 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 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 maximise the perimeter to area ratio (contrary to the usual advice to minimise edge, e.g. Fraver 1994, and references therein).

What are the lessons and directions for future research?

Area is an important factor for population persistence and 'area effects' dominate the literature on habitat fragmentation. Though edge is frequently measured, 'edge effects' are not always differentiated from 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). 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 now we see a behavioural response in meadow voles that may force ecologists to rethink whether reductions in population size are caused by loss of safe 'matrix', or are mediated through the length of edge habitat. Carefully designed experiments such as those outlined here may be needed to explore, more fully, the relative implications of area versus edge in habitat-fragmentation research. But it is also crucial to note that different patterns, such as those dependent on distance, may emerge under lower regimes of disturbance than simple habitat loss.

It is impossible to understand populations and communities without incorporating behaviour. Adaptive behaviours affect the dynamics of populations, the structure of communities, and may translate to patterns in the landscape (see Ostfeld *et al.* 1999). 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. I hope that other ecologists will also use behaviour and its associated optimisation research program

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

Acknowledgements

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Appendix 1: Small mammal live-trapping census data from an abandoned hay field outside Thunder Bay, Ontario.

Species	Sex	Age *	No. individuals	No. captures
Microtus pennsylvanicus	F	Adult	73	218
		Juv.	25	32
	M	Adult	76	165
		Juv.	22	27
Tamias minimus	M	Adult	1	1
Sorex cinerus	NA	NA	NA	8
S. arcticus	NA	NA	NA	1

*Juvenile *M. pennsylvanicus* were less than 20 g. NA signifies that insectivores were not marked, aged, or sexed.

The focal species in this study was the meadow vole, *Microtus pennsylvanicus*. The meadow vole is a generalist herbivorous rodent of 35 to 60 g whose average home range is less than 0.3 ha (Reich 1981; minimum recorded size 144 m^2, Dooley and Bowers 1996). Meadow voles can reproduce often and year-round, becoming sexually mature at 4-5 weeks of age and having a 21 day gestation time (Reich 1981).

Appendix 2: Site description of abandoned hay field outside Thunder Bay, Ontario, including common field plant species, potential vole predators (Kurta 2000, National Geographic 2000) and photos. Adjacent woodlands contained forest tree species typical of the Great-Lakes St. Laurence region including jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*). The site is an abandoned hay field that was planted with red pine (seedlings were less than 0.5 m tall during the study). Photos below show (A) vegetation structure and relief of the field and (B) a disturbed patch (4-m radius).

Common plants found at field site	**Potential *M. pennsylvanicus* predators**	**Potential *M. pennsylvanicus* predators continued**
Sedges and grasses	**Carnivores**	**Raptors**
Carex spp. (2 main species)	*Mephitis mephitis*	*Buteo platypterus*
Danthonia spicata	*Martes americana*	*Buteo jamaicensis*
Phleum pratense	*Martes pennanti*	*Falco sparverius*
Elymus trachycaulus	*Lynx canadensis*	*Falco columbarius*
Forbs	*Lynx rufus*	*Haliaeetus leucocephalus*
Lotus corniculatus	*Felis catus*	*Lanius excubitor*
Rosa acicularis	*Canis latrans*	*Accipiter striatus*
Fragaria virginiana	*Canis lupus*	*Accipiter gentilis*
Ranunculus acris	*Canis familiaris*	**Owls**
Taraxacum spp.	*Vulpes vulpes*	*Asio otus*
Solidago spp.	*Procyon lotor*	*Bubo virginianus*
Tree	*Mustela erminea*	*Strix varia*
Pinus resinosa	*Mustela frenata*	*Strix nebulosa*
	Mustela vison	*Aegolius acadicus*
	Mustela nivalis	*Aegolius funereus*
	Insectivore	**Corvids**
	Blarina brevicauda	*Cyanocita cristata*
	Shrike	*Perisoreus canadensis*
	Circos cyaneus	*Corvus brachyrhynchos*
		Corvus corax

A

B

Appendix 3: Schedule of fieldwork during summer, 2003: A = tracking tube activity, Mow = when risky patches were created (or re-defined), S = seed placement, T = live-trapping. Each letter represents one plot sampled randomly.

	Plot type				
Date	**control (0 m)**	**4 m**	**6 m**	**8 m**	**no. plots sampled**
May 19 - 23	T	T	T	T	16
May 26 - 30	A,S	A	S,S	-	5
June 2 - 6	S,S,S	A,S	A,A	A	8
June 9 - 13	T	T	T	T	16
June 16 - 20	A,A,A	S,S	-	A,S,S	8
June 23 - 27	-	A,A,S	A,A,S	A,A,S,S	10
July 5 - 7	Mow	Mow	Mow	Mow	16
July 7 - 11	T	T	T	T	16
July 14 - 18	A,S,S	A,S	A,A	S	8
July 21 - 25	A,S	S	A,S,S	A,A	8
July 26 - 29	Mow	Mow	Mow	Mow	16
July 28 - Aug. 1	T	T	T	T	16
August 4 - 8	S	A,S	A,S	A,A,S	8
August 10 - 14	A,A	A,A,S	S	S,S	8
August 15 - 19	T	T	T	T	16