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Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*

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Models of patch use (Brown 1992) make a number of qualitative predictions regarding when a forager should quit feeding from depletable food patches that vary in predation risk. We tested for these effects using free-living fox squirrels, *Sciurus niger*, foraging for sunflower seeds mixed into a sand matrix. We used giving-up density (GUD: food remaining in patches following a day of foraging) as a surrogate for quitting harvest rate. We used near (bush) and away (open) from trees as risky and safe microhabitats for patches. And, we augmented seeds to the environment to depress the marginal value of food to the squirrels. GUDs were higher in the open than in the bush microhabitat. Augmenting food to either the bush or open microhabitats increased GUDs in both microhabitats. Augmenting food caused the difference in GUDs between the bush and the open microhabitats to increase.

1. Introduction

For the ecology of prey species, the non-lethal effects of predators (= predators scare prey) may be more important than the lethal effects of predators (= predators kill prey) (Kotler & Holt 1989). This has been particularly apparent in the way that predators influence the foraging behavior of their prey. Foraging theory and models of patch use have provided a successful framework for detecting and measuring non-lethal effects of predators (see Lima & Dill 1990).

Brown (1992) analyzes four patch use models to evaluate how a forager should trade off the conflicting demands for food and safety. The models yield a number of shared predictions. Foragers should:

i) demand a higher feeding rate from risky than safe patches,
ii) demand a higher feeding rate as the marginal value of food declines, and
iii) as the value of food declines, demand an even higher feeding rate premium to forage in risky patches.

The first prediction has been verified by numerous studies (Sih 1980, Grubb & Greenwald 1982, Werner et al. 1983, see Lima & Dill 1990 for a review) and has demonstrated the need for considering safety along with energy when studying feeding ecology. The second prediction states that a starving individual or an individual in a low energy state has less to lose from being preyed upon than a well-fed individual (Dill & Fraser 1984, Godin & Sproul 1988, Lima 1988). The third prediction states that risky patches become even less desirable relative to safe patches as the animal becomes better fed.

Here, we would like to use a field experiment to consider the question of how thoroughly a forager should utilize a patch that offers both food and danger. As our goals:

1) We discuss several methodologies for measuring empirically the forager's tradeoff between food and safety, and
2) we apply one of these methodologies (measuring giving-up densities in manipulated food patches) to test the models' general predictions.

Using free-living fox squirrels (*Sciurus niger*), we test the predictions that:

i) giving-up densities should be higher in the risky habitat,
ii) decreasing the marginal value of food should increase giving-up densities in both safe and risky patches, and
iii) decreasing the marginal value of food should increase the giving-up density in the risky patch relative to the giving-up density in the safe patch.

2. Measuring patch use under predation risk

A number of titration methodologies have been used to measure the additional feeding rate required to make a forager sacrifice safety. These experimental methods find the combinations of feeding rate and predation risk that elicit indifferent behavior by the forager. Food abundance or giving-up density is often used as a surrogate for feeding rate and habitat is often used as a surrogate for predation risk.

Under one methodology, the experimenter adjusts the feeding rate in non-depleting food patches. The feeding rate in patches that vary in predation risk are then adjusted until the forager or foragers show no preference for one patch over the other. In the laboratory, Nonacs & Dill (1990) offered ants (*Lasius pallitaris*) two feeding sources that varied in quality and risk. The combinations of food quality and risk that yielded indifference was determined by measuring patch preferences across ten different pairings of patch qualities.

Using free-ranging blue tits (*Parus caeruleus*), Todd & Cowie (1990) used a Skinner box regulated by computer as a food patch. Distance from cover was used to vary predation risk. Following a two hour period, the effort required to obtain a food item from a patch was increased for the more frequently used patches. Adjustments in patch delivery rates were continued until the birds used the feeders with equal frequency. A higher rate of delivery was required to get birds to forage with equal frequency in the risky open habitat.

Another methodology uses non-depleting food patches and species that commonly feed in groups. Under an ideal free distribution, individuals of the feeding group should distribute themselves among food patches in a way that equalizes the fitness rewards among patches (for empirical support with rock doves, *Columbia livia*, see Lefebvre 1983). Abrahams & Dill (1989) offered guppies (*Poecilia reticulata*) two feeders that varied in terms of the presence or absence of a predator. The distribution of ten guppies at these two feeders under different food delivery rates determined the energy equivalence of risk. While the patches were non-depleting the distribution of guppies among patches created a situation where each guppy experienced a higher feeding rate at the risky patch. This technique should be useful under both field and laboratory conditions when studying group feeding species that conform to the expectation of an ideal free distribution.

A third methodology for titrating the tradeoff between feeding rate and predation risk, uses the forager's giving-up density within depletable food patches (Brown 1988). Rather than the experimenter varying a feeding rate schedule, the forager varies its feeding rate as it exploits the patch. This can usually be effected by mixing a known amount of food into a quantity of non-food matrix. In such a patch, the forager's feeding rate declines with patch residency time (Kotler & Brown 1990). Differences in giving-up densities between patches that vary in predation risk measure the forager's indifference to risk and feeding rate. Furthermore, the GUD of the forager may reveal other useful information regarding foraging efficiencies, missed opportunity costs, and metabolic costs of foraging.

3. Methods

3.1. Study site and organism

In this experiment we tried to influence the marginal value of food ($\partial F/\partial e$) by augmenting food to the environment of fox squirrels at the Morton Arboretum, Lisle, Illinois, USA (25 miles west of Chicago). The arboretum's 600 ha offer a diversity of habitats: deciduous forest, coniferous plantation, meadow, prairie grassland, and mowed lawns. A diverse assemblage of sciurid rodents inhabit these habitats: fox squirrel, thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), eastern chipmunk (*Tamias striatus*), gray squirrel (*S. carolinensis*), southern flying squirrel (*Glaucomys volans*), and woodchuck (*Marmota monax*). At the arboretum, these sciurid species face a natural community of predators. Red-tailed hawk (*Buteo jamaicensis*), Cooper's hawk (*Accipiter cooperii*), great-horned owl (*Bubo virginianus*), gray fox (*Urocyon cineroargentatus*), red fox (*Vulpes vulpes*), and coyote (*Canis latrans*) are resident throughout the year and a variety of other predators are occasional visitors (Walters 1987).

3.2. Experimental protocol

We used three sites located along woodland/meadow boundaries. Sites were at least 0.5 km apart. Each site had three stations at least 50 m apart. At each station we had the "bush" microhabitat (either at the base of a tree or 1–2 m inside the woodland) and the "open" microhabitat (in the meadow 2–3 m from the tree or woods of the bush microhabitat). Within each microhabitat of each station, we placed three experimental food patches side by side. The layout required 54 food patches (3 sites × 3 stations × 2 microhabitats × 3 side-by-side patches). By conducting the experiments during the winter, we were able to insure feeding by fox squirrels only (chipmunks, thirteen-lined squirrels, and woodchucks were inactive, flying squirrels are nocturnal, and gray squirrels are restricted to the deeper woods at the arboretum).

Food patches consisted of plastic nursery trays (55 × 28 × 6 cm) filled with a measured amount of unshelled sunflower seed mixed thoroughly into 4 liters of sifted sand (commercial bank sand). These trays offer a food patch wherein the harvest rate of a squirrel declines as it depletes the food in the patch. The density of seeds remaining in a food patch following harvest by a forager is its giving-up density (GUD). Insofar as harvest rates are a function of food abundance, GUDs provide an estimate of the quitting harvest rates.

Food patches were established early in the morning and left all day for the squirrels to harvest. In the afternoon, the remaining seeds were sieved from each tray and later cleaned of debris and weighed to provide a measure of the GUD. To confirm the presence of fox squirrels, we relied on direct observations of squirrels feeding from seed trays and on footprints and body marks left in seed trays.

On a site by site basis, we augmented food by scattering one cup of sunflower seed within a 2 m radius of either the bush or open trays of a station. We had three food augmentation treatments:

i) no augmentation of the stations at a site,
ii) augmentation of the bush microhabitat of all stations at a site, and
iii) augmentation of the open microhabitat of all stations at a site.

On a given day, all stations of a site received the same augmentation treatment. Food was augmented in the morning and the GUDs collected that afternoon were used to measure the effect.

As an unrelated and additional experiment to test for the effect of sunflower chaff on the squirrel's foraging behavior (squirrels husk the sunflower seeds within the patches and drop the chaff into the sand) we varied the initial conditions of the triplet of patches within a microhabitat of a station. The three initial conditions were

i) 10 g of sunflower seeds (one scoop with a four dram vial),
ii) 10 g of sunflower seeds (one scoop) and twice the volume of chaff (two scoops), and
iii) 30 g of sunflower seeds (three scoops).

The augmentation experiment followed a 3 × 3 Latin Square design. On a given day, each augmentation treatment was present at one of the sites; and after three days each site experienced each of the augmentation treatments. The Latin Square was repeated twice in time. This required six days of data collection (November 17, 18, 21, 24, 30, and December 1, 1989).

Titrating the tradeoff between safety and feeding rates with GUDs in food patches does not require continuous or lengthy direct observations of the sequence of behaviors leading to the GUDs. This allows the collection of data from many more patches than would be possible if patches were continuously monitored by observers or video cameras. During the experiment, we observed squirrel foraging behavior via spot checks. These observations showed that from one to three squirrels would visit a station. When food was augmented to the environment, squirrels would usually begin by collecting this food before feeding from the experimental patches. Following a brief sampling of the triplet of patches (less than a minutes time) feeding usually commenced in the richest patch of the bush microhabitat, and as this patch became depleted the forager would move onto the other patches of the triplet or move to the rich tray of the open microhabitat. Within 10–15 minutes of commencing feeding, all patches of a station had usually been fed from. By moving frequently from patch to patch, squirrels tended to deplete the patches of a station in parallel rather than sequentially. We observed no unexpected or unusual feeding behaviors that would make us suspect the validity of the results.

3.3. Predictions

In terms of predation risk, the placement of food patches in the bush and open microhabitats should provide safe and risky food patches, respectively. Observational (Smith & Follmer 1972) and experimental (Lima et al. 1985, Kraus & Smith 1987, Dill & Houtman 1989) evidence suggests that predation risk is higher for fox squirrels in the open than bush microhabitat (Temple 1987).

Prediction 1

Using GUDs as surrogates for harvest rates, GUDs should be higher in the open than the bush microhabitat.

The augmentation of food should provide the squirrels with additional feeding opportunities and with additional food. The additional feeding opportunities should increase the squirrels' missed opportunity cost (they now have better things to do with their time). Furthermore, the squirrels' marginal valuation of food should decline in response to augmentations of either the bush or open microhabitats (under the assumption that there are diminishing returns to fitness from net energy gain).

The increase in missed opportunity cost and the decrease in the marginal value of food should apply to all of a squirrels' activities. For this reason, augmenting food in the bush microhabitat should influence GUDs in both the bush and open microhabitats. By augmenting just the bush or open microhabitat, we can show (Brown & Alkon 1990) that shifts in missed opportunity costs or food valuations extend to behavior in both microhabitats (such effects should be environment-wide).

Prediction 2

In response to augmenting either microhabitat, GUDs should increase for two reasons. First, missed opportunity costs should increase (this assumes that having more food or being able to obtain food more easily makes other activities more valuable). Second, even if the missed opportunity cost does not increase, the cost of predation should increase because the lower valuation of food increases the marginal rate of substitution of energy for safety (Brown 1992).

Prediction 3

Decreasing the value of food increases the difference in quitting harvest rates between the open and bush microhabitats (see equations 5 of Brown 1992).

4. Results

The data were analyzed as an ANOVA with fixed and random effects, and with nested variables. The variables day, site, and augmentation form the three variables of the Latin Square. They are not fully crossed and so only main effects can be tested. Station is a variable that is nested within site. Initial abundance for the chaff experiment and microhabitat are variables fully crossed with the variables of the Latin Square. Initial analyses showed that all of the interaction effects between initial abundance (or microhabitat) and the variables of the Latin Square were not significant (most generated $F < 1$). For this reason, all but two of the interaction effects were dropped from the ANOVA model.

In the ANOVA model, the interaction between augmentation and microhabitat, and augmentation and initial abundance were retained along with the main and nested effects. The first interaction tests whether microhabitat-specific augmentations have microhabitat-specific effects (we predict a non-significant interaction, see Prediction 2). The second interaction verifies that initial conditions of patches should not alter the effects of the augmentations (we expect a non-significant interaction effect).

For two reasons we logarithmically transformed GUDs in the analyses. First, this tends to normalize the data and remove the tendency for variance to increase with the mean. Second, the relationship between harvest rate and GUD tends to be non-linear (Kotler & Brown 1990) and decelerating. Hence, logarithm of the GUD may provide a more linear relationship to quitting harvest rate. The ANOVA model yielded a good fit to the data ($r^2 = 0.60$) and all main effects were significant (Table 1).

GUDs were higher in the open than bush microhabitat, providing evidence that squirrels trade-off feeding rate and predation risk in their foraging behavior (Fig. 1). The initial abundance of food also strongly influenced GUDs. The mean GUDs (backtransformed) for one scoop of seeds and no chaff, one scoop of seeds and two scoops of chaff, and three scoops of seeds were 2.41, 2.70, and 5.11 g, respectively. Interestingly, the addition of chaff does not seem to interfere with their foraging process within patches. The effect of initial conditions is due primarily to the addition of seeds rather than chaff.

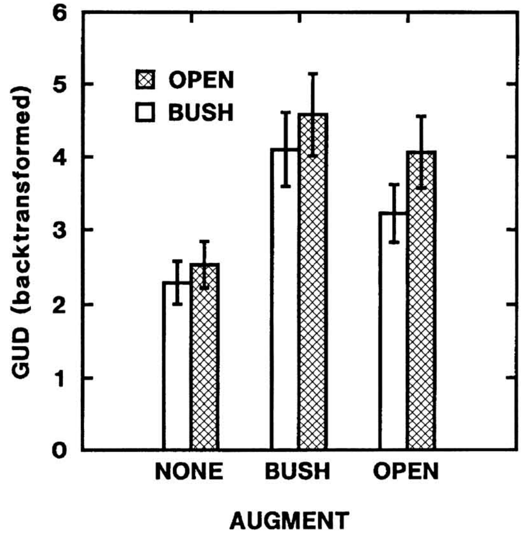

Fig. 1. The effect of microhabitat (BUSH and OPEN) and the addition of food to the environment (AUGMENT) on giving-up densities (GUD) in grams. Regardless of the food addition treatment, GUDs were higher in the risky (OPEN) than safe (BUSH) microhabitat. When food was added to the bush (BUSH) or open (OPEN) microhabitats, GUDs increased in patches of both microhabitats relative to the control treatment of no food augmentation (NONE). The error bars give the standard error around each mean (each bar has a sample size of 54).

The above analysis shows that the interaction effects of augmentation with microhabitat and initial abundance were not significant (Table 1). The analysis, though, is not appropriate for testing the direct effect of augmentation. This is because augmentations occurred at the level of site and all of the GUD measurements for a particular site on a given day may not be true replicates. To avoid this inflation of data points, we calculated a mean GUD for each combination of day and site (the mean of the logarithmically transformed GUDs). This yielded eighteen data points that were analyzed as an ANOVA without interaction effects. Day ($F_{5,8} = 4.02$, $P < 0.05$), site

($F_{2,8}$ = 11.35, P <.005), and augmentation ($F_{2,8}$ = 13.4, P < 0.005) all had significant effects on GUDs (r^2 =.90). In response to either augmenting the bush or open microhabitats, GUDs increased in both the bush and open microhabitats (Fig. 1).

To test Prediction 3 we must factor out the effect of GUDs in the bush microhabitat from GUDs in the open and then test for the residual effect of augmentation on GUDs in the open microhabitat. For a fixed GUD in the bush microhabitat, we want to know whether GUDs in the open microhabitat change in response to the augmentation treatments. To do this, we used an ANCOVA where GUD in the open microhabitat was the dependent variable, GUD in the bush microhabitat was the covariate, and augmentation, site, and initial abundance were group variables. First, we tested for homogeneity of slopes by considering the main effects and the interaction effects of bush with augmentation, site, and initial abundance. As these interaction effects were not significant ($F_{2,146}$ = 0.33, $F_{2,146}$ = 0.74, and $F_{2,146}$ = 0.91, respectively), we assumed that slopes were homogeneous and dropped these interactions from the analysis. By initially including a bush squared term (not significant, $F_{1,146}$ = 0.23, and subsequently dropped from the analysis), we tested for non-linearities in the relationship between bush and open GUDs.

The subsequent ANCOVA (r^2 = 0.78) revealed a significant effect of augmentation on the difference between GUDs in the bush and open microhabitats (Table 2). In response to the augmentation, fox squirrels required a higher GUD in the open microhabitat for a given GUD in the bush microhabitat. Relative to GUDs in the bush, GUDs in the open increased by 0.35 and 0.31 g in response to augmenting the open or bush microhabitat, respectively.

5. Discussion

By using GUDs as a surrogate for quitting harvest rate we were able to use the patch use behavior of fox squirrels to test three predictions of foraging under predation risk. In accord with the expectation that predation risk is higher away from trees than near trees (Lima et al. 1985, Temple 1987, Newman & Caraco 1987), fox squirrels had higher GUDs in the open than bush microhabitat. In response to augmenting food to the environment, GUDs increased in both risky and safe patches. And, for any GUD in the safe

Table 1. The ANOVA testing for the effects of microhabitat and initial abundance, and for possible interaction effects of microhabitat and initial abundance with augmentation. In this model, the logarithm of giving-up density is the dependent variable. Day, site, and augmentation are the factors of the Latin Square. Microhabitat and initial abundance are factors fully crossed with all other factors. Station is a factor nested within site and so the mean sum of squares of station is used as the error term when testing for the effect of site. The complete model gives r^2 = 0.604. ** = P < 0.01, *** = P < 0.001.

Variables	*df*	Mean Square	*F*-ratio
Microhabitat (Mh)	1	1.23	6.79 **
Initial abundance (Ia)	2	15.0	82.96 ***
Day	5	2.49	13.70 ***
Augmentation (Ag)	2	8.86	48.79 ***
Site	2	7.40	8.98 ***
Station	6	0.824	4.53 ***
Mh × Ag	2	0.260	1.43
Ia × Ag	4	0.065	0.36
Error	297	0.182	

Table 2. The ANCOVA testing for the effect of augmentation on the relationship between giving-up densities (GUD) in the bush and open microhabitats. The dependent variable is GUD in the open microhabitat. The covariate is the corresponding GUD in the bush microhabitat. The group variables are augmentation, site, and initial abundance. The interaction effects of the group variables with the covariate were not significant and so we assumed that slopes were homogeneous and dropped the interaction terms from the analysis. The ANCOVA model gives r^2 = 0.778. Augmenting food to the environment significantly increases GUDs in the open relative to GUDs in the bush. * = P < 0.025, ** = P < 0.01, *** = P < 0.001

Variables	*df*	Mean Square	*F*-ratio
Bush	1	391.7	213.76 ***
Augmentation	2	6.78	3.70 *
Initial abundance	2	9.15	4.99 **
Site	2	5.15	2.81
Error	152	1.83	

microhabitat, fox squirrels had a higher GUD in the risky microhabitat in response to food augmentation.

In the field experiments, we rotated food addition treatments on a daily basis and performed separate augmentations of the bush and open microhabitats. By conducting microhabitat specific augmentations, we could verify that the missed opportunity cost of foraging and the marginal valuation of food are environment-wide and not habitat specific (Brown 1988, Brown & Alkon 1990). For instance, augmenting the bush microhabitat raised GUDs in both the bush and open patches. The daily rotation of food additions assumes that squirrels can adjust their valuation of energy on a daily basis and that there is negligible carry-over of this effect to the next day. After factoring out the effect of the day's treatment, we found no effect of the previous day's treatment on GUDs the following day. This result is noteworthy for two reasons. First, our augmentation was not so large as to significantly alter behavior for several days. Second, short-term (daily) and local (microhabitat specific) changes in the environment cause measurable changes in patch use while having little effect on the state of the forager.

These short-term changes in the marginal value of food may better explain the results of experiments by Lima et al. (1985) and Valone & Lima (1987) on squirrels and birds, respectively. In these experiments, the animals frequently carried food items from risky patches (where they were harvested) to protective cover (where the food was consumed). Interestingly, during a feeding bout some food items were consumed in the risky habitat and others were carried to cover. This partial rather than all-or-nothing transportation of food items was interpreted as the forager striking an ideal balance between the probability of surviving predation and the fitness value of net energy gain. This view requires that the forager's probability of surviving predation changes significantly during a foraging bout. For squirrels, this may be unlikely during any given ten or fifteen minute feeding bout. An alternative explanation says that the feeding rate of the forager significantly alters its valuation of food. As less food is carried and more food is consumed within the risky patch (increasing the feeding rate), the marginal value of food declines and the cost of predation increases. Under this interpretation, the overall probability of surviving predation remains virtually unchanged and carrying a fraction of food strikes a balance between the marginal value of food and the cost of predation. When food is augmented as in these experiments, it is probably true that the marginal value of food changes more quickly than the probability of surviving predation; both of these terms influence the cost of predation and the subsequent trade-off between safety and feeding rate.

The previous paragraph illustrates the importance of understanding the components that comprise the cost of predation. Following Brown (1992), these components include the fitness value of energy, F (Model 4), the probability of surviving predation, p (Models 1–3), the predation rate, μ (Models 1–4), and the marginal value of energy, $\partial F/\partial e$ (Models 1–4). Experiments that manipulate aspects of predation risk may be influencing one or several of these factors. Because the latter two terms, μ and $\partial F/\partial e$, are the respective derivatives of the former two terms, p and F, most experiments on foraging under predation risk probably influence μ and $\partial F/\partial e$ much more strongly than p and F. For instance, experiments that use spatial and temporal habitats as surrogates for predation risk are mostly manipulating habitat-specific differences in μ (e.g. moonlight avoidance in rodents, Lockard & Owings 1974). Introduction of predators or cues of predation risk probably change perceptions of μ more strongly than perceptions of p (e.g. aviary experiments with rodents and owls; Brown et al. 1988, Kotler et al. 1991). Studies that manipulate the state of the animal by food deprivation (e.g. Lima 1988) or augmenting food in the environment (e.g. this study) probably strongly influence $\partial F/\partial e$ while having smaller if not negligible effects on F. In the present study the augmentation probably increased the squirrels' foraging time and increased their net rate of energy gain; this will decrease p slightly, increase F slightly, and mostly decrease $\partial F/\partial e$.

Based on the modeling (Brown 1992), manipulations of μ or $\partial F/\partial e$ should have powerful effects on patch use. In all models, doubling predation risk or halving the marginal value of food will double the predation cost of foraging in a patch. For this reason, patch use has and will continue to provide an excellent empirical means for assaying predation risk, testing models of the non-lethal effects of predators, and documenting the population and community level consequences of predation risk.

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