

Vigilance, patch use and habitat selection: Foraging under predation risk

Joel S. Brown*

Department of Biological Sciences, University of Illinois at Chicago, 845 W. Taylor Street, Chicago, IL 60607, USA

ABSTRACT

To balance conflicting demands for food and safety from predation, feeding animals have two useful tools. First, they can vary the amount of time they devote to harvesting patches that vary in predation risk and feeding rates. Second, they can use vigilance to trade-off food and safety while feeding from a food patch. I present a model for predicting how an optimal forager should jointly use these two tools. Factors influencing the use of these tools include encounter rate with predators, predator lethality in the absence of vigilance, effectiveness of vigilance in reducing predator lethality, the marginal value of energy to the forager and the forager's survivor's fitness. Patch-use behaviours influenced by these factors include vigilance level, quitting harvest rate and giving-up density (GUD). All three of these patch-use behaviours should increase in response to an increase in encounter rate with predators, predator lethality and the forager's survivor's fitness, and decrease with an increase in the marginal value of energy. In response to increasing the effectiveness of vigilance, vigilance should increase and the GUD and quitting harvest rate should decline. The amount of food left by a forager in a depletable food patch, the GUD, provides an empirical link for testing the model's predictions. Giving-up densities should increase with increasing predation risk, and GUDs should increase with declining food-density-specific harvest rates. Differences in GUDs among food patches attributable to differences in quitting harvest rates measure the contribution of time allocation to managing differences in predation risk. Differences in GUDs attributable to differences in food-density-specific harvest rates measure the contribution of vigilance to managing predation risk.

Keywords: ecology of fear, foraging theory, giving-up density, habitat selection, patch use, predation risk, quitting harvest rate, time allocation, vigilance.

INTRODUCTION

Two approaches have been taken to understanding foraging under predation risk. The first considers how a forager should allocate its time among activities that vary in feeding opportunities and predation risk. The second considers how a forager should use vigilance to trade-off feeding rates and predation risk while engaged in a particular activity. Lima and Dill (1990) characterize the safety of a feeding activity as the probability of surviving predation. This probability has two components. The first represents the rate of encounters

* e-mail: squirrel@uic.edu

with predators while engaged in the feeding activity and the second involves the total time engaged in the activity. Most foraging animals simultaneously use vigilance to influence the former and time allocation to influence the latter. Here, I combine these two approaches by asking how the forager should jointly use time allocation and vigilance to offset predation risk. Using foraging theory as a framework, the model makes predictions regarding how manipulations of predation risk and food should jointly influence habitat selection, vigilance, giving-up densities (GUDs) and quitting harvest rates in depletable food patches. The theory shows that vigilance activity and quitting harvest rates do not provide accurate gauges of habitat-specific costs of predation. Because they integrate contributions of vigilance and harvest rates, GUDs should provide an accurate measure of predation costs.

Vigilance as a response to predation risk

Although the rate of fatal encounters is influenced by the numbers and aptitudes of predators, this rate may in part be under the behavioural control of the feeding organism. By adopting particular alert behaviours (e.g. prairie dogs; Hoogland, 1979), changing feeding modes (e.g. grey squirrels; Newman *et al.*, 1988) and paying attention to the alarm calls of others (e.g. woodpeckers; Sullivan, 1984), the forager may be able to reduce the rate of fatal encounters. To characterize the vigilance trade-off between food intake rate and predation risk, Fraser and Gilliam (1987) defined the tenacity index as 'the forager's attitude towards hazard in terms of the degree to which it maintains its feeding rate when a predator is introduced'. However, vigilance may carry a price. Lima (1990) discusses several models in which vigilance represents a trade-off between safety and feeding rates within a food patch (Lima, 1988a). Most models have been interested in how group size influences the optimal vigilance behaviour of the individual (Bertram, 1978; Pulliam *et al.*, 1982; Dehn, 1990; McNamara and Houston, 1992). These models do not address how the forager should allocate foraging time among food patches or habitats.

Time allocation among food patches as a response to predation risk

A forager can influence its safety by the way it allocates time among different activities that differ in risk and/or feeding rates. When the most profitable feeding patch incurs the least risk, this patch should be favoured over all other patches (Nonacs and Dill, 1990). More likely, patch choice requires a trade-off 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 are more willing to take risks than well-fed salmon; Dill and 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, 1992, 1993). Theories that model patch use and habitat selection under predation risk all make the prediction that foragers should demand higher feeding rates from risky than from safe habitats (Gilliam and Fraser, 1987, 1988; Brown, 1988, 1992; Houston *et al.*, 1993). These models, however, do not address the question of how vigilant the forager should be while in a particular food patch.

Combining vigilance and time allocation

I introduce vigilance into Brown's (1988, 1992) model of patch use under predation risk. The model assumes that a forager's harvest rate in a patch declines as the patch's resources deplete. Upon quitting the patch, the GUD (the resources remaining in the patch; Brown, 1988) represents the point at which the forager's quitting harvest rate no longer exceeds its perceived metabolic, predation and missed opportunity costs of foraging. Within each food patch, I allow the forager to select both its vigilance level and its GUD. I then use the results of the model to make predictions regarding the effect of various factors on the forager's level of vigilance, quitting harvest rate and GUD. These factors include the forager's encounter rate with predators, the predator's lethality, the effectiveness of vigilance in reducing lethality, the forager's survivor's fitness and the forager's valuation of resources.

The following theory, while crucial to understanding the model's assumptions and logic, may be tedious and opaque to some readers. As a prelude, Table 1 provides the model's testable predictions. Here are some highlights. A forager is likely to vary both its time allocation and vigilance among habitats. While somewhat complementary tools for managing predation risk, changes in time allocation or vigilance will dampen changes in the other. The forager's allocation of time and vigilance to a depletable food patch determines its GUD. In general, the forager's optimal level of vigilance co-varies positively with its GUD. Only under changes in the effectiveness of vigilance does vigilance level co-vary negatively with GUD. With respect to actual predation risk, changes in predator numbers, predator lethality and the effectiveness of vigilance result in a positive relationship between GUDs and predation risk. Conversely, changes in the marginal value of energy or survivor's fitness results in a negative relationship between GUDs and actual predation risk.

MODELLING TIME ALLOCATION AND VIGILANCE

Consider a forager that decides how to allocate time among food patches and that also decides its rate of vigilance within each food patch. Let the forager realize fitness following T time units (for birds and mammals, T is the period of time from one breeding event to the next and it may include such periods as over-wintering). The forager's finite growth rate (per time) is the product of F (survivor's fitness: expected fitness gain in the absence of predation) and p (safety: the probability of surviving predators to realize the gain in fitness)

Table 1. Predictions for the effects on GUDs, vigilance level, quitting harvest rate and predation risk in a patch from increasing (1) encounter rate with predators (m), (2) predator lethality ($1/k$), (3) effectiveness of vigilance (b), (4) forager's survivor's fitness (F) and (5) the marginal value of energy ($\partial F/\partial e$)

	Giving-up density	Vigilance rate	Quitting harvest rate	Predation risk
Encounter rate with predators	↑	↑	↑	↑
Predator lethality	↑	↑	↑	↑
Effectiveness of vigilance	↓	↑ at low b ↓ at high b	↓	↓
Survivor's fitness	↑	↑	↑	↓
Marginal value of energy	↓	↓	↓	↑

(Lima *et al.*, 1985; Brown, 1988, 1992; Abrams, 1991). Natural selection should result in the following:

$$\max pF \text{ with respect to } t \text{ and } u \text{ subject to } \sum_{i=1}^n t_i = T \quad (1)$$

where $t = (t_1, \dots, t_n)$ represents time allocated by the forager to n different activities that can include both foraging and non-foraging activities, and $u = (u_1, \dots, u_n)$ represents the fraction of time devoted to vigilance while the forager engages in a particular activity ($0 < u_i < 1$ for all $i = 1, \dots, n$). Let p and F be influenced by t and u . The probability of surviving predation can be increased by shifting time from a risky to a safe activity, or by increasing the level of vigilance while engaged in an activity. With respect to a foraging activity, let t_i and u_i influence F via the forager's energy state, where fitness in the absence of predation increases with energy state. Energy state can be increased by shifting foraging time from a poor patch to a rich patch, or by decreasing the level of vigilance while harvesting a patch.

When rich patches are risky and poor patches are safe, then switching time from safe to risky patches increases the animal's survivor's fitness but also increases its probability of being killed by a predator. In contrast, increasing the amount of vigilance while engaged in a foraging activity decreases the animal's survivor's fitness and decreases its probability of being preyed upon: increasing u_i decreases F and increases p . Time allocation and vigilance become tools that the forager can use for balancing food and safety.

Before determining the optimal values for time allocation and vigilance, it is useful to consider in more detail the effects of time allocation and vigilance on the animal's survivor's fitness and the animal's probability of surviving predation.

Effect of patch use and vigilance on the animal's survivor's fitness

Assume that vigilance and time spent foraging alter the forager's survivor's fitness, F , through effects on net energy gain, e (i.e. $F[e(u, t)]$). In the absence of vigilance, let the forager's harvest rate, f , in a food patch be approximated by Holling's disc equation (Holling, 1965):

$$f = \frac{aN}{(1 + ahN)} \quad (2)$$

where a is the forager's encounter probability on food items (Hassell, 1978), h is the forager's handling time on a food item and N is the remaining number of food items within the patch. When a forager quits a food patch, N is the GUD and it increases with increasing f according to the relationship (found by rearranging Equation 2):

$$N = \frac{f}{a(1 - hf)} \quad (3)$$

In the presence of vigilance, let the forager's harvest rate be reduced proportionally by the amount of vigilance to $(1 - u)f$ (Houston *et al.*, 1993).

Spending more time harvesting resources from the i th food patch has the following effect on the forager's survivor's fitness:

$$\frac{\partial F}{\partial t_i} = \left(\frac{\partial F}{\partial e} \right) \left(\frac{\partial e}{\partial t_i} \right) = \left(\frac{\partial F}{\partial e} \right) [(1 - u_i)f_i - c_i] \quad (4)$$

where $\partial F/\partial e$ is the effect of net energy gain on the forager's survivor's fitness, $(1 - u_i)f_i$ is the current rate of resource harvest from the patch, and c_i is the energetic cost of foraging (this assumes that the energetic costs of vigilance, searching for food items and handling food items are the same). The effect of increasing time in a patch is the product of the forager's net rate of energy gain and the effect of energy on the forager's survivor's fitness.

Increasing the amount of vigilance while in the i th food patch has the following effect on the forager's survivor's fitness:

$$\frac{\partial F}{\partial u_i} = \left(\frac{\partial F}{\partial e} \right) \left(\frac{\partial e}{\partial u_i} \right) = \left(\frac{\partial F}{\partial e} \right) (-f_i t_i) < 0 \quad (5)$$

where $\partial e/\partial u_i = -f_i t_i$. The loss of net energy gain in a patch from increased vigilance is the product of the GUD stated in terms of f_i (see Equation 3) and the total time allocated to the patch, t_i .

So long as net energy gain from a patch is positive, $(1 - u_i)f_i > c$, then Equation (4) gives the increase in the forager's survivor's fitness from spending more time in a food patch, and Equation (5) gives the decrease in the forager's survivor's fitness from increasing the rate of vigilance.

Effect of patch use and vigilance on predation risk

Let μ_i represent the instantaneous risk of death from predation while foraging in patch i . I assume that this mortality rate does not vary with time spent in a food patch; that is, μ_i is independent of t_i . This means that the early and late stages of a foraging bout are equally risky.

Let the instantaneous risk of predation decline with the forager's rate of vigilance. In determining the relationship between vigilance and predation risk, consider three aspects of predation. The first of these is the encounter rate of predators with the forager, m . This parameter increases with the abundance of predators, the activity of predators and the ability of the predators to detect a forager. If the predator only captures one prey at a time and the prey forage as a group, m may decline with group size and represent the dilution effect (Bertram, 1978; Dehn, 1990). The second aspect considers the lethality of the predator in the absence of vigilance by the forager, k . Let this parameter be the forager's ability to escape a predator given the forager was not vigilant. This parameter increases with decreasing predator lethality and with other sources of information regarding the approach of a predator (alarm calls of others and other sensory information not directly tied to the individual's own vigilance). When foragers form groups, k may increase with group size and represent the benefit to the prey of 'many eyes' (Powell, 1974; Bertram, 1978; Dehn, 1990). The third aspect considers the effectiveness of vigilance in reducing the lethality of a predator, b . This parameter increases with the increased ability of the forager to make good an escape as a result of its own vigilance. These assumptions regarding vigilance and predation risk lead to the following relationship between vigilance and predation risk:

$$\mu_i = \frac{m_i}{k_i + b_i u_i} \quad (6)$$

and the following effect of vigilance on predation risk:

$$\frac{\partial \mu_i}{\partial u_i} = \frac{-m_i b_i}{(k_i + b_i u_i)^2} < 0 \quad (7)$$

The effect of vigilance in reducing predation risk increases with the prey's encounter rate with predators, m , the predator's lethality, $1/k$, and the effectiveness of vigilance, b .

Effect of patch use and vigilance on safety

The probability of surviving predation can be expressed as:

$$p = \exp\left(-\sum_{i=1}^n \mu_i t_i\right) \quad (8)$$

and the effects of vigilance and time on safety can be written as:

$$\frac{\partial p}{\partial u_i} = -p t_i \frac{\partial \mu_i}{\partial u_i} > 0 \quad (9)$$

$$\frac{\partial p}{\partial t_i} = -p \mu_i < 0 \quad (10)$$

By spending time in a food patch, safety declines in proportion to the patch's predation risk. By increasing vigilance within a food patch, safety increases proportionally with the amount of time allocated to the patch.

OPTIMAL LEVEL OF TIME ALLOCATION AND VIGILANCE

The technique of Lagrange multipliers can be used to determine the optimal allocation of time and vigilance among activities. Let ϕ be the Lagrange multiplier for the time constraint $\sum t_i = T$. Lagrange multipliers give the marginal fitness cost or benefit associated with relaxing the constraint (Chiang, 1974). As such, ϕ is the missed opportunity cost of not engaging in alternative activities (Brown and Alkon, 1990). The first-order necessary conditions for maximizing Equation (1) with respect to vigilance, u_i , and time, t_i , respectively, are:

$$F \frac{\partial p}{\partial u_i} + p \frac{\partial F}{\partial u_i} = 0 \quad (11)$$

$$F \frac{\partial p}{\partial t_i} + p \frac{\partial F}{\partial t_i} - \phi = 0 \quad (12)$$

These conditions apply when the optimal value for t_i is greater than zero and when the optimal value for u_i is greater than zero and less than 1: $t_i^* > 0$ and $u_i^* \in (0,1)$. To determine the optimal level of vigilance within a food patch and the optimal time to devote to a food patch, we can substitute the expressions for $\partial p / \partial u_i$, $\partial F / \partial u_i$, $\partial p / \partial t_i$ and $\partial F / \partial t_i$ into Equations (11) and (12), respectively. The optimal level of vigilance can be found by substituting Equation (5) for the effect of vigilance on the forager's survivor's fitness and Equation (9) for the effect of vigilance on safety into Condition (11):

$$u_i^* = \sqrt{\frac{m_i F}{f_i b_i (\partial F / \partial e)}} - \frac{k_i}{b_i} \quad (13)$$

The optimal amount of vigilance increases with the encounter rate with predators, m_i , and the animal's survivor's fitness, F . The optimal amount of vigilance decreases with the GUD, f_i , and the marginal value of energy, $\partial F / \partial e$. Vigilance increases with the predator's lethality, $1/k_i$. Time spent in the patch, t_i , influences the optimal level of vigilance through the GUD only. As such, the initial abundance of resources in the patch has no direct effect on the optimal rate of vigilance. The optimal value of vigilance at first increases and then decreases with the effectiveness of vigilance, b_i . There exists a threshold level of b such that, below this level, Equation (13) is negative and $u_i^* = 0$. When vigilance is not very effective, there is little point to vigilance. When the effectiveness of vigilance is very great, little vigilance is required (Fig. 1).

The actual predation risk while in a food patch after accounting for vigilance can be found by substituting u_i^* from Equation (13) into Equation (6) for μ_i :

$$\mu_i(u_i^*) = \sqrt{\frac{m_i f_i (\partial F / \partial e)}{b_i F}} \quad (14)$$

The actual risk of predation experienced by the forager becomes modified by its optimal level of vigilance. In response to vigilance, actual predation risk while harvesting a patch should increase with the encounter rate with predators, the GUD and the marginal value of energy. Predation risk should decrease with the animal's survivor's fitness and the effectiveness of vigilance. Interestingly, actual predation risk should be independent of the predator's lethality in the absence of vigilance.

The optimal amount of time to spend in a patch can be found implicitly by substituting Equation (4) for the effect of patch residence time on the forager's survivor's fitness, and Equation (10) for the effect of patch residence time on safety into Condition (12):

$$(1 - u_i) f_i - c_i - \frac{\mu_i F}{\partial F / \partial e} - \frac{\phi}{p(\partial F / \partial e)} = 0 \quad (15)$$

The four terms of Equation (15) correspond to the quitting harvest rate, metabolic cost of foraging, the predation cost and the missed opportunity cost, respectively. A forager should leave a patch when the patch harvest rate equals the sum of the three foraging costs (Brown, 1988, 1992).

If it is optimal to spend some but not all time vigilant, $u^* \in (0, 1)$, then Equation (14) for μ can be substituted into (15) to give:

$$(1 - u_i) f_i - c_i - \sqrt{\frac{m_i f_i F}{b_i (\partial F / \partial e)}} - \frac{\phi}{p(\partial F / \partial e)} = 0 \quad (16)$$

and Equation (13) for the optimal level of vigilance can be substituted into Equation (16):

$$f_i \left(1 + \frac{k_i}{b_i} \right) - c_i - 2 \sqrt{\frac{m_i f_i F}{b_i (\partial F / \partial e)}} = \frac{\phi}{p(\partial F / \partial e)} \quad (17)$$

The forager selects its time allocation to produce the GUD that satisfies Equation (17).

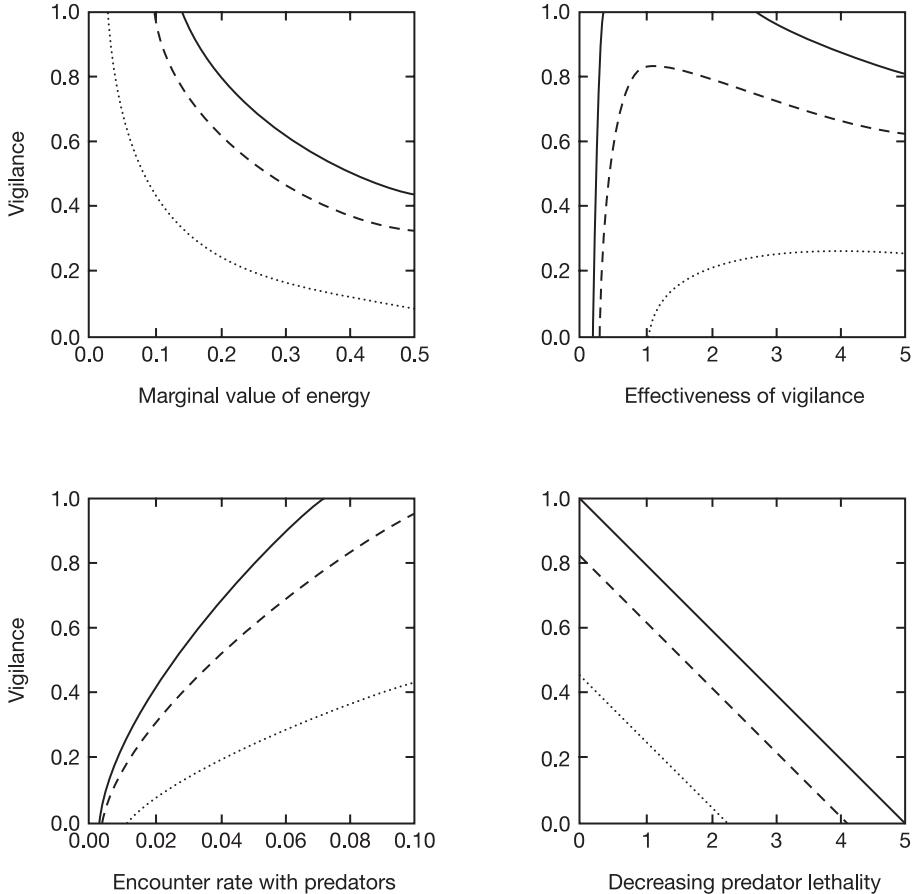


Fig. 1. The effects of the marginal value of energy, effectiveness of vigilance, encounter rate with predators and predator lethality on the optimal level of vigilance for food abundances (solid, dashed and dotted lines represent high, medium and low food abundances, respectively). Below a threshold level of the marginal value of energy, the optimal level of vigilance is 1. Below a threshold level of the effectiveness of vigilance, predator lethality or encounter rate with predators, the optimal level is no vigilance. For illustration purposes, $\partial F/\partial e = 0.2$, $b = 5$, $m = 0.05$, $k = 1$ and $f = 0.1$, 0.15 and 0.5 for low, medium and high food levels, respectively.

Because Condition (17) is transcendental in f , an explicit equation cannot be derived for the GUD.

Equation (17) can be simplified by considering two scenarios that determine the missed opportunity cost represented by ϕ . In one scenario, the forager exhausts all fitness-enhancing activities by the end of the time period T , and in the other the forager experiences an infinitely repeating environment and remains continuously active harvesting resources.

In the first scenario (depleting environment), assume that the forager finds it optimal to spend time inactive and resting in a refuge. Assume that the forager, while resting, expends energy at rate $c_o < c_i$, harvests no resources, experiences negligible predation risk, and receives no additional benefits from engaging in possible alternative activities such as grooming, rearing offspring and securing matings (these would be considered activities

separate from ‘resting’). In this scenario, the missed opportunity cost ϕ is given by (Brown, 1992; Brown *et al.*, 1994):

$$-c_o = \frac{\phi}{p(\partial F/\partial e)} \quad (18)$$

and Equation (17) can be rewritten as:

$$f_i \left(1 + \frac{k_i}{b_i} \right) - (c_i - c_o) - 2 \sqrt{\frac{m_i f_i F}{b_i (\partial F / \partial e)}} = 0 \quad (19)$$

In the second scenario (non-depleting environment), assume that the forager does not deplete the resources of the environment, that there are always additional and profitable food patches awaiting exploitation, and that the forager’s population size has reached equilibrium ($pF = 1$). In this case, the forager does not retreat to a refuge, but remains active for the duration of the time period. In this scenario, the missed opportunity cost is zero (i.e. $\phi = 0$). In a non-depleting environment where the forager’s population growth rate is positive ($pF > 1$), the missed opportunity cost is positive ($\phi > 0$), and vice versa when the population growth rate is negative ($pF < 1 \Rightarrow \phi < 0$).

JOINT USE OF VIGILANCE AND TIME ALLOCATION

For a given set of parameters, there will be a particular optimal level of vigilance, u^* , and optimal level of time allocation among patches, t^* , that maximizes the forager’s fitness. Equations (11) and (12) can be used to determine the difference in GUDs and quitting harvest rates in two patches (1 and 2) that differ in their risk characteristics (encounter rate with predators, predator lethality and/or the effectiveness of vigilance):

$$(1 - u_2^*) f_2 - (1 - u_1^*) f_1 = \frac{F(\mu_2 - \mu_1)}{\partial F / \partial e} \quad (20)$$

where optimal vigilance levels and predation risks come from Equations (13) and (14), respectively.

From Equation (20), the joint use of vigilance and time allocation lie on a continuum characterized by two extremes of vigilance levels and time allocation. At one extreme, the forager may manage predation risk entirely through time allocation, keeping vigilance levels constant among patches that vary in predation risk: set $u_1 = u_2$ in (20). When vigilance levels do not vary between two patches, differences in the forager’s patch-specific GUDs measure the differences in patch-specific risks of predation: $(f_1 - f_2)$ is directly proportional to $(\mu_1 - \mu_2)$ (Fig. 2).

At the other extreme, the forager may sacrifice its feeding rate in the risky habitat by adopting a level of vigilance in the risky habitat such that the risk of mortality is now equal between the ‘safe’ (patch 1) and ‘risky’ (patch 2) habitats: that is, $\mu_1(u_1) = \mu_2(u_2)$ because $u_1 < u_2$. In this case, the forager should leave each patch at the same quitting harvest rate where $(1 - u_1) f_1 = (1 - u_2) f_2$. To achieve this, the forager must have a higher GUD in the risky than in the safe habitat ($f_1 > f_2$), but equal quitting harvest rates. When vigilance completely compensates for habitat-specific risks of predation, habitat-specific differences in GUDs measure the feeding cost of using vigilance: $(f_1 - f_2)$ is directly proportional to $(u_1 - u_2)$ (Fig. 2).

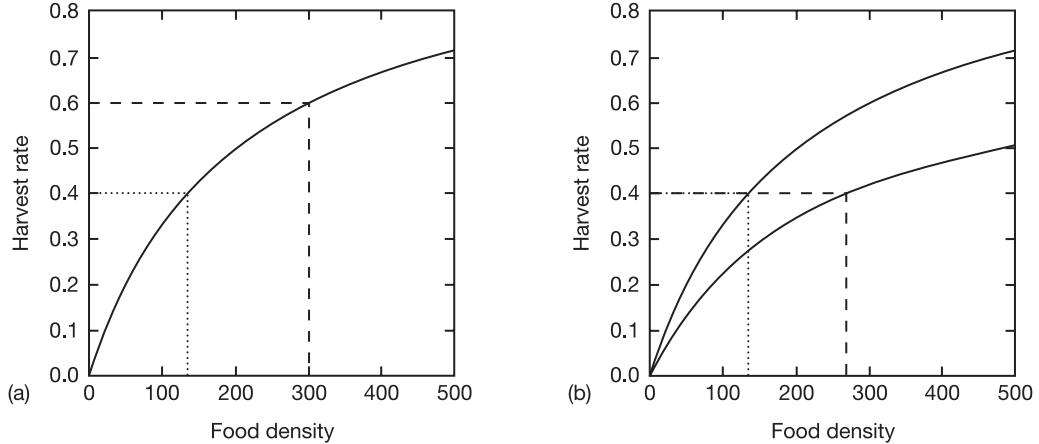


Fig. 2. The two ways in which a forager can respond to food patches varying in predation risk (dotted and dashed lines refer to low- and high-risk patches, respectively). The solid line shows the relationship between the harvest rate, $(1 - u)f$, and food density. In (a) the forager uses the same level of vigilance in both patches and balances the patch differences in predation risk by requiring a higher quitting harvest rate and higher GUD in the risky (dashed line) than in the safe (dotted line) patch. In (b) the forager equalizes predation risk between the two patches by being more vigilant in the risky (lower harvest rate curve) than in the safe (upper harvest rate curve) patch. In this case, the forager has the same quitting harvest rate in each patch, but still has a higher GUD in the risky than in the safe patch. Differences in GUDs attributable to differences in quitting harvest rates measure differences in predation risk, whereas differences in GUDs attributable to different harvest rate curves measure differences in vigilance levels.

We can use the results of Equation (20) to make two predictions regarding how GUDs and quitting harvest rates in depletable food patches measure the forager's joint use of time allocation and vigilance to manage feeding in patches that differ in predation risk:

- *Time allocation:* differences in the forager's giving-up density attributable to differences in the quitting harvest rate measure the actual mortality differences between foraging in one patch than another. This difference represents the contribution of time allocation to managing predation risk.
- *Vigilance:* differences in the forager's giving-up density attributable to different patch-specific harvest rates measure the contribution of vigilance to managing predation risk.

Joint changes in vigilance and time allocation

The forager's joint choice of vigilance level and time allocation depend on such factors as encounter rate with predators, predator lethality and effectiveness of vigilance. Vigilance and time allocation also depend upon the energy state of the forager and its marginal valuation of energy. Condition (13) for vigilance and Condition (15) for time allocation provide a means for predicting the effects of the salient parameters and functions on the giving-up density, f , rate of vigilance, u , and quitting harvest rate, $(1 - u)f$. To do this (see the Appendix), I will use the implicit function theorem to differentiate Expression (15) for f ,

Expression (13) for u , and $(1 - u)f$ with respect to m , k , b , F and $\partial F/\partial e$, respectively, under the assumption that the use of a single patch has negligible effect on the forager's survival probability, p , survivor's fitness, F , and missed opportunity cost, ϕ .

- *Encounter rate with predators*: in response to an increased encounter rate with predators, the forager should increase its giving-up density, increase its rate of vigilance and increase its quitting harvest rate (Fig. 3). Actual predation risk will increase (Fig. 4).
- *Predator lethality*: in response to increasing the predator's lethality, the forager should increase its giving-up density, increase its rate of vigilance and increase its quitting harvest rate (Fig. 3). Actual predation risk will increase (Fig. 4).
- *Forager's survivor's fitness and marginal value of energy*: in response to increasing the forager's survivor's fitness, or decreasing the forager's marginal value of energy, the forager should increase its giving-up density, increase its rate of vigilance and increase its quitting harvest rate (Fig. 5). Actual predation risk will decrease (Fig. 4).

The above effects all involve the forager jointly using vigilance and time allocation to balance food and safety. When used jointly, the effects are damping, in that the GUD rises and falls less than otherwise in the absence of adjustments in vigilance. Vigilance increases or decreases less than otherwise in the absence of changes in GUDs. Changes in the marginal value of energy, the forager's survivor's fitness, encounter rate with predators and the predator's lethality all result in similar and concordant changes in GUD, vigilance and quitting harvest rate. A rising GUD is associated with increased vigilance and an increased quitting harvest rate (Table 1).

- *Effectiveness of vigilance*: increasing the effectiveness of vigilance decreases the giving-up density, increases (at low b) or decreases (at high b) vigilance and greatly reduces the quitting harvest rate (Fig. 5). Actual predation risk will decline (Fig. 4).

Changing the effectiveness of vigilance, b , results in amplified changes in the GUD and vigilance. The decrease in quitting harvest rate is associated with a decline in predation risk. Effectiveness of vigilance is the only factor that can result in an inverse relationship between GUD and vigilance (Table 1).

The above results are general in that they do not depend on the exact nature of the environment, alternative fitness-enhancing activities or the missed opportunity cost. While the missed opportunity cost does not influence the direction in which each parameter influences vigilance, GUDs and quitting harvest rates, it does influence the magnitude of the effects. The effect of a factor on vigilance is always more extreme in a non-depleting than in a depleting environment. This has to do directly with the sign of the missed opportunity cost: negative in a depleting environment and zero in a non-depleting environment. In a depleting environment, resting safely in the burrow while saving energy is a valuable activity. This increases the cost of vigilance. In a non-depleting environment, the cost of vigilance is merely the foregone energy from not foraging. In a depleting environment, the energy cost of vigilance sums the foregone energy as well as the additional energetic cost of activity ($c_i - c_o$). As a consequence:

- *Effect of missed opportunity cost*: vigilance should be higher in a non-depleting than in a depleting environment.

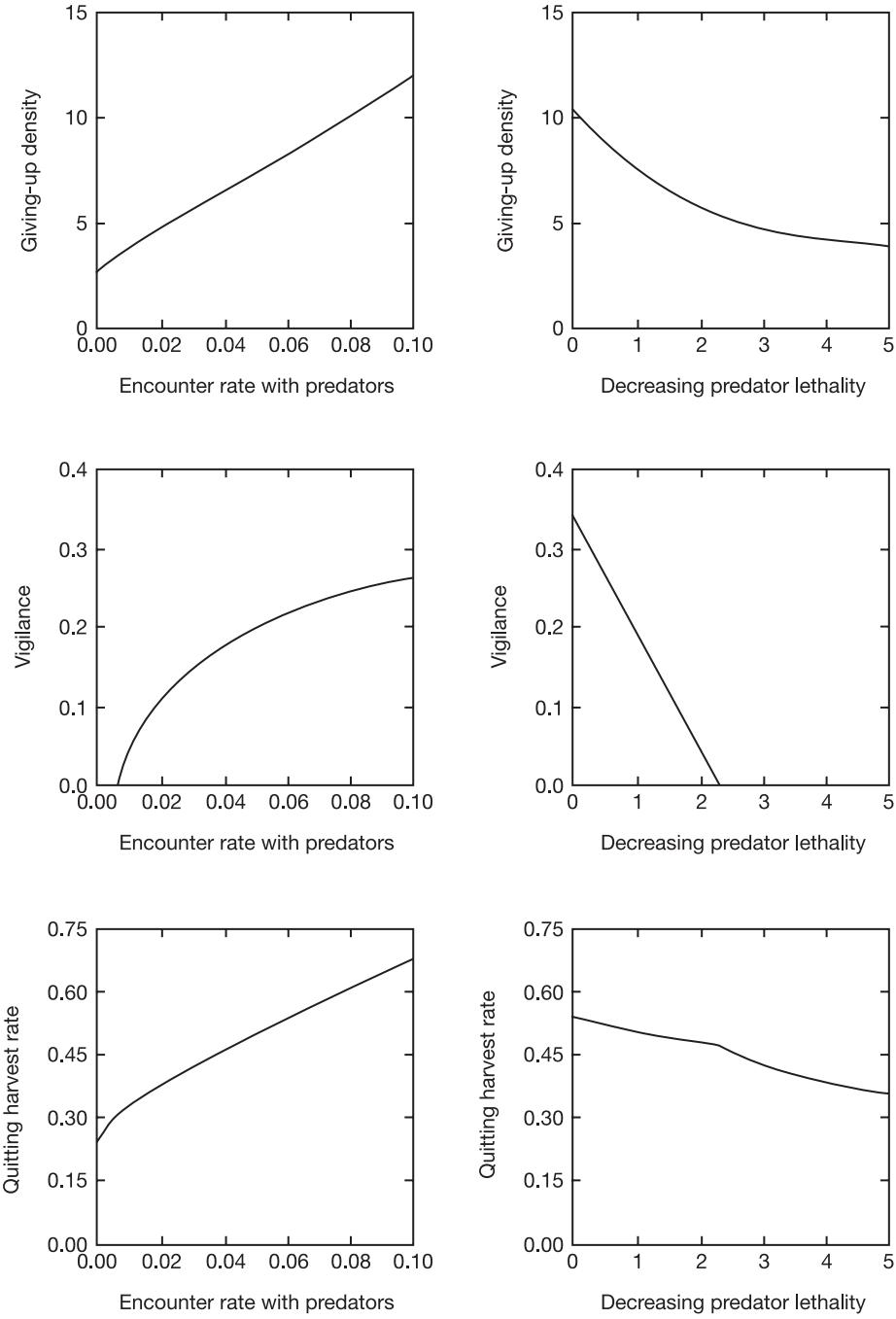


Fig. 3. The effects of encounter rate with predators and decreasing predator lethality on three measures of a forager's patch use behaviour: GUD, optimal level of vigilance and quitting harvest rate. For most baseline parameter settings, see Fig. 2. For feeding rates, the forager's encounter probability and handling time were set to: $a = 0.1$ and $h = 0.25$.

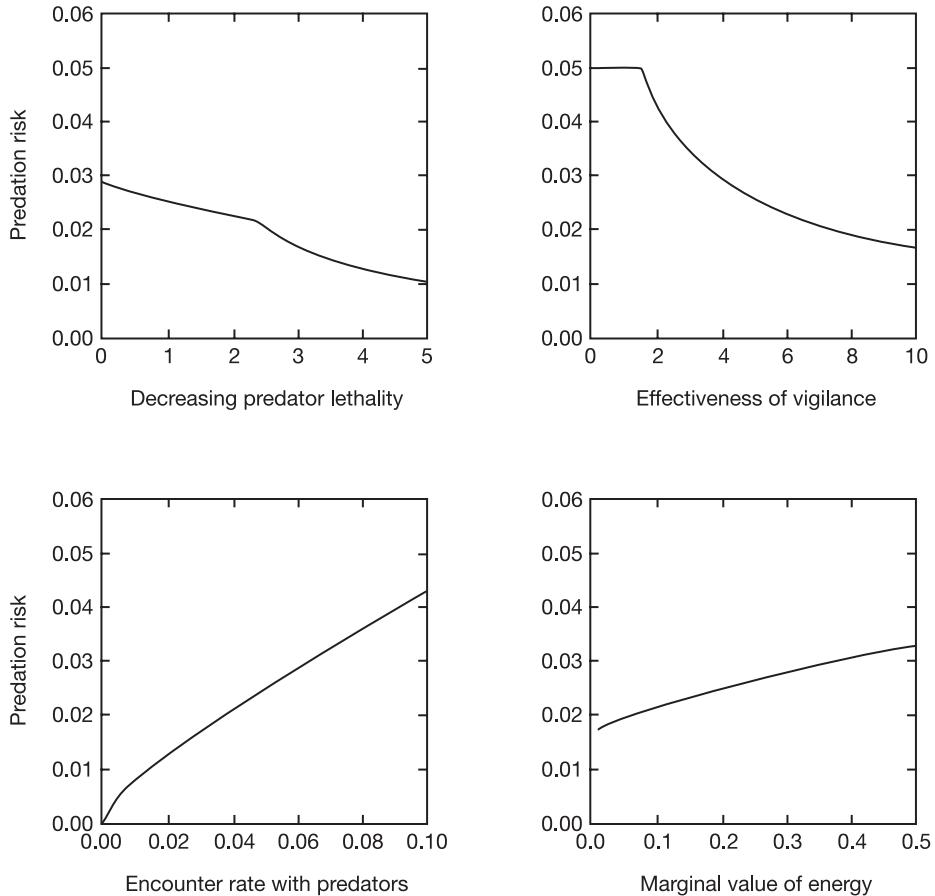


Fig. 4. The actual predation risk experienced by the forager after it has adjusted its patch-use behaviour to the effects of predator lethality, effectiveness of vigilance, encounter rate with predators and marginal value of energy. For baseline parameter settings, see Figs 2 and 3.

VIGILANCE AND GIVING-UP DENSITIES IN RISKY VERSUS SAFE ENVIRONMENTS

The above analyses have considered the effects of predation risk on foraging behaviour in an environment where risk varies among food patches. In such a situation, the forager's survivor's fitness and marginal valuation of energy remain constant from patch to patch – each patch is assumed to have only a small effect on the forager's survivor's fitness, F , or probability of surviving predation, p . When risk varies among food patches, the forager adjusts its patch-use strategy accordingly from patch to patch.

At a scale greater than patches, different environments may afford greater or lesser amounts of safety, either because of different frequencies of safe and risky patches or because the food patches of one environment may be overall more risky than those of another. If animals cannot move freely among environments and are constrained to live their entire lives within a particular environment, then in the long term there should be an inverse relationship between the probability of surviving predation, p , and its survivor's

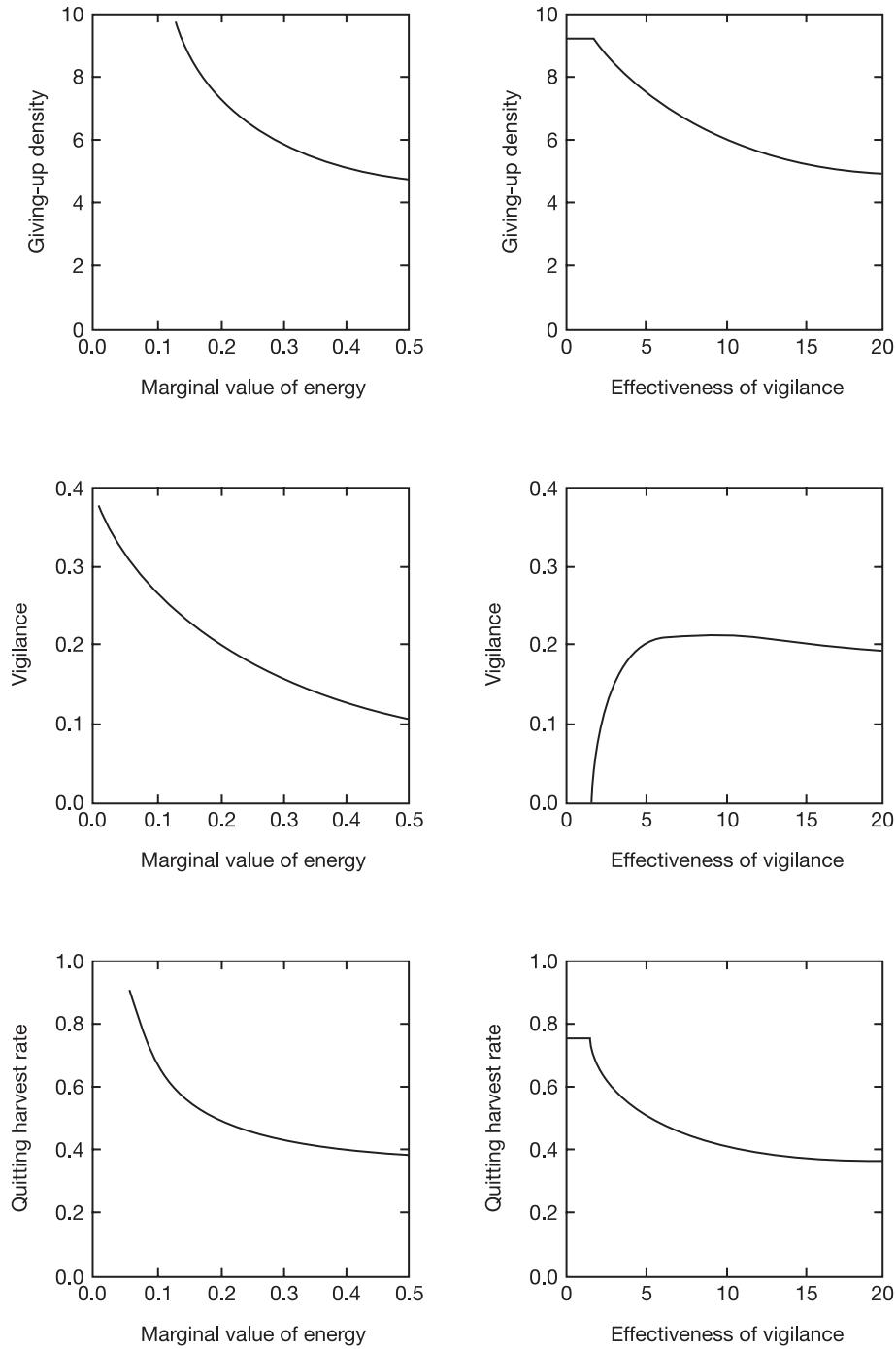


Fig. 5. The effects of predator lethality and effectiveness of vigilance on the forager's GUD, optimal level of vigilance and quitting harvest rate. For baseline parameter settings, see Figs 2 and 3.

fitness, F (Moody *et al.*, 1996). As a result, the safe environment offers a higher p and concomitantly lower F .

Two forces will jointly contribute to a higher GUD, quitting harvest rate and vigilance level in the risky than in the safe habitat. First, the risky environment may be so because of either a higher encounter rate with predators or greater predator lethality, both of which produce higher GUDs, quitting harvest rates and vigilance levels in a manner analogous to their effects among risky and safe patches within an environment. Second, the higher survivor's fitness, F , and lower marginal value of energy, $\partial F/\partial e$ (if there are diminishing returns to fitness from energy gain), in the risky environment will magnify the increased levels of GUDs, quitting harvest rates and vigilance.

- *Effect of scale on patch-use strategies:* differences in the forager's patch-use strategies with respect to giving-up densities, quitting harvest rates and vigilance levels should be more extreme when predation risk varies among environments than when predation risk varies among patches within an environment.

Two environments may differ in risk as a result of differences in the effectiveness of vigilance. Foragers in the environment with a lower effectiveness of vigilance will have magnified increases in GUDs and quitting harvest rates. But, the difference in vigilance between the safe (effective vigilance) and risky (ineffective vigilance) environments is ambiguous. In the risky environment, the ineffectiveness of vigilance selects for less vigilance, whereas the increased survivor's fitness of foragers in the risky environment selects for more vigilance.

DISCUSSION

A forager's cost of predation increases with predation risk, increases with the forager's survivor's fitness and decreases with the forager's marginal value of food (Brown, 1992; Houston *et al.*, 1993). The forager can respond to its cost of predation by choosing the amount of time to spend in the food patch and/or by adopting a particular level of vigilance. In this way, a forager has two tools at its disposal for balancing conflicting demands for food and safety: time allocation and vigilance. Via time allocation, a forager can trade-off safety and energy by exploiting food patches in safe habitats to lower levels than patches in risky habitats (Gilliam and Fraser, 1987; Brown, 1988). Via vigilance, a forager can trade-off food and safety while exploiting a given food patch (Fraser and Gilliam, 1987).

In using these tools, the forager selects for each patch its optimal rate of vigilance (= proportion of time spent vigilant, number of scans, duration of scanning, etc.) and its GUD. In response to increasing the forager's survivor's fitness or decreasing its marginal value of energy, both vigilance and GUD should increase. The increased vigilance results in a lower risk of predation. When differences in vigilance levels correspond to the forager's survivor's fitness, actual risk varies inversely with vigilance. In response to increasing the forager's encounter rate with predators or the predator's lethality in the absence of vigilance, both vigilance and GUD should increase; actual risk varies directly with vigilance. In response to increasing the effectiveness of vigilance, the forager should decrease its GUD. The relationship between vigilance and the effectiveness of vigilance should be humped-shaped, although the adjustments of GUD extend the region over which vigilance increases with the effectiveness of vigilance (Table 1).

Under some circumstances, the forager's optimal level of vigilance will be zero. In this case, the forager will only have time allocation at its disposal for mediating situation-dependent risks of predation. For vigilance to be greater than zero, the effectiveness of vigilance must be sufficiently large, the predator sufficiently lethal in the absence of vigilance, and there must be a sufficiently high encounter rate with predators.

Houston *et al.* (1993) and Newman (1991) used stochastic dynamic programming to address foraging under predation risk. Houston *et al.* (1993) considered a scalar-valued anti-predator strategy that can either represent vigilance while feeding or time allocation between a feeding habitat and a refuge. In either case, the anti-predator strategy trades off food and safety in a manner analogous to the vigilance strategy of the present model. The three general results include: (1) a forager will demand a higher rate of feeding from a risky than from a safe habitat; (2) increasing the encounter rate with predators increases the forager's rate of vigilance; and (3) increasing the forager's energy state (analogous to survivor's fitness of the present model) will increase the forager's vigilance. The present model advances these predictions by considering the joint use of vigilance and time allocation as a vector-valued anti-predator strategy, and by dividing predation risk into the three components of encounter rate with predators, predator lethality in the absence of vigilance and the value of vigilance in reducing predator lethality. In terms of patch-use behaviour and vigilance, the present model permits a more general and complete set of predictions (Table 1).

Newman (1991) considered patch use under predation risk. In his model, predation risk was a property of the foraging environment at large, and the forager managed risk by deciding how much time to spend foraging versus how much time to spend in a refuge. While foraging, the animal selected its optimal GUD and then allocated time among patches so as to achieve this GUD. (Newman does not consider GUDs explicitly, but many of his predictions can be couched in terms of GUDs.) Increasing the travel time between patches and increasing the initial abundance of food within patches increases GUDs. Interestingly, increasing environment-wide predation risk does not influence GUDs. This probably has to do with the forager selecting a GUD which maximizes some measure of net energy gain while out of its refuge. Predation risk does not influence this rate-maximizing GUD, but it does influence the allocation of time between foraging and the refuge. In my model, predation risk is assumed to vary among activities and food patches within the environment. The forager's goal is to find its optimal GUD and vigilance level for each food patch. On pp. 13 and 15, I consider environment-wide changes in predation risk. There, GUDs do increase with increasing environment-wide predation risk because patch quality and survivor's fitness are allowed to increase concomitantly with risk. The same would happen in Newman's model.

My model represents an extension of static models of patch use under predation (Gilliam and Fraser, 1987; Brown, 1988, 1992). I selected the approach in preference to a dynamic programming model because: (1) at stationarity (when a time-dependent strategy is independent of the actual point of time), many dynamic programming models can be translated into a static optimization analogue and vice versa; (2) most of the useful and testable predictions will be in terms of the static consequences (e.g. average rates of vigilance, quitting harvest rates, GUDs and average amounts of food harvested) of behavioural sequences, not in terms of the actual sequences themselves; and (3) the dynamic programming analogue of the present model would probably be sufficiently cumbersome to obscure general predictions and their rationale. However, time-dependent variables would reveal an

additional tier of predictions pertaining to the time course of vigilance within a patch (which might vary with patch quality in interesting ways) and the distributions of vigilance behaviours and GUDs among patches of the same quality.

Thoughts on how to apply and test the theory

A forager's use of depletable food patches provides a means of experimentally measuring the joint contributions of vigilance behaviour and time allocation to the forager's management of food and safety. This can be done by combining Fraser and Gilliam's (1987) tenacity index to the concept of GUDs (Brown, 1988). Differences in GUDs between risky and safe habitats should result from differences in quitting harvest rates and differences in harvest rate curves (harvest rate as a function of food abundance). The difference in quitting harvest rate measures the residual habitat-specific differences in predation risk that have been managed through time allocation (Fig. 2). The differences in harvest rate curves measure the tenacity index and this difference measures the contribution of vigilance to the forager's management of habitat-specific differences in predation risk.

Four types of measurements can be used to apply and test the theory: (1) the animal's GUDs in food patches under different conditions that influence the cost of predation (e.g. risky and safe microhabitats; Brown, 1988, 1989); (2) the animal's cumulative harvest rate curve in the patches under each condition (Kotler and Brown, 1990; Brown *et al.*, 1994); (3) the amount of vigilance employed by the animal under the different conditions; and (4) the time spent by the animal in the food patches. The condition-dependent harvest rate curves can be used to convert the GUDs into quitting harvest rates. In this way, information is available on GUDs, quitting harvest rates, amount of vigilance and time allocation.

Consider fox squirrels (*Sciurus niger*) or grey squirrels (*Sciurus carolinensis*) feeding near versus away from large trees in a savanna or open woodland. As expected, these squirrels have lower GUDs near than away from trees (Brown *et al.*, 1992; Bowers *et al.*, 1993; Brown and Morgan, 1995). This difference may be due to a greater effectiveness of vigilance near than away from trees. Having spotted a predator, the squirrel's chance of escaping increases with proximity to a tree (Dill and Houtman, 1989). If so, then squirrels should have higher vigilance, a slower rate of food harvest, and spend much more time in food patches near than away from trees. We have found that fox squirrels are more vigilant near than away from trees (J. Brown and W. Bachman, unpublished), and Newman *et al.* (1988) found that grey squirrels feed slower from the same quality food patch near than away from trees.

In the Negev Desert, Israel, Indian crested porcupines (*Hystrix indica*) were shown to have higher GUDs in habitats lacking vegetation cover and on moonlit nights (Brown and Alkon, 1990). Moonlight may greatly increase the porcupine's encounter rate with threatening predators (possibly humans and leopards). If so, then porcupines should have higher vigilance and lower harvest rate curves on moonlit than dark nights. Levacov (1996) found that porcupines, in an enclosure feeding from controlled food patches, had lower harvest rate curves (= higher vigilance) and higher quitting harvest rates (= greater residual risk of predation) on bright than on dark nights. At a site in Arizona, kangaroo rats (*Dipodomys merriami*) revealed a higher cost of predation in the bush than open microhabitat during the summer and the reverse during the winter (Brown, 1989). This may represent a seasonal shift in the threat of owls (*Tyto alba*) and rattlesnakes (*Crotalus atrox* and *C. scutulatus*), where the encounter rate with owls and snakes is higher in the open and bush microhabitats, respectively (Brown *et al.*, 1988; Brown, 1989; Bouskila, 1995). While not measured,

microhabitat-specific levels of vigilance should change accordingly with the seasonal changes in snakes and owls.

Cassini (1991) measured both vigilance and time allocation in guinea pigs feeding near (safe) and far (risky) from cover. Guinea pigs foraged longer away from cover than near cover, and they had higher rates of vigilance to compensate for these longer forays into the risky habitat. Illius and Fitzgibbon (1994) predicted that smaller ungulates (gazelle, wildebeest and buffalo) should be more vigilant than larger ungulates because they have more spare time at any given level of forage quality. Alternatively, smaller ungulates may be more vigilant as a result of a higher encounter rate with predators (gazelle have more predators than buffalo), and a higher predator lethality in the absence of vigilance (buffalo have a high likelihood of escape even when ambushed by lions; Schaller, 1972).

In response to risk from house cats (*Felis cattus*), Lendrem (1983) found that tits (*Parus caeruleus*) accepted reduced feeding levels (lower giving-up densities) and were less vigilant as feeding height above the ground increased. This may result from the reinforcing effects of lower encounter rate with cats and reduced lethality of cats as height increases. Cresswell (1994) found that large flocks of redshanks experienced less predation risk as a result of a combined dilution effect (lower individual encounter rate with predators) and confusion effect (reduced predator lethality). Accordingly, redshanks were less vigilant in large flocks and foraged at lower prey abundances (= lower GUDs?). In addition, redshanks were less vigilant during cold snaps (higher marginal value of energy?) and more vigilant in or near cover (higher predator lethality?).

Vigilance, time allocation and energy state compression among foragers

Individuals within a population may vary in their energy state, either by chance or as a result of dominance hierarchies. The optimal use of vigilance and time allocation should compress the variability among individuals in their energy states (Lima, 1988b). Individuals with above-average energy states should be more vigilant and shift their foraging time from risky to safe microhabitats. Both of these actions will tend to enhance survivorship but result in a lower net gain of energy than the average individual. The energy state of these individuals should converge towards the mean. Individuals with below-average energy states should be less vigilant and shift activity from safe to risky habitats. While sacrificing survivorship, these behaviours will yield a higher rate of energy gain than the average individual. In this way, trade-offs in food and safety among habitats, and the option to use vigilance to trade-off food and safety within habitats, serve to compress individuals within a population around the mean energy state.

Community-level consequences of vigilance and time allocation

The contribution of vigilance behaviour and residual predation risk to the forager's cost of predation has important implications for the predator. That portion of the cost of predation resulting from vigilance represents foregone energy that does not contribute to feeding predators. In the extreme, consider a forager that eliminates predation risk through its vigilance behaviour. Such a forager incurs a potentially large cost of predation yet provides no sustenance for the predators. On the other hand, the portion of the cost of predation resulting from residual predation risk does feed predators. The forager's higher quitting harvest rate provides the increase in growth and reproduction needed to compensate for

predator-induced mortality. The mortality component of the forager's cost of predation represents energy being passed directly up the trophic chain to the predators (Brown *et al.*, 1994).

The relative use of vigilance versus time allocation to manage food and safety may influence the number of trophic levels in a food chain. Animals that manage the cost of predation via vigilance (foregoing food to reduce the actual risk of predation) may promote shorter food chains; these animals forego feeding themselves and their predators. Animals that use little vigilance and manage risk via time allocation (demanding a higher feeding rate to compensate for a higher risk of predation) may promote longer food chains; these animals enhance feeding themselves and their predators. In this way, the effectiveness of vigilance in reducing predation risk influences the animal's use of vigilance, which may in turn have consequences for the abundance of predators and the numbers of trophic levels.

Within a food-web, via apparent competition, other prey species may sustain a larger population size of predators than otherwise could exist (Holt, 1977; Holt and Lawton, 1994). This increases a prey's encounter rate with predators and obliges it to be more vigilant, increase its GUD and forego otherwise profitable feeding opportunities. A large fraction of the fear response of Negev porcupines (Brown and Alkon, 1990) and Illinois fox squirrels (Brown *et al.*, 1992; Brown and Morgan, 1995) probably represents this kind of behavioural apparent competition, in which other prey support the wolves, hyenas, jackals and leopards that frighten porcupines, and the great-horned owls, red-tailed hawks, coyotes and red foxes that frighten fox squirrels. Via shared predators, different prey species influence each others' vigilance, GUDs and patch use.

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REFERENCES

- Abrams, P.A. 1991. Life history and the relationship between food availability and foraging effort. *Ecology*, **72**: 1242–1252.
- Bertram, B.C.R. 1978. Living in groups: Predators and prey. In *Behavioural Ecology* (J.R. Krebs and N.B. Davies, eds), pp. 64–96. Oxford: Oxford University Press.
- Bouskila, A. 1995. Interactions between predation risk and competition: A field study of kangaroo rats and snakes. *Ecology*, **76**: 165–178.
- Bowers, M.A., Jefferson, J.L. and Kuebler, M.G. 1993. Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). *Oikos*, **66**: 229–236.
- Brown, J.S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.*, **22**: 37–47.
- Brown, J.S. 1989. Desert rodent community structure: A test of four mechanisms of coexistence. *Ecol. Monogr.*, **59**: 1–20.
- Brown, J.S. 1992. Patch use under predation risk: I. Models and predictions. *Ann Zool. Fenn.*, **29**: 301–309.

- Brown, J.S. and Alkon, P.U. 1990. Testing values of crested porcupine habitats by experimental food patches. *Oecologia*, **83**: 512–518.
- Brown, J.S. and Morgan, R.A. 1995. Effects of foraging behaviour and spatial scale on diet selectivity: A test with fox squirrels. *Oikos*, **74**: 122–136.
- Brown, J.S., Kotler, B.P., Smith, R.J. and Wirtz, W.O., II. 1988. The effects of owl predation on the foraging behaviour of heteromysid rodents. *Oecologia*, **76**: 508–515.
- Brown, J.S., Morgan, R.A. and Dow, B.D. 1992. Patch use under predation risk: II. A test with fox squirrels, *Sciurus niger*. *Ann. Zool. Fenn.*, **29**: 311–318.
- Brown, J.S., Kotler, B.P. and Valone, T.J. 1994. Foraging under predation: A comparison of energetic and predation costs in a Negev and Sonoran Desert rodent community. *Austr. J. Zool.*, **42**: 435–448.
- Cassini, M.H. 1991. Foraging under predation risk in the wild guinea pig, *Cavia aperea*. *Oikos*, **62**: 20–24.
- Chiang, A.C. 1974. *Fundamental Methods of Mathematical Economics*, 2nd edn. New York: McGraw Hill.
- Cresswell, W. 1994. Flocking is an effective anti-predator strategy in redshanks, *Tringa totanus*. *Anim. Behav.*, **47**: 433–442.
- Dehn, M.M. 1990. Vigilance for predators: Detection and dilution effects. *Behav. Ecol. Sociobiol.*, **26**: 337–342.
- Dill, L.M. and Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav. Ecol. Sociobiol.*, **16**: 65–71.
- Dill, L.M. and Houtman, R. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool.*, **67**: 233–235.
- Fraser, D.F. and Gilliam, J.F. 1987. Feeding under predation hazard: Responses of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behav. Ecol. Sociobiol.*, **21**: 203–209.
- Gilliam, J.F. and Fraser, D.F. 1987. Habitat selection under predation hazard: A test of a model with foraging minnows. *Ecology*, **68**: 1856–1862.
- Gilliam, J.F. and Fraser, D.F. 1988. Resource depletion and habitat segregation by competitors under predation hazard. In *Size-structured Populations: Ecology and Evolution* (B. Ebenman and L. Persson, eds), pp. 173–184. New York: Springer-Verlag.
- Hassell, M.P. 1978. *The Dynamics of Arthropod Predation*. Princeton, NJ: Princeton University Press.
- Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.*, **45**: 1–60.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.*, **12**: 197–229.
- Holt, R.D. and Lawton, J. 1994. The ecological consequences of shared predators. *Ann. Rev. Ecol. Syst.*, **25**: 495–520.
- Hoogland, J.L. 1979. The effect of colony size on individual alertness of prairie dogs (Sciuridae: *Cynomys* spp.). *Anim. Behav.*, **27**: 394–407.
- Houston, A.I., McNamara, J.M. and Hutchinson, J.M.C. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Phil. Trans. R. Soc. Lond. B*, **341**: 375–397.
- Illiis, A.W. and Fitzgibbon, C. 1994. Costs of vigilance in foraging ungulates. *Anim. Behav.*, **47**: 481–484.
- Kotler, B.P. 1992. Behavioral resource depression and decaying perceived predation in two species of coexisting gerbils. *Behav. Ecol. Sociobiol.*, **30**: 239–244.
- Kotler, B.P. and Brown, J.S. 1990. Harvest rates of two species of gerbilline rodents. *J. Mammal.*, **71**: 591–596.
- Kotler, B.P., Brown, J.S. and Hasson, O. 1991. Owl predation on gerbils: The role of body size, illumination, and habitat structure on rates of predation. *Ecology*, **71**: 2249–2260.

- Kotler, B.P., Blaustein, L. and Brown, J.S. 1992. Predator facilitation: The combined effects of snakes and owls on the foraging behaviour of gerbils. *Ann. Zool. Fenn.*, **29**: 199–206.
- Kotler, B.P., Brown, J.S., Slotow, R.H., Goodfriend, W.L. and Strauss, M. 1993. The influence of snakes on the foraging behavior of gerbils. *Oikos*, **67**: 309–316.
- Lendrem, D.W. 1983. Predation risk and vigilance in blue tits (*Parus caeruleus*). *Behav. Ecol. Sociobiol.*, **14**: 9–13.
- Levacov, D. 1996. Predation risk and the foraging behavior of the Indian crested porcupine (*Hystrix indica*). Unpublished MSc thesis, Ben-Gurion University, Beer Sheva, Israel (in Hebrew).
- Lima, S.L. 1988a. Vigilance and diet selection: The classical diet model reconsidered. *J. Theor. Biol.*, **132**: 127–143.
- Lima, S.L. 1988b. Initiation and termination of daily feeding in dark-eyed juncos: Influences of predation risk and energy reserves. *Oikos*, **53**: 12–26.
- Lima, S.L. 1990. The influence of models on the interpretation of vigilance. In *Interpretation and Explanation in the Study of Animal Behavior*, Vol. II (M. Bekoff and D. Jamieson, eds), pp. 246–267. Boulder, CO: Westview Press.
- Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.*, **68**: 619–640.
- Lima, S.L., Valone, T.J. and Caraco, T. 1985. Foraging-efficiency–predation-risk trade-off in the grey squirrel. *Anim. Behav.*, **33**: 155–165.
- McNamara, J.M. and Houston, A.I. 1992. Evolutionarily stable levels of vigilance as a function of group size. *Anim. Behav.*, **43**: 641–658.
- Moody, A.L., Houston, A.I. and McNamara, J.M. 1996. Ideal free distributions under predation risk. *Behav. Ecol. Sociobiol.*, **38**: 131–143.
- Newman, J.A. 1991. Patch use under predation hazard: Foraging behavior in a simple stochastic environment. *Oikos*, **61**: 29–44.
- Newman, J.A., Recer, G.M., Zwicker, S.M. and Caraco, T. 1988. Effects of predation hazard on foraging ‘constraints’: Patch use strategies in grey squirrels. *Oikos*, **53**: 93–97.
- Nonacs, P. and Dill, L.M. 1990. Mortality risk versus food quality trade-offs in a common currency: Ant patch preferences. *Ecology*, **71**: 1886–1892.
- Powell, G.V.N. 1974. Experimental analysis of the social value of flocking in starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.*, **22**: 501–505.
- Pulliam, H.R., Pyke, G.H. and Caraco, T. 1982. The scanning behaviour of juncos: A game theoretical approach. *J. Theor. Biol.*, **95**: 89–103.
- Schaller, G.B. 1972. *The Serengeti Lion: A Study of Predator–Prey Relations*. Chicago, IL: University of Chicago Press.
- Sullivan, K.A. 1984. Information exploitation by downy woodpeckers in mixed species flocks. *Behaviour*, **91**: 294–311.

APPENDIX

Below are the effects of changing the encounter rates with predators, m , decreasing predator lethality, k , effectiveness of vigilance, b , the forager's survivor's fitness, F , and the marginal value of energy $\partial F/\partial e$ on the forager's GUD, f , vigilance level, u , and quitting harvest rate, $(1 - u)f$. The analyses apply to situations where $u^* \in (0, 1)$.

To determine effects on the GUD, f , Equation (19) is most useful:

$$f\left(1 + \frac{k}{b}\right) - (c - c_o) - 2\sqrt{\frac{mfF}{b(\partial F/\partial e)}} = 0$$

The effect of a term, say m , can be found by implicitly differentiating Equation (19) with respect to m where f is considered to be a function of m . The derivative, $\partial f/\partial m$, can then be found by rearranging the result.

To determine effects on vigilance, u , the following form of Equation (15) is most useful:

$$(c - c_o) = (1 - u^*)f - \sqrt{\frac{mfF}{b(\partial F/\partial e)}} \quad (21)$$

The effect of m can be found by differentiating Equation (13) with respect to m where f is considered to be a function of m . Next substitute $\partial f/\partial m$ into the result and then factor until one term equals the right-hand side of (21). At this point $(c - c_o)$ can be substituted for the factor.

To determine effects on the quitting harvest rate, $(1 - u)f$, the following form of Equation (21) is most useful:

$$(1 - u^*)f = (c - c_o) + \sqrt{\frac{mfF}{b(\partial F/\partial e)}} \quad (22)$$

The effect of m can be found by implicitly differentiating the right-hand side of (22) with respect to m where f is considered to be a function of m . The effect of m on f , $\partial f/\partial m$, can then be substituted into the result. I followed the above procedures to determine the effects of m , k , b , F and $\partial F/\partial e$, respectively.

Effects of the encounter rate with predators, m :

$$\begin{aligned} \frac{\partial f}{\partial m} &= \left(\frac{1}{1 - u^*} \right) \sqrt{\frac{fF}{mb(\partial F/\partial e)}} > 0 \\ \frac{\partial u^*}{\partial m} &= \left(\frac{c - c_o}{2f(1 - u^*)} \right) \sqrt{\frac{F}{mfb(\partial F/\partial e)}} > 0 \\ \frac{\partial(1 - u^*)f}{\partial m} &= \sqrt{\frac{fF}{4mb(\partial F/\partial e)}} + \frac{F}{2b(1 - u^*)(\partial F/\partial e)} > 0 \end{aligned}$$

Effects of decreasing predator lethality, k :

$$\begin{aligned} \frac{\partial f}{\partial k} &= \frac{-f}{b(1 - u^*)} < 0 \\ \frac{\partial u^*}{\partial k} &= \frac{-(c - c_o)}{bf(1 - u^*)} - (1 - u^*)f < 0 \\ \frac{\partial(1 - u^*)f}{\partial k} &= \left(\frac{1}{2b(1 - u^*)} \right) \sqrt{\frac{mF}{b(\partial F/\partial e)}} < 0 \end{aligned}$$

Effects of the effectiveness of vigilance, b :

$$\frac{\partial f}{\partial b} = \frac{-fu^*}{b(1 - u^*)} < 0$$

$$\frac{\partial u^*}{\partial b} = \frac{k - 2bu^*(1 - 2u^*)}{2b^2(1 - u^*)}$$

$$\frac{\partial(1 - u^*)f}{\partial b} = \left(\frac{-u^*}{2b(1 - u^*)} \right) \sqrt{\frac{mf}{b(\partial F/\partial e)}} - \left(\frac{1}{2b} \right) \sqrt{\frac{mfF}{b(\partial F/\partial e)}} < 0$$

The effect of b on u^* is humped-shaped; $\partial u^*/\partial b$ is positive for lower values of b and negative for higher values of b . The decline in GUD with b encourages a positive relationship between b and u^* and shifts the peak of the relationship to higher values of b .

Effects of the forager's survivor's fitness, F :

$$\frac{\partial f}{\partial F} = \left(\frac{1}{1 - u^*} \right) \sqrt{\frac{mf}{bF(\partial F/\partial e)}} > 0$$

$$\frac{\partial u^*}{\partial F} = \left(\frac{c - c_o}{2f(1 - u^*)} \right) \sqrt{\frac{m}{bfF(\partial F/\partial e)}} > 0$$

$$\frac{\partial(1 - u^*)f}{\partial F} = \sqrt{\frac{mf}{4bF(\partial F/\partial e)}} + \frac{m}{2b(1 - u^*)(\partial F/\partial e)} > 0$$

Effects of the marginal value of energy, $\partial F/\partial e$:

$$\frac{\partial f}{\partial(\partial F/\partial e)} = \left(\frac{-1}{(\partial F/\partial e)(1 - u^*)} \right) \sqrt{\frac{mfF}{b(\partial F/\partial e)}} < 0$$

$$\frac{\partial u^*}{\partial(\partial F/\partial e)} = \left(\frac{-(c - c_o)}{2f(1 - u^*)} \right) \sqrt{\frac{mF}{bf(\partial F/\partial e)}} < 0$$

$$\frac{\partial(1 - u^*)f}{\partial(\partial F/\partial e)} = \left(\frac{-1}{2(\partial F/\partial e)} \right) \sqrt{\frac{mfF}{b(\partial F/\partial e)}} - \frac{mF}{2b(1 - u^*)(\partial F/\partial e)^2} < 0$$

