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Patch use under predation risk: I. Models and predictions

Joel S. Brown

Brown, J. S., Department of Biological Sciences, University of Illinois, Box 4348, Chicago, IL, 60680, USA

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Patch use under predation risk requires animals to trade off needs for safety and food. I consider within a common framework four ways of modeling how safety and energy influence fitness. These models make similar predictions for when a forager should stop feeding from depletable patches that vary in predation risk. In accord with Brown (1988), patches should be abandoned when the harvest rate no longer compensates for the metabolic, predation, and missed opportunity costs of foraging. In accord with Gilliam & Fraser (1987), safe and risky patches should be left at the same ratio of predation risk to net feeding rate when the alternative activities include resting in a safe refuge to save energy. The quitting harvest rate of the forager within a food patch should be sensitive to predation risk and to the marginal value of food (the fitness value of an additional food item). Quitting harvest rates should be higher in food patches with higher predation risk. Quitting harvest rates and the costs of predation should increase as the marginal value of food decreases. The difference in quitting harvest rates between patches with high and low predation risk should increase as the marginal value of food decreases. Fortunately, the shared qualitative predictions of these models have and can be tested. Unfortunately, distinguishing among the models' differing quantitative predictions shall prove challenging.

1. Introduction

In ecology, predators have been primarily viewed as agents of mortality that influence the abundance and population dynamics of their prey (Rosenzweig & MacArthur 1963, Taylor 1984). The prey were modeled as passive victims of this interaction. Issues of importance include the dynamical stability and properties of predator-prey or multi-trophic level systems (Hassell 1978, Gilpin 1979, Pimm 1982), the importance of indirect effects such as apparent competition (Holt 1977, Kerfoot & Sih 1987), and the influence of the predators' functional response (Holling 1965, Royama 1971, Murdoch & Oaten 1975).

Experimental work by Werner et al. (1983) and Sih (1980) showed how prey respond actively to the presence of predators by reducing activity or by shifting activity to safer habitats. This has been followed by much important and novel research that identifies the numerous and often subtle ways predators influence the behavior of their prey (see Lima & Dill 1990 and references therein). These non-lethal effects of predators on their prey may sometimes be more important than the actual killing of prey by predators (Kotler & Holt 1989). Non-lethal effects of predators may strongly influence behavior, intraspecific interactions, competitive interactions (Liebold 1988, Persson 1991, Werner 1991, Kohler 1992), and interactions between the prey and its food (Abrams 1984, 1989).

Foraging theory provides a framework for addressing the question of how an animal should seek its food while not becoming food for its predators. When its food occurs patchily, a forager can influence its safety by the way it allocates time among food patches that may vary in predation risk. When the most profitable feeding patch incurs the least risk then this patch should be favored over all other patches (Nonacs & Dill 1990). More likely situations occur when patch choice requires a tradeoff between feeding rate and predation risk. Factors that influence whether to opt for a riskier patch include the state of the forager (hungry coho salmon, *Oncorhynchus kisutch*, are more willing to take risks than well-fed salmon, Dill & Fraser 1984), direct or indirect cues of predation risk (Brown et al. 1988), time since last exposure to a predator (Kotler 1992), and the species of forager (Brown 1989, Kotler et al. 1991).

In response to predation risk, a number of models exist that predict how much time a forager should devote to foraging (Abrams 1991) and how the forager should allocate this time among food patches (Gilliam & Fraser 1987, 1988, Brown 1988). Abrams (1982, 1987, 1991) considered a family of fitness functions relating safety and feeding rates, and considered how foraging time should be influenced by short-term and long-term changes in food abundances.

Gilliam & Fraser (1987, 1988) developed a patch use model that makes the elegant prediction that foragers should utilize the patch that offers the lowest predation risk, μ, to harvest rate ratio, f: the "μ/f" rule. When food patches are depleted, this predicts that all food patches should be left at the same ratio. Hence, more food should be left behind in risky than poor patches. While this prediction has received empirical support (Gilliam & Fraser 1987, Gotceitas 1990), an additional prediction that foraging time should decline as food abundance increases has generally been refuted (Gilliam & Fraser 1987, Valone & Brown 1989, Mitchell & Brown 1990).

Brown (1988) generalized the marginal value theorem (Charnov 1976) to include predation risk and alternative activities. The model predicts that a forager should leave a patch when the harvest rate no longer exceeds the sum of metabolic, predation, and missed opportunity costs of foraging (Brown 1988). In accord with Abrams (1991), time spent foraging should increase with short-term or localized increases in food abundance (Mitchell and Brown 1990) whereas predictions become ambiguous for long-term or widespread increases in food abundance. This model has been used to investigate cues of predatory risk (Brown et al. 1988, Kotler et al. 1991), and habitat differences in perceived predation risk (Brown 1989, Brown & Alkon 1990).

Here, I would like to model the question of how thoroughly a forager should utilize a patch that offers both food and danger. As my goals:

1) I consider four different functional forms for how food and safety influence fitness (see Abrams 1991) and I consider the optimal allocation of time by a forager to a safe and a risky food patch.
2) I discuss the general predictions that emerge from the four fitness models. In particular, I focus on the importance of the marginal value of food in determining the use of risky and safe patches (see Lima 1988).
3) Within this modeling framework, I contrast and compare the derivation and predictions of Gilliam and Fraser's (1987, 1988) and Brown's (1988) model of patch use under predation risk.

2. Modeling patch use under predation risk

Papers by Gilliam & Fraser (1987), Brown (1988), and Abrams (1991) have produced at least four ways of combining predation risk and feeding rates into a fitness function. In the context of depletable food patches, all can consider a forager that has T time units to devote to n activities where t_i is the amount of time devoted to the ith activity. For convenience and applicability to the experimental procedures to follow, denote activities 1 and 2 as foraging in food patches 1 and 2, respectively. The other $n - 2$ activities can include foraging or engaging in any other alternative activities. The question of interest is how much time, t_1 and t_2, should a forager devote to food patches 1 and 2, respectively.

Let activities 1 and 2 contribute to the expected number of surviving offspring, F, that result from the acquisition of energy, e, over a period of T time units. Net energy, e, is either an increasing or decreasing function of t_1 and t_2 (depending upon whether more energy is harvested than expended while exploiting the food patch), and F is an increasing function of e. Furthermore, activities 1 and 2 incur predation risk and influence the forager's probability of surviving, p, until the end of the time period, T. Hence, p is a decreasing function of t_1 and t_2. Let μ_i be the instantaneous risk of predation while engaged in activity i. Let the probability of surviving predation be given by:

$$p = e^{-\Sigma\mu_i t_i}$$

Let f_1 and f_2 denote the forager's harvest rate from patches 1 and 2, respectively, and let c_1 and c_2 denote the energetic cost of exploiting patches 1 and 2, respectively. Under these definitions (and their associated assumptions):

$$\partial e/\partial t_1 = f_1 - c_1$$

$$\partial e/\partial t_2 = f_2 - c_2$$

Finally, assume that patches are depletable in the sense that a forager's harvest rate declines with time spent in the patch; i.e. $\partial f_1/\partial t_1 < 0$ and $\partial f_2/\partial t_2 < 0$.

Model 1

Gilliam & Fraser (1987) assumes that natural selection favors an allocation of time among activities that maximizes safety subject to the constraint that enough energy is harvested to insure a sufficient value for F. Treating energy as a constraint rather than as an input into fitness means that any surplus energy above the constraint level has no value and that energy below the constraint level has effectively infinite value.

Such a model may apply to certain non-reproductive stages or non-reproductive periods in the life of a forager. For instance, non-reproductive or larval life-history stages may require a certain amount of energy for attaining the next developmental stage. In a steady state population where maturation time does not influence fitness, then natural selection may select for a feeding strategy that maximizes the probability of surviving until the next life-history stage (Werner 1991). In other organisms this model may approximate conditions during non-reproductive seasons (e.g. over-winter survival in birds), particularly if surplus energy acquired during the non-breeding season has negligible value during the breeding season.

Model 1 can be thought of as minimizing the probability of death by predation while maintaining or attaining some specified level of energy reserves:

$$\text{Max } p \text{ subject to } F \geq k \text{ and } \Sigma t_i = T \quad \text{(1a)}$$

Model 2

The opposite extreme to Model 1 views natural selection as favoring a strategy that maximizes the fitness reward of energy and other activities, F, subject to the constraint that some minimum level of safety is insured. This model may have little biological relevance because almost by definition safety is a component of fitness rather than a constraint. But, foraging models that only consider energy gain and not safety may come close to implicitly assuming such a model. Foraging models that only consider energy as an input into fitness make the assumption that either predation risk does not exist, predation risk does not vary among available activities, or predation risk must be reduced or maintained behaviorally below some threshold level after which the forager attempts to maximize the expected number of surviving offspring (Model 2):

$$\text{Max } F \text{ subject to } p \geq k \text{ and } \Sigma t_i = T \quad \text{(1b)}$$

Model 3

For species that reproduce frequently relative to the time span under consideration, an appropriate measure of fitness may be the difference between reproduction and mortality. Most ecological models of predator-prey population dynamics (see Taylor 1984) take a form where fitness is the per capita growth rate in the absence of predation minus the predation rate. This assumes that current net energy gain is either instantaneously or irrevocably converted into fitness in a manner that cannot be nullified by predation. Biologically, this requires either a rapid conversion of energy into offspring relative to predation, or social structures in which several individuals collectively (and continuously) raise offspring. If a number of individuals share in the rearing of offspring then the death of one parent or helper does not necessarily nullify or greatly alter the parent's past contribution to the present offspring. Such a model can be approximated as the sum of surviving offspring and safety (Abrams 1991).

$$\text{Max } F + p \text{ subject to } \Sigma t_i = T \tag{1c}$$

where $F + p$ is the finite rate of increase over T time units, N_{t+T}/N_t.

Model 4

In iteroparous species that only realize fitness following the T time units and in many difference equation models of predator-prey dynamics (e.g. Nicholson & Bailey 1935), a more appropriate measure of fitness may be fitness in the absence of predation multiplied by the probability that the organism survives from predators to realize fitness. When food intake is not instantly converted into offspring, predation may nullify the value of previous food intake. For instance, in many organisms, parents must survive most or all of the breeding season before any feeding effort devoted to offspring and growth has any fitness value.

Most organisms probably fit a model where natural selection favors maximizing the product of surviving descendants (expressed as F+1 in an iteroparous species) and safety (Lima et al. 1985, Brown 1988, Abrams 1991).

$$\text{Max } p(F+1) \text{ subject to } \Sigma t_i = T \tag{1d}$$

where $p(F+1)$ is the finite rate of increase over T time units.

For each of these models, the technique of Lagrange multipliers can be used to characterize the optimal allocation of time among activities (Brown & Venable 1986, Brown 1988, Brown & Alkon 1990 provide examples within this context). The technique forms a Lagrangian function by ascribing a Lagrange multiplier to each constraint. Let Φ_t be the multiplier for the time constraint $\Sigma t_i = T$ in all four models, let Φ_F be the energy constraint $F \geq k$ in model 1, and let Φ_p be the safety constraint $p \geq k$ in model 2. Lagrange multipliers give the marginal fitness cost or benefit associated with relaxing the constraint (Chiang 1974). As such, Φ_t is the missed opportunity cost of not engaging in alternative activities (Brown & Alkon 1990), and $\Phi_F \leq 0$, $\Phi_p \leq 0$ are the marginal fitness costs resulting from having to meet a certain energy or safety requirement, respectively.

The time constraint multiplier, Φ_t is negative if the organism exhausts all of its fitness enhancing activities during the time period; or it is positive if the organism still has fitness enhancing activities remaining at the end of the time period. The energy constraint multiplier, Φ_F, and the safety constraint multiplier, Φ_p, must be negative when activities involve a trade-off between feeding rate and safety. When feeding occurs in depletable food patches, such a tradeoff results from the forager's feeding activity. Under this tradeoff, increasing the energy constraint obliges the forager to expose itself to additional predation risk, and increasing the safety threshold obliges the forager to reallocate time from high feeding-rate patches to safer low feeding-rate patches.

The Lagrangian function for each model is given by:

$$\text{Model 1: } L = p + \Phi_t(T - \Sigma t_i) + \Phi_F(k - F) \tag{2a}$$
$$\text{Model 2: } L = F + \Phi_t(T - \Sigma t_i) + \Phi_p(k - p) \tag{2b}$$
$$\text{Model 3: } L = F + p + \Phi_t(T - \Sigma t_i) \tag{2c}$$
$$\text{Model 4: } L = p(F+1) + \Phi_t(T - \Sigma t_i) \tag{2d}$$

and the necessary conditions for the optimal amount of time to devote to activity i, t_i^*, are:

$$\text{Model 1: } \partial L/\partial t_i = \partial p/\partial t_i - \Phi_t - \Phi_F(\partial F/\partial e)(\partial e/\partial t_i) = 0 \tag{3a}$$
$$\text{Model 2: } \partial L/\partial t_i = (\partial F/\partial e)(\partial e/\partial t_i) - \Phi_t - \Phi_p(\partial p/\partial t_i) = 0 \tag{3b}$$
$$\text{Model 3: } \partial L/\partial t_i = \partial p/\partial t_i + (\partial F/\partial e)(\partial e/\partial t_i) - \Phi_t = 0 \tag{3c}$$

Model 4: $\partial L/\partial t_i =$

$$(F+1)(\partial p/\partial t_i) + p(\partial F/\partial e)(\partial e/\partial t_i) - \Phi_t = 0 \tag{3d}$$

The above necessary conditions only apply to those activities actually engaged in by the forager; equations (3a–d) only apply when $t_i^* > 0$.

Equations (3a–d) can be used to determine when a forager should leave food patch $j = 1,2$. To do this substitute into equations (3a–d) the relationships $\partial p/\partial t_j = -\mu_j p$ and $\partial e/\partial t_j = f_j - c_j$, and solve for the quitting harvest rate, f_j:

Model 1: $f_j =$

$$\mu_j p /[-\Phi_F(\partial F/\partial e)] + \Phi_t / [-\Phi_F(\partial F/\partial e)] + c_j \tag{4a}$$

Model 2: $f_j =$

$$-\Phi_p \mu_j p /[(\partial F/\partial e)] + \Phi_t / [(\partial F/\partial e)] + c_j \tag{4b}$$

Model 3: $f_j =$

$$\mu_j p /[(\partial F/\partial e)] + \Phi_t / [(\partial F/\partial e)] + c_j \tag{4c}$$

Model 4: $f_j =$

$$\mu_j (F+1) /[(\partial F/\partial e)] + \Phi_t / [p(\partial F/\partial e)] + c_j \tag{4d}$$

Each of these expressions gives the harvest rate at which the forager should abandon a food patch and seek another food patch or another activity. The left hand side of each equation is the forager's quitting harvest rate. The first term of the right hand side is the cost of predation (in units of harvest rate), the second term is the missed opportunity cost of not using time elsewhere (in units of harvest rate), and the third term is the metabolic cost of foraging. In each model, the cost of predation includes the predation rate, μ, multiplied by the marginal rate of substitution of safety for harvest rate. It is the marginal rate of substitution that converts something like predation rate into a common currency of harvest rate (see Caraco 1979, Brown 1988).

Each of these models can be used to determine how a forager should trade off feeding rates and predation rates between patches that vary in predation risk. If the patches are equal in all respects save predation risk then $c_1 = c_2$ and if the optimal amount of time to devote to patches 1 and 2 are positive then equations (4a–d) can be used to show:

$$\text{Model 1: } f_2 - f_1 = (\mu_2 - \mu_1)/[-\Phi_F(\partial F/\partial e)] \tag{5a}$$

$$\text{Model 2: } f_2 - f_1 = -\Phi_p(\mu_2 - \mu_1)/[\partial F/\partial e] \tag{5b}$$

$$\text{Model 3: } f_2 - f_1 = p(\mu_2 - \mu_1)/[\partial F/\partial e] \tag{5c}$$

$$\text{Model 4: } f_2 - f_1 = (F+1)(\mu_2 - \mu_1)/[\partial F/\partial e] \tag{5d}$$

Under depletable food patches, equations (5a–d) give the difference in quitting harvest rates between two food patches that vary in predation risk.

2.1. The "μ/*f*" rule

None of the four models necessarily results in a patch quitting rule that equalizes, among patches, the ratio of predation risk to feeding rate. However, Gilliam & Fraser (1987) in making this prediction made an additional assumption. They assumed that the forager finds it worthwhile to spend time in a refuge. While in the refuge the forager experiences no predation risk and harvests no food.

To see how this additional assumption influences the four models, let t_3 represent time devoted to "resting" in a refuge where predation risk is negligible ($\mu_3 = 0$) and no food can be harvested ($f_3 = 0$ and so $\partial e/\partial t_3 = -c_3$). The necessary conditions for t_1^*, t_2^*, and t_3^* can be found by considering equations (4a–d) for j = 1,2,3. The equations generated for j = 3 can be used to derive an expression for the Lagrange multiplier of the time constraint. This expression for Φ_t can be substituted into equations (4a–d) for $j = 1,2$. These can be re-arranged to show that at t_1^* and t_2^*:

$$\mu_1/(f_1 - c_1 + c_3) = \mu_2/(f_2 - c_2 + c_3) \tag{6}$$

Equation (6) holds for all four models. Equation (6) is the "μ/*f*" rule when the energetic cost of foraging is different than the energetic cost of remaining in the refuge (as derived by Gilliam & Fraser 1987, 1988). As such, the "μ/*f*" rule emerges not from the assumptions of Model 1 but from the assumption that the forager finds it optimal to devote time to an activity that influences fitness only through the expenditure of energy.

In a similar vein, the prediction of Brown (1988) that foragers should abandon a food patch when the harvest rate no longer exceeds the sum of predation, metabolic, and missed opportunity costs does not depend upon the assumptions of Model 4, but emerges as a general result of all four models. In this way, the predictions of Gilliam & Fraser (1987) and Brown (1988) are simply different ways of examining the same models. Equations (5a–d) are in the spirit of Brown (1988) and show the feeding rate premium that a forager should demand when feeding in a risky patch. Equation (6) restates the result of Gilliam & Fraser (1987).

2.2. General properties and predictions

While the four models have different functional forms they make similar predictions regarding the use of food patches.

1. In all four models, a forager should leave a patch when its harvest rate no longer exceeds the sum of metabolic, predation, and missed opportunity costs of foraging.

2. When the alternative activity is resting in a safe refuge, and energy and safety are the only inputs into fitness (simplifying assumptions of Gilliam and Fraser 1987) then patches should be left at the same ratio of predation risk to net feeding rate: the "μ/f" rule.

3. The quitting harvest rate should be higher in the food patch with the higher predation risk (the right hand sides of equations 5a–d are positive if $\mu_2 > \mu_1$; recall that for models 1 and 2, Φ_F and Φ_p are negative, respectively). If $\mu_2 > \mu_1$ then $f_2 > f_1$. This commonplace prediction has been verified by numerous studies (Sih 1980, Grubb & Greenwald 1982, Werner et al. 1983, see Lima & Dill 1990 for a review).

4. The response to predation risk depends upon the state of the animal and the marginal value of energy, $\partial F/\partial e$. Inspection of equations (4a–d) shows that lowering the marginal value of energy increases the cost of predation. As a result, decreasing the value of energy increases the quitting harvest rates within food patches 1 and 2, regardless of which patch has the higher risk of predation: decreasing $\partial F/\partial e$ increases both f_1 and f_2. More generally, the state of an individual should influence its willingness to trade off safety and feeding rates (McNamara and Houston 1986). A number of studies have shown how a starving individual or an individual in a low energy state will tolerate greater predation risk for the same energetic reward than a well-fed individual (Dill & Fraser 1984, Godin & Sproul 1988, Lima 1988).

5. Also, for a given feeding rate in the safe patch, the feeding rate in the risky patch should increase as the marginal value of energy declines. Inspection of equations (5a–d) shows how decreasing $\partial F/\partial e$ increases $f_1 - f_2$. Above some level of health, most organisms probably experience diminishing returns to fitness from additional energy, $\partial^2 F/\partial e^2 < 0$. Hence, a well fed animal should require a greater feeding rate premium in the risky patch than a hungry animal (for empirical support see Godin & Smith 1988, Lima 1988).

2.3. Distinguishing among the models

With respect to patch use, the four models all make the same qualitative predictions. The models only differ in their quantitative predictions. When fitness involves maximizing the probability of surviving predation (Model 1), then increasing the energy constraint (increasing F) results in a smaller cost of predation and a smaller difference in quitting harvest rates between risky and safe food patches (increasing F increases the magnitude of Φ_F). When fitness involves maximizing the fitness reward of energy (Model 2), then increasing the safety constraint (p) results in a larger cost of predation and a larger difference in quitting harvest rates between risky and safe patches (increasing p increases the magnitude of Φ_p). Depending upon the magnitude of the energy constraint and the safety constraint, respectively, the cost of predation in Models 1 and 2 can be much larger or smaller than the predation costs in Models 3 and 4.

Comparisons of the cost of predation between Models 3 and 4 are less ambiguous. When fitness is an additive rather than multiplicative function of offspring (F) and safety (p), the cost of predation is lower; $p < 1$ in equation (4c) must be less than $(F+1) > 1$ in equation (4d). Similarly the difference in quitting harvest rates between risky and safe patches will always be smaller in the additive model than in the multiplicative model: compare equations (5c) and (5d), respectively.

A forager's patch use behavior probably will not reveal which of the four models is most appropriate. Detailed information on an organisms life history will probably provide the only means for selecting among the different models.

3. Discussion

This paper examined, within a single framework, the popular approaches to modeling foraging in patches under predation risk. Gilliam & Fraser (1987, 1988) and Brown (1988) provide two models. Gilliam & Fraser (1988) used the probability of surviving predation subject to an energy constraint as their fitness function (see Model 1). From this they derive the "μ/f" rule for leaving all patches at the same ratio of predation risk and feeding rate. Brown (1988) used the product of safety and value of energy gain as a fitness function (see Model 4) to show that a forager should leave a patch when its feeding rate no longer compensates for the metabolic, predation, and missed opportunity costs of foraging ($H = C + P + MOC$).

Using four different fitness formulations, I examined the domains of the "μ/f" and "$H = C + P + MOC$" rules. The former rule applies to all four models under the assumption that the forager's optimal allocation of time includes resting in a refuge to conserve energy and/or avoid predation. The latter rule applies to all four models under the assumption of diminishing returns to fitness from net energy gain and the assumption that energy leaves unchanged or enhances the value of other fitness enhancing activities. Finally, the two rules represent different ways (compare equations 5 and 6) of viewing the same optimal allocation of time among foraging in risky and safe patches.

Confusion over the proper domain of the "μ/f" rule may explain some of the discrepancies in the literature. Gilliam & Fraser (1987) and Gotceitas (1990) support the prediction of using food patches that minimize "μ/f" but do not support the prediction that foraging time should decline as food patch quality increases (Gilliam & Fraser 1987, Mitchell & Brown 1990, Abrams 1991). The resolution of this discrepancy probably lies in decoupling the "μ/f" rule from a particular fitness function. The "μ/f" rule may apply while the assumption that foragers attempt to maximize the probability of surviving predation (Model 1) is probably false.

Abrahams & Dill (1989) see their formulation of safety and feeding rates as different: "We assumed that habitat quality is determined by the additive effects of energy and risk, whereas Gilliam & Fraser (1987) assumed that it is determined by the *ratio* of mortality rate to feeding rate...". As in the case of Brown (1988) versus Gilliam & Fraser (1987), this discrepancy results from viewing the optimal allocation of time in terms of either additive (equations 5) or multiplicative (equation 6) components.

The models considered here use static optimization techniques to analyze patch use under the assumption that the forager influences predation risk through its allocation of time among activities that vary in predation risk. An alternative approach uses dynamic optimization to consider the effects of predation risk on foraging behavior (Mangel & Clark 1988, Ludwig & Rowe 1990). Abrams (1991) discusses some of the advantages of using static optimization. These include ease of analysis, generality of results, and, if the actual temporal sequence of the forager's behavior is not under investigation, then dynamic optimization models may yield, as yet, few additional insights (see Mangel & Clark 1988 for some of the advantages of using dynamic optimization).

Besides altering time allocation among patches to influence predation risk, many foragers can use vigilance behaviors to alter the risk of predation while engaged in a particular activity (see Lima & Dill 1990 and references therein). Models of vigilance consider how a forager should trade off safety and feeding rates within a food patch (Lima 1990). In the models of patch use considered here, the forager trades off safety and feeding rates by allocating time among food patches. A more complete picture of foraging will emerge when vigilance and time allocation are combined into the same model.

The four 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.

By using giving-up densities as a surrogate for quitting harvest rate, Brown et al. (1992) were able to use the patch use behavior of fox squirrels (*Sciurus niger*) to test these three predictions. Depletable food patches placed near and away from trees provided safe and risky patches, respectively. In response, squirrels had higher giving-up densities away from trees than near trees. To lower the squirrels' marginal valuation of food, sunflower seeds were augmented to the natural environment. In response, giving-up densities increased in both risky and safe patches. And, for any giving-up density in the safe microhabitat, fox squirrels had a higher giving-up density in the risky microhabitat in response to food augmentation.

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