REVIEW

Hazardous duty pay and the foraging cost of predation

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Abstract

We review the concepts and research associated with measuring fear and its consequences for foraging. When foraging, animals should and do demand hazardous duty pay. They assess a foraging cost of predation to compensate for the risk of predation or the risk of catastrophic injury. Similarly, in weighing foraging options, animals tradeoff food and safety. The foraging cost of predation can be modelled, and it can be quantitatively and qualitatively measured using risk titrations. Giving-up densities (GUDs) in depletable food patches and the distribution of foragers across safe and risky feeding opportunities are two frequent experimental tools for titrating food and safety. A growing body of literature shows that: (i) the cost of predation can be big and comprise the forager's largest foraging cost, (ii) seemingly small changes in habitat or microhabitat characteristics can lead to large changes in the cost of predation, and (iii) a forager's cost of predation rises with risk of mortality, the forager's energy state and a decrease in its marginal value of energy. In titrating for the cost of predation, researchers have investigated spatial and temporal variation in risk, scale-dependent variation in risk, and the role of predation risk in a forager's ecology. A risk titration from a feeding animal often provides a more accurate behavioural indicator of predation risk than direct observations of predator-inflicted mortality. Titrating for fear responses in foragers has some well-established applications and holds promise for novel methodologies, concepts and applications. Future directions for expanding conceptual and empirical tools include: what are the consequences of foraging costs arising from interference behaviours and other sources of catastrophic loss? Are there alternative routes by which organisms can respond to tradeoffs of food and safety? What does an animal's landscape of fear look like as a spatially explicit map, and how do various environmental factors affect it? Behavioural titrations will help to illuminate these issues and more.

Keywords

Cost of predation, fear, giving-up densities, habitat selection, isodars, optimal foraging, predation, predation risk, risk titrations.

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INTRODUCTION

The incentive behind 'hazardous duty' or 'combat' pay is straightforward: the person risks injury or perhaps death in exchange for additional benefits. Similarly, the phrase, 'Is it worth the risk?' captures the idea of balancing rewards (monetary, goods, or utility) with the consequence of a catastrophe. One starts with seemingly irreconcilable currencies. How does one put a monetary price on being alive, or balance a sense of well-being and satisfaction with a crippling injury? Yet, we humans answer the question of

whether it is worth the risk every time we get behind the wheel of a car, climb a ladder, look over a cliff, or get out of bed. Somehow we balance diverse costs and benefits. We place a price on risk taking.

Alfred Lord Tennyson in 1850 penned 'nature, red in tooth and claw'; a phrase replete with, among other things, predation imagery. While seeking food, the forager itself risks becoming food. In response to predation risk, animals balance food and safety (McNamara & Houston 1987; see Lima & Dill 1990). Instead of foraging in a manner that maximizes energy gain or resource acquisition, a forager may

accept a lower rate of gain if it also means greater safety from predators. Alternatively, to get a forager to accept greater risks requires offering greater benefits. Most of the time and in most places, feeding animals experience a positive relationship between feeding opportunities and predation risk. This relationship is likely sculpted by the foragers themselves. In safe circumstances, resources and foraging opportunities become more thoroughly depleted and vice versa under risky circumstances (Hugie & Dill 1994; Brown 1998). Like hazardous duty pay, the forager places an energetic or resource valuation on death or risk of injury. A cost must be assessed on the risk of catastrophe.

The fact that animals exchange food and safety is well documented. Animals do treat predation risk as a cost of foraging. Younger backswimmers (*Notonecta* sp.) shift feeding to safer and less rewarding places in the face of older and cannibalistic backswimmers (Sih 1980). The re-introduction of wolves into Yellowstone was manifested in greater elk (*Cervus elaphe*) vigilance and lower feeding rates (Laundre *et al.* 2001). Hungry juncos (*Junco hyemalis*) increased feeding rates relative to less hungry birds by opting for the riskier open habitat (Lima 1988). Researchers have suggested (McNamara & Houston 1990, 1994; Clark & Eckman 1995; but see Brodin 2001) how fat levels in wintering birds such as tits (*Parus* sp.) may balance the risk of starvation (the fatter the better) with the risk of predation (leaner is better for agility and escape). Foragers will accept higher risks when returns are higher. To do this, foragers must assess risk in terms of energy or other resources. Yet, measuring the foraging cost of predation experimentally is a challenge.

Foraging theory shows how animals should use the marginal rate of substitution (MRS) of energy for safety to place an exchange rate on varied inputs into fitness. The per capita growth rate or fitness associated with a feeding strategy is the ultimate hard currency of natural selection acting on anti-predator behaviours. The ratio of the fitness consequences of being killed by a predator with the fitness consequences of energy gain provides the MRS of energy for safety (Brown 1988, 1992). Empirically, choice experiments provide the means for getting animals to reveal the foraging cost of predation and their MRS of energy for safety. The cost of predation is usually measured quantitatively or qualitatively with a behavioural titration experiment. Either energy reward or predation risk is continuously varied until the animal reveals a point of indifference between a low-reward/low-risk option and a high-reward/high-risk option (Kotler & Blaustein 1995).

Here we provide a synthesis of the concepts and methodologies for getting animals to reveal their foraging cost of predation through titrations of food and safety. We begin by briefly reviewing the models from foraging theory that consider predation risk. These models define the cost of

predation as a mathematical equation for fear, identify the MRS of food for safety, and make predictions for the quantitative and qualitative nature of predation risk as a foraging cost. We then discuss the measurable foraging strategies available to an animal for titrating food and safety – these include the use of time allocation, tenacity, apprehension and vigilance. Our main focus will be on the application of these concepts and the methodologies for revealing costs of predation through behavioural titrations. The literature offers a delightful spectrum of taxa, approaches and insights regarding the foraging cost of predation. We conclude with the broader context of applying the cost of predation to any situation involving the risk of catastrophic injury or death. We also provide a prospectus of future directions and techniques.

FORAGING COST OF PREDATION

Consider an animal foraging under predation risk. Let predation risk, μ (units of per time), be the forager's instantaneous rate of being preyed upon while engaged in some risky activity. Let the reward from foraging, f (items, joules, or moles per unit time), be the instantaneous or expected harvest rate of resources while foraging under predation risk. Let a forager have a number of alternative foraging choices that vary in risk, μ, and reward, f. These choices may represent different habitats. Or, the forager may balance risk and reward by varying its level of vigilance. How should the forager rank the fitness value of these choices (Brown 1992)?

Gilliam & Fraser (1987) derived a rule whereby fitness is maximized when the forager chooses the habitat or foraging tactic that minimizes μ/f. This rule is quite robust and applies across a variety of fitness functions and ecological scenarios. In particular, it applies to situations where the forager has among its activities the option of remaining safely dormant within its burrow or nest. Furthermore, appropriate adjustments can be made to the reward for energetic costs of foraging, c, and the cost of dormancy, c_0. In this case, the rule becomes 'select the foraging option that minimizes $\mu/(f + c_0 - c)$'. This is an effective rule for ranking choices, but as a ratio, it does not reveal the foraging cost of predation. We do not yet have a titration of food and safety.

The use of depletable food patches provides such a titration. Here, patch harvest rate, f, declines with resource harvest. How thoroughly should the forager use such a food patch? The answer to this question includes the cost of predation if there is risk associated with patch use. The cost of predation depends on how risk and resources combine to determine fitness. Let $F(e)$ be the survivor's fitness. It gives fitness in the absence of predation (expressed as a finite growth rate). Assume that F increases with net energy gain, e. Let p be the probability of surviving predation over

the finite time interval. This probability is influenced by the cumulative exposure of the individual to risky situations. As more time is allocated to risky situations, p declines; as more time is allocated to safer situations, p increases.

Consider four fitness formulations. Each of these formulations shares a time constraint such that the time devoted to all activities must sum to the total time available:

(1) Max p subject to $F \geq k$
(2) Max F subject to $p > k$
(3) Max $F + p$
(4) Max $p \cdot F$

The first considers an organism attempting to maximize the probability of surviving over some time interval with the requirement of maintaining a certain energy state. This model can be appropriate for animals surviving through a juvenile or larval stage to adulthood, or to animals that must survive through a non-breeding season. The second model considers an organism that attempts to maximize its state while maintaining a threshold level of survivorship. Given that survivorship is a component of fitness rather than a constraint, this model seem less applicable. This safety constraint can provide an approximation for fitness maximization when the modeller wants the objective function to merely be net energy gain. The third model fits the classic predator–prey models closely where fitness is the difference between per capita growth rate in the absence of predation and the per-prey predation rate. This model applies to situations where there is: (i) a rapid conversion of energy gain into offspring, (ii) communal raising of young, or (iii) full compensation by the surviving mate so that the death of a parent or helper does not jeopardize the current state and investment in offspring. The fourth model is probably most applicable to food-safety tradeoffs where an organism's fitness is its survivor's fitness (or net reproductive value in dynamic programming models; see Houston *et al.* 1993) multiplied by the probability of achieving this fitness. In this case, a forager must survive over some finite time period before realizing its fitness potential.

Brown (1992) derived the optimal patch use strategy for each of these fitness formulations. In all cases, a food patch should be left when the benefits of the reward rate, H, no longer exceeds the sum of metabolic, C, predation, P, and missed opportunity, MOC, costs of foraging: $H = C + P + \text{MOC}$. In this formulation, H and f are the same, and C and c are the same. They have units of energy per unit time, items per unit time or units of resource per unit time. The missed opportunity cost of foraging, MOC, places a value on alternative fitness enhancing activities. These are the activities that an animal forgoes by spending time in the current food patch (see Brown 1999 for how this cost can be calculated for different scenarios). Finally, there is the cost of predation, P, which we consider in detail below.

In the following equations (one for each fitness formulation), the term on the left hand side is H, and terms on the right hand side are C, $\boldsymbol{P}$, and MOC, respectively:

$$\text{Model 1}: f = c + \frac{\boldsymbol{\mu p}}{\boldsymbol{\Phi_F(\partial F/\partial e)}} + \frac{\Phi_t}{\Phi_F(\partial F/\partial e)}$$

$$\text{Model 2}: f = c + \frac{\boldsymbol{\mu p \Phi_P}}{\boldsymbol{\partial F/\partial e}} + \frac{\Phi_t}{\partial F/\partial e}$$

$$\text{Model 3}: f = c + \frac{\boldsymbol{\mu p}}{\boldsymbol{\partial F/\partial e}} + \frac{\Phi_t}{\partial F/\partial e}$$

$$\text{Model 4}: f = c + \frac{\boldsymbol{\mu F}}{\boldsymbol{\partial F/\partial e}} + \frac{\Phi_t}{p(\partial F/\partial e)}$$

In all of these models, $\partial F/\partial e$ is the marginal value of energy and Φ_t is the marginal fitness value of time if the time constraint were relaxed by providing more time. In model 1, Φ_F is the marginal survivorship value of favourably adjusting the energetic-state constraint. In model 2, Φ_P is the marginal value of relaxing the survivorship constraint.

In all these models, the cost of predation (shown in bold in each of the above equations) has units of energy per unit time or resources per unit time. The currency of risk, μ, is converted into the currency of f by multiplying the predation risk by the MRS of energy for safety. The MRS depends upon the fitness formulation. For instance, in model 4, this MRS is the ratio of survivor's fitness to the marginal value of energy. Hence in model 4, the energetic cost of predation is the predation risk multiplied by survivor's fitness divided by the marginal fitness value of energy: $\boldsymbol{\mu F/(\partial F/\partial e)}$. Houston *et al.* (1993) derive the same cost of predation for dynamic programming models.

In terms of titrating food and safety, the patch use models predict that:

(1) a forager will demand a higher feeding rate from risky than safe patches (hazardous duty pay should equal P),
(2) a forager will demand a higher feeding rate as the marginal value of food declines, and
(3) as the value of food declines, a forager will demand an even higher feeding rate premium to forage in risky patches.

The above represent the conceptual tools for measuring the foraging cost of predation. In the next section, we consider the foraging tactics available to animals for effecting this titration of food and safety.

TACTICS AND TOOLS FOR BALANCING FOOD AND SAFETY

Foragers have a variety of complementary behaviours for balancing food and safety. These include time allocation, tenacity and the use of apprehension or vigilance.

Time allocation

By time allocation, we refer to where a forager spends time, when it spends that time, and for how long it remains at each location. Such decisions affect the types and amounts of resources encountered – and therefore harvest rate – and the types and amounts of predators encountered – and therefore risk of predation. An animal can adjust both exposure to risk and the amount of resources harvested by selecting habitats and microhabitats, the season or time of day for foraging and the duration of time spent foraging from a patch. A forager exploits opportunities by allocating more time towards resource-rich times and places. A forager avoids hazards by shifting time from risky to safe times and places.

There must be spatial and temporal variability in resources and predation risk for time allocation to be meaningful. For kangaroo rats (*Dipodomys* sp.) and pocket mice (genus *Perognathus* and *Chaetodipus*) in the Sonoran Desert, seed densities in the soil may vary a dozen-fold over the space of a few metres (Price & Reichman 1987). Similarly, different types of resources that vary in energetic content, nutritional content, handling time and encounter probabilities may be available in different places and at different times. With regards to predators, the types and densities of predators may vary among habitats (Svanback & Eklov 2003), across seasons (Brown 1989) and at different times of the day (e.g. Kotler *et al.* 2002). In aquatic habitats, encounter rates of juvenile perch (*Perca fluviatilis*) with large predators and cannibalistic conspecifics in littoral habitats are far lower than in pelagic habitats (Bystrom *et al.* 2003; Persson & De Roos 2003). At a Sonoral Desert site, the types and numbers of snakes, hawks and owls vary seasonally with the predators' distinctive migratory, breeding and dormancy habits (Brown 1989). Just as importantly, the encounter rate of predators with their prey and the lethality of the predator can vary with habitat and microhabitat structure (e.g. redshanks, *Tringa totanus*, feeding near and away from cover, Cresswell 1994). Structural elements such as shrubs or cliff faces can conceal prey from predators (Rosenzweig 1973) and can hinder the ability of a predator to successfully attack prey (Kotler *et al.* 1988, 1991; Longland & Price 1991). In the following section, we examine how such spatial and temporal variability in resource abundances and predation risk permit several kinds of behavioural titrations involving time allocation.

Giving-up densities

When the scale of variability in food and safety is small and/or when food patches become depleted, one can use quitting harvest rates or giving-up densities (GUD) to titrate for food and safety. Todd & Cowie (1990) set automatic feeders within two microhabitats that differed in risk for foraging tits (*Parus caeruleus*). The birds, as expected, preferred to feed in the safer, close-to-cover microhabitat when all feeders offered the same reward rate. By increasing the reward rate within the risky, far-from-cover microhabitat, the researchers were able to determine the tit's point of indifference where the higher harvest rate offered by the feeder in the more dangerous microhabitat offset its higher risk. Based on model (4) above, this point of indifference should occur when:

$$f_r - f_s = \frac{F(\mu_r - \mu_s)}{\partial F / \partial e}$$

where f is feeding rate and the subscripts 's' and 'r' refer to safe and risky microhabitats respectively. Thus, differences in quitting harvest rates between safe and risky situations will be affected by the difference in risk, by the energetic state of the forager and by its survivor's fitness.

Rather than setting harvest rates experimentally, the researcher can let the forager deplete a food patch and determine its quitting harvest rate from when it exits the patch. As measuring an animal's quitting harvest rate can be tricky, it is more common to measure GUDs as a surrogate for quitting harvest rate. The GUD is the amount of food remaining in a depletable food patch after a forager has ceased harvesting the patch (Brown 1988). The approach relies on a monotonic relationship between the food remaining within the patch and the forager's expected harvest rate. As remaining food abundance declines, so too does the forager's harvest rate. Eventually, the forager should reach the point where f no longer exceeds foraging costs, and it should quit the patch and seek another or seek some other fitness-enhancing activity (Fig. 1).

When food patches do not vary in C or MOC then:

(1) GUDs should be higher in the risky than safe habitat or scenario,
(2) GUDs should be higher for the forager with the higher energy state or survivor's fitness, F (Brown 1992; Clark 1994),
(3) GUDs should be lower for the forager with the higher marginal value of energy, $\partial F / \partial e$.

When measuring the cost of predation using GUDs, the gain curve (cumulative harvest vs. time spent harvesting the patch) should exhibit diminishing returns (Brown 1988; Price & Correll 2001) so that the slope of the gain curve (the forager's expected instantaneous harvest rate) declines with time spent in the patch (Fig. 1). Olsson *et al.* (2001) developed a protocol for testing for diminishing returns
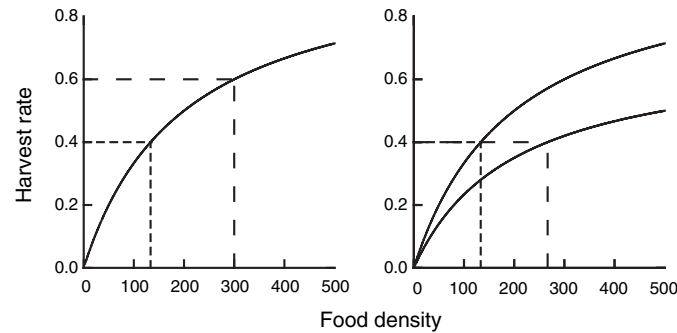
Figure 1 Patch use in depletable food patches can be used to titrate the cost of predation when there are diminishing returns to exploiting a patch. The graphs show how the forager's expected instantaneous harvest rate increases with the remaining abundance of resources in the patch. The first panel shows how the forager's GUD increases with the risk of predation. The increased risk of predation increases the forager's cost of predation. Hence, it requires a higher quitting harvest rate from the patch (horizontal dashed line) than a patch with a lower cost of predation (vertical dotted line). To achieve the higher quitting harvest rate in the risky patch the forager must leave the patch at a higher GUD (vertical dashed line) than the safer patch (vertical dotted line). The second graph relates to using vigilance to manage higher predation risk. The graph assumes that the forager uses vigilance in the safer patch to achieve the same level of safety as in the safe patch. But, this higher level of vigilance means that harvest rate curve in the risky patch is lower than that in the safe patch. As risk in the safe and risky patches are now equal, the cost of predation in each is now equal. But, this still results in a higher GUD in the risky patch (intersection of dashed line with lower harvest rate curve) than in the safe patch (intersection of dotted line with higher harvest rate line).

and the shape of the gain curve. The protocol uses measures of initial prey density, current prey density and time spent searching by the forager for prey within patches. For starlings (*Sturnus vulgaris*) probing for mealworms in an experimental food patch with moist sand, they found that starlings exhibited diminishing returns and that these diminishing returns came both from patch depletion and from 'negative stirring' in which the search technique of the starlings actually made it more difficult to find the remaining mealworms.

The GUDs in risky situations are higher than those under safe conditions. In aviary experiments with direct (owls) and indirect (lights) cues of predation risk, GUDs for desert rodents were consistently higher on nights with owls or lights than on nights without (Brown *et al.* 1988; Kotler *et al.* 1991). In these same experiments, GUDs were lower in the bush microhabitat (safe) than in the open microhabitat (risky). Following a night with owls, it takes one to seven nights (depending on the species of gerbil, *Gerbillus* sp.) for fear levels to return to 'baseline' (Kotler 1992).

Fewer studies have looked at the effect of survivor's fitness (*F*) on GUDs. Olsson *et al.* (2002) compared in aviaries the GUDs of starlings from a good environment (high reproductive success, *F*) with those from a poor environment. Indeed, the starlings from the poor environment had lower GUDs than those from the high quality environment. Under natural conditions, white-footed mice (*Peromyscus leucopus*) from a high quality

environment (based on higher fitness) had higher GUDs than those from a lower quality environment (Morris & Davidson 2000). Similarly, lesser-spotted woodpeckers (*Dendrocopos minor*) with higher quality territories (based on reproductive success) exhibited higher GUDs (Olsson & Holmgren 1998).

More studies have used GUD titrations to show how decreasing the marginal value of energy increases GUDs. In these experiments, animals in aviaries (e.g. gerbils, Kotler 1997; starlings, Olsson *et al.* 2002) or free-living animals (fox squirrels, *Sciurus niger*; Brown *et al.* 1992) are given a food augmentation that presumably reduces their marginal value of energy. Augmenting with food increases GUDs, and this increase is often more pronounced in risky than safe microhabitats (Brown *et al.* 1992) and in the presence of predators (Kotler 1997).

GUDs have generally been measured by making an experimental food patch that includes a container, substrate (this increases search time and encourages diminishing returns) and food. Natural GUDs pose challenges in terms of measuring initial and ending abundances, and in identifying the quality and quantity of the resource as perceived by the foraging animal. Olsson *et al.* (1999) were able to measure the natural GUDs of lesser-spotted woodpeckers in Sweden. Upon leaving a branch, the branch was collected and X-rayed to determine the number of items removed (empty cavities) and the number of food items remaining (cavities containing a particular beetle larvae).

Density-dependent habitat selection

The ideal free distribution of density-dependent habitat selection (Fretwell & Lucas 1970; Fretwell 1972) provides another context for letting animals use time allocation as a means of titrating the exchange rate of food and safety (Gilliam & Fraser 1988). In models of density-dependent habitat selection under predation risk (Moody *et al.* 1996; Brown 1998; Grand 2002), individuals should distribute themselves among habitats so that the average fitness rewards from each habitat are equal. This can be carried out at two scales.

At a small scale, animals may be part of the same flock, herd or foraging group, and they may have the option of splitting up between two foraging choices that vary in food and safety. As more individuals select one of the options, the feeding rate from that option declines and it is assumed that predation risk remains independent of group size [otherwise predation risk must be calibrated for group size as well; see Schwinning & Rosenzweig (1990) and van Baalen & Sabelis (1999) for habitat selection when both prey and predators respond to habitat quality]. As they are from the same group, it is assumed that the individuals have the same survivor's fitness and marginal value of energy [see Grand & Dill (1999), for modelling of this when individuals are asymmetric in terms of predation risk and competitive abilities]. If the food reward from the feeding option is fixed and divided equally among the individuals selecting the option, then individuals should distribute themselves so that:

$$\frac{f_r}{N_r} - \frac{f_s}{N_s} = \frac{F(\mu_r - \mu_s)}{\partial F/\partial e}$$

where N_r and N_s refer to the numbers of individuals using the risky and safe feeding options respectively.

With GUDs in depletable food patches, the forager selects the GUDs that balance feeding rates from safe and risky patches. With habitat selection, a group of individuals balances feeding rates from safe and risky habitats. With small-scale habitat selection:

(1) More individuals should occupy the safe than risky feeding option, if each option offers the same feeding opportunities ($f_r = f_s$).
(2) The disparity in numbers between the two options should amplify with an increase in survivor's fitness (F), or a decrease in the marginal value of energy ($\partial F/\partial e$).

Density-dependent habitat selection can also provide a food vs. safety titration at large spatial scales where individuals can only move irregularly among safe and risky habitats, and where individuals are likely to spend most of their lives within one or the other habitat. Morris (1988) has developed the concept of isodars to examine how habitats vary quantitatively and qualitatively. An isodar is a plot of the number of individuals in habitat B as a function of individuals in habitat A. The actual measurement of isodars requires either manipulating the numbers of individuals, or taking advantage of temporal variation in total population size (Morris 1988, 1996). Based on an ideal free distribution, individuals should distribute themselves among habitats in a manner that equalizes fitness opportunities:

$$p_r F_r(N_r) = p_s F_s(N_s)$$

where it is assumed that the probability of surviving predation is lower in the risky than safe habitat, $p_r < p_s$, and so survivor's fitness must be higher in the risky habitat: $F_r(N_r) > F_s(N_s)$. If $F(N)$ has the same functional form in both habitats, then it requires that fewer individuals occupy the risky than safe habitat: $N_r < N_s$. If one were to measure GUDs in the two habitats one would find:

$$f_r(N_r) - f_s(N_s) = \frac{F_r \mu_r}{\partial F_r/\partial e_r} - \frac{F_s \mu_s}{\partial F_s/\partial e_s}$$

The qualitative predictions for density-dependent habitat selection at a large spatial scale remain the same for GUDs in different microhabitats or the ideal free distribution at small spatial scales. But, because $F_r(N_r) > F_s(N_s)$ and $\partial F_r/\partial e_r < \partial F_s/\partial e_s$ (if there are diminishing returns to survivor's fitness from net energy gain), the feeding rate premium in the risky habitat must be even higher than it would be for patches in equivalently safe and risky microhabitats. Morris (2001), in measuring both GUDs and isodars of the deer mouse (*Peromyscus maniculatus*), revealed strong and consistent roles for predation risk at both small and large spatial scales.

Vigilance

Vigilance allows an organism to balance food and safety while engaged in a particular activity. Vigilance occurs when an animal switches effort from harvesting food to detecting predators. Measures of vigilance may have units of scans per unit time, or percent of time spent scanning. In general, vigilance should increase with the animal's expected encounter rate with predators, predator lethality in the absence of vigilance, the value of vigilance in reducing the risk of mortality and the forager's survivor's fitness. Vigilance should decline with the quality of the animal's feeding opportunity, and its marginal value of energy (Brown 1999). For group foragers, per individual vigilance generally declines with group size (McNamara & Houston 1992) as a consequence of the many eyes effect (Powell 1974), dilution effect (Bertram 1978; Dehn 1990) confusion effect (Cresswell 1994), or increased interference.

Because of these properties, vigilance can provide a behavioural indicator of predation risk or the forager's situation. Guinea pigs (*Cavia aperea*) find feeding away from cover more dangerous, while redshanks find the opposite. In both cases, guinea-pigs and redshanks exhibit more vigilance while feeding in their more dangerous microhabitat (Cassini *et al.* 1991; and Cresswell 1994, respectively). Gurung (2003) tested for vigilance in blue sheep (*Pseudovis nayaur*) as an indicator for the presence of snow leopards (*Uncia uncia*) in the Anapurna region of Nepal. Blue sheep displayed more vigilance in areas with snow leopard populations than those areas without. Furthermore, within snow leopard areas, blue sheep were more vigilant when a snow leopard was currently present in the sheep's valley as opposed to when it was away in another valley.

Even when vigilance is used to mitigate the risk of predation, the forager's GUD will rise in the risky situation (Brown 1999). In the case of using vigilance, the GUD rises not because the cost of predation rises but because the vigilant forager requires a higher resource abundance to maintain the same harvest rate (Fig. 1).

Tenacity

Tenacity as defined by Fraser & Gilliam (1987) refers to the ability of the forager to maintain harvest rates in the face of increasing risk of predation. High tenacity may occur for at least three reasons. First, foragers may be relatively invulnerable to predators. Desert rodents above 100 g appear irregularly in the diets of owls (Kotler 1985) and may have little to fear from them. Next, foragers may be poor at detecting the presence of predators and be incapable of altering foraging behaviour. Mosquito larvae (*Culiseta longiareolata*) provide one such example (Kiflawi *et al.* 2003; Blaustein *et al.* 2004). Finally, foragers may modulate the risk of predation through other behavioural means such as apprehension and vigilance.

By apprehension, we mean any attention directed away from the task of harvesting resources and directed towards ascertaining the types and whereabouts of predators (Dall *et al.* 2001). Apprehension manifests the tradeoffs associated with multi-tasking. Complete attention to foraging tasks may maximize harvest rates, but at the price of total ignorance of the approach or attack of a predator. Complete attention to predators may make predator detection and escape maximally likely at the expense of effective harvesting of resources. While engaged in a foraging activity, we expect the forager to select an optimal level of apprehension that balances food harvest with predator detection. Vigilance is a form of apprehension where the forager alternates, according to some schedule, short or long bouts of efficient harvesting with short or long bouts of attention directed primarily towards predator detection.

Tenacity and apprehension prove useful in situations where vigilance behaviours are difficult to measure or interpret. Fox squirrels in suburban Chicago often continue handling acorns even as a house cat approaches, without any detectable change in behaviour (at least to a human observer). Suddenly, at its own choosing, the squirrel will effect an escape in a manner suggesting the squirrel's awareness of the cat's movements.

Measuring the ability of a forager to maintain task performance in the face of risk can provide a useful behavioural indicator of predation risk. In this regard, gerbils (*Gerbillus andersoni* and *G. pyramidum*) are known to show heightened apprehension when predators are most active, in riskier microhabitats, and during moonlit hours of the night when predators are most lethal (Kotler *et al.* 2002). They also show heightened apprehension when their energetic state has been augmented (Kotler *et al.* 2004). In regard to vigilance, Belding's ground squirrels (*Spermophilus beldingi*) whose state had been enriched, increased both the amount of time spent vigilant and the intensity of vigilance (Bachman 1993). In addition, juncos whose state had been forced to deteriorate spent less time in vigilance (Lima 1995). The deprived juncos harvested food faster than non-deprived birds, as did birds foraging in flocks compared with those foraging alone.

BEHAVIOURAL TITRATIONS OF RISK

The literature offers diverse examples of behavioural titrations that reveal various facets of the cost of predation. We present some of them below, in the context of what they reveal about the cost of predation and its consequences.

How big is the cost of predation?

Brown *et al.* (1994) obtained field measurements of environmental conditions and patch use for two species of gerbils, a kangaroo rat (*Dipodomys merriami*), and a ground squirrel (*Spermophilus tereticaudus*). They measured the relationship between resource density and harvest rate in laboratory experiments (Kotler & Brown 1990; Brown *et al.* 1994), and estimated energetic costs of foraging from laboratory measurements of the temperature-dependent metabolic rates of each species (Chew & Chew 1970; Linder 1988; Morgan & Price 1992) and the allometric relationship between body size and cost of locomotion (calculated for speed equal to 0) (Calder 1984). Missed opportunity costs typically range from zero to the negative of the resting metabolic rate and were treated as being equal to zero [see Brown (1999) for the rationale for estimating this cost]. These values allowed them to calculate a minimum estimate of the cost of predation by subtracting
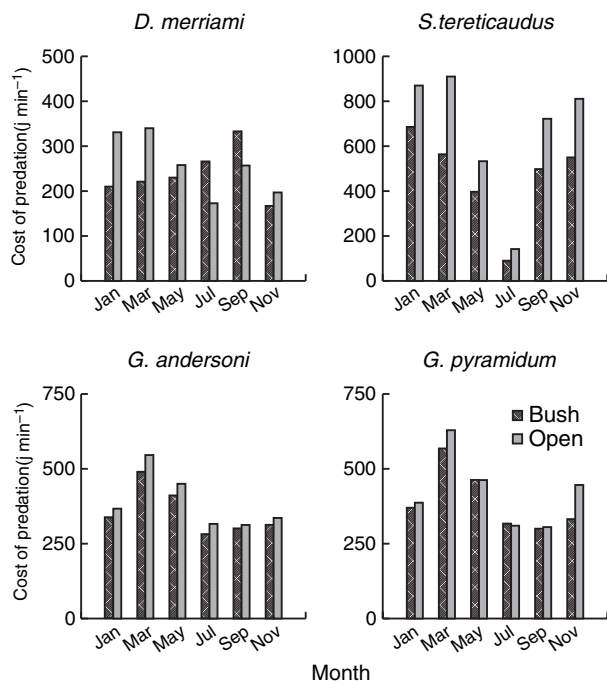
Figure 2 The cost of predation (in units of J m^{-1}) for four species of desert rodents. Each graph shows how a species' cost of predation varies with month and with microhabitat (bush vs. open). Merriam's kangaroo rat (*Dipodomys merriami*) and the round-tailed ground squirrel (*Spermophilus tereticaudus*) co-occur at sites in the Sonoran Desert, Arizona (Brown 1989), and Allenby's gerbil (*Gerbillus andersoni*) and the greater Egyptian sand gerbil (*G. pyramidum*) co-occur on sand dune habitats in the Negev Desert, Israel (Brown *et al.* 1994).

the energetic cost of foraging from the quitting harvest rate estimated from the GUD.

For the four species, the energetic cost of predation varied over seasons and between bush and open microhabitats (Fig. 2). For the gerbils, the cost of predation varied from no less than 80% to over 91% of foraging costs (260 up to 595 J min^{-1}); for the ground squirrel, the cost of predation varied from 47 to 89% (95 up to 930 J min^{-1}); for the kangaroo rat, the cost of predation varied from 52 to 83% (100 up to 375 J min^{-1}).

A more subtle demonstration of the importance of the cost of predation comes from comparing foraging costs in the bush versus the open microhabitat. Typically, the open is perceived by desert rodents as being the more dangerous microhabitat because of risk of predation by owls (Kotler *et al.* 1988, 1991; Longland & Price 1991), but snakes appear to render the bush microhabitat more dangerous (Kotler *et al.* 1993; Bouskila 1995). The premium required for foraging in the open microhabitat rather than the bush microhabitat ranged from 22 J min^{-1} up to 114 J min^{-1} for the gerbils and from 52 J min^{-1} up to 335 J min^{-1} for the ground squirrels. The kangaroo rat

required an additional 167 J min^{-1} to forage in the open in February, but required an additional 93 J min^{-1} to forage in the bush in July. This reversal may reflect the seasonal activities of rattlesnakes. For all four species, foraging costs were overwhelmingly dominated by the cost of predation. Sometimes the additional reward required for foraging in the open was up to five times the direct energetic costs of foraging.

The above example has the advantage of requiring data that are easy to obtain in the field (GUDs and local meteorological data) and physiological measurements that often are available in the literature. The shortcoming is that it depends on laboratory measurements of harvest curves that may not be accurate for field conditions. A second type of titration can be employed to overcome this.

In a large aviary, two gerbils species, *G. a. allenbyi* and *G. pyramidum*, experienced risk of predation from barn owls (*Tyto alba*) (Kotler & Blaustein 1995). Seed trays placed in bush and open microhabitats provided resource patches in which GUDs could be measured. Trays in both bush and open microhabitat started with the same initial amounts of seeds. Then, the initial amounts of seeds in trays in the open were increased (keeping amounts in the bush constant) until equal amounts of seeds were removed by gerbils from the bush and open microhabitats. At this point, the two microhabitats are of equal value to the gerbils. This experiment involved both types of titrations, that performed by the gerbils and manifested through their GUDs, and that performed by the investigators. At the point where total seeds removed was equal for both microhabitats, the microhabitats were equal in both marginal value and total value.

For *Gerbillus a. allenbyi*, the two microhabitats were of equal value when open trays initially contained eight times more seeds than trays in the bush microhabitat. For *G. pyramidum*, open trays required four times more food than bush trays for the two microhabitats to be of equal value. These results accord with field estimates showing that predation represents 91% of foraging costs for *G. a. allenbyi* and as little as 80% of the foraging costs for *G. pyramidum*.

Several titration experiments have estimated the foraging cost of predation using habitat selection. Abrahams & Dill (1989) used guppies (*Poecilia reticulata*) in aquaria under threat of predation from cichlids (*Cichlasoma* sp.) and gouramis (*Trichogaster leeri*) (Abrahams & Dill 1989). Here, the experimenters created two patches that differed in risk (one side of the aquarium contained a predator) and resource supply rate. By allowing several guppies to choose their patches simultaneously, the researchers could estimate the energetic cost of predation from the differences in harvest rates per forager. Indubitably more guppies occupied the safe half relative to the risky half of the
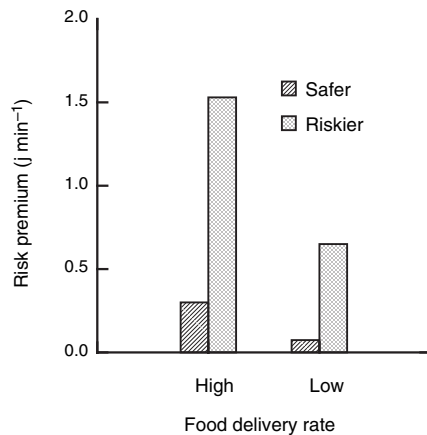
Figure 3 The additional cost of predation for female guppies (*Poecilia reticulata*) to use a risky vs. a safe resource patch (data from Abrahams & Dill 1989). Two aspects of the aquarium environment were varied: food delivery rates (high vs. low), and the riskiness of the risky food patch (safer vs. riskier). The premium for using the risky food patch relative to a safe food patch increased with food delivery rate and with the riskiness of the risky food patch.

aquarium. Two manipulations increased the difference in the foraging cost of predation. One treatment involved varying the risk level at the risky side of the aquarium through the position of the feeder. The other involved increasing the food delivery rate to each side of the aquarium, which should increase the foraging cost of predation via a reduction in the marginal value of energy. For females, in the low risk situation, the energetic premium for using the risky microhabitat ranged from 0.074 J min^{-1} in the low food treatment to 0.30 J min^{-1} in the high food situation. In the high risk treatment, the energetic premium for using the risky microhabitat rose from 0.65 to 1.53 J min^{-1} (Fig. 3).

Abramsky *et al.* (2002) used the foraging behaviour of *G. a. allenbyi*, and the ideal free distribution to estimate the costs associated with predation risk. Experiments were conducted in two pairs of enclosures. Risk of predation was introduced to one subplot of each enclosure either by simulating the light of a full moon or by flying trained owls over the experimental subplots. This typically reduced gerbil activity on the risky plot. Seeds were then added to the risky subplot until activity levels became equal on both sides. To compensate for the extra risk imposed by the moonlight treatment, 4.24–8.47 g of seeds per gerbil had to be added nightly to the illuminated subplot. To compensate for the owl-flight treatment, 4.24–5.64 g of seeds had to be added to the risky subplot.

Nonacs & Dill (1990) offered ant colonies two patches that varied in food quality and in predation risk. A larger species of ant provided the predators. They could

determine the point at which the colony was indifferent to using a low risk, low food-quality patch relative to a high risk, high food-quality patch. With a per load mortality risk of 1.7% at the high risk patch, the ant colonies required a premium of 17 µg of colony growth per load in order for each patch type to be used equally (the average worker weighs 1.37 mg).

Habitat variation in perceived predation risk

By placing depletable food patches across a range of microhabitats, it is possible to use GUDs to titrate for microhabitat variation in perceived predation risk. By far the most frequent result shows that microhabitats near cover (bush) have lower GUDs and are perceived as safer than microhabitats away from cover (open). Besides the examples discussed above, examples with rodents include: Namib desert gerbils (Hughes & Ward 1993), pygmy rock mouse (*Petromyscus collinus*, Brown *et al.* 1998), multimammate mouse (Mohr *et al.* 2003), degu (Yunger *et al.* 2002), white-footed mouse (Morris & Davidson 2000), common spiny mouse (*Acomys caharinus*, Mandelik *et al.* 2003), laboratory rat (*Rattus norvegicus*, Arcis & Desor 2003), deer mouse (Morris 1997), chipmunk (*Tamias striatus*, Bowers *et al.* 1993), fox squirrel (Brown & Morgan 1995), and grey squirrel (*Sciurus carolinensis*, Bowers *et al.* 1993). In birds, bobwhites, *Colinus virginianus*, had lower GUDs in the bush than open microhabitat (Kohlmann & Risenhoover 1996).

Variation in GUDs have titrated for predation risk along habitat axes that include increasing GUDs with distance from burrow (13-lined ground squirrel, *Spermophilus tridecemlineatus*; Thorson *et al.* 1998), and decreasing GUDs with the amount of vegetation cover at a Negev Desert site (Indian crested porcupine, *Hystrix indica*; Brown & Alkon 1990). House mice, *Mus musculus*, in an agricultural landscape in Australia had their lowest GUDs along fence rows and their highest in mowed fields. These habitat differences in GUDs collapsed when the mice saw precipitous drops in their survivor's fitness (Ylonen *et al.* 2003). A similar pattern of lower GUDs with increasing grass and vegetation cover has been shown for voles, *Microtus* sp., both in Europe (Jacob & Brown 2000) and in North America (Pusenius & Schmidt 2002). GUDs of European starlings and American robins (*Turdus migratorius*) increased sharply in going from shrub margins into a lawn at 2 m increments (Oyugi & Brown 2003).

Mountain lions (*Felis concolor*) ambush mule deer (*Odocoileus hemionus*) within forest patches and along their margins. In a region in southern Idaho, USA, the mountain lions occupy woodlots of Douglas fir and are absent from woodlots of mountain mahogany. Accordingly, mule deer had lower GUDs in mountain mahogany than Douglas fir (Altendorf *et al.* 2001). Along transects with feeding stations

50 m inside the woods, a station at the forest edge, and 50 m away from the woods into the adjacent scrubland, mule deer had their lowest GUDs in the shrubland and their highest in the forest interior. But, this microhabitat effect was only associated with Douglas fir and not mountain mahogany.

Some studies reveal animals and situations in which the open microhabitat offers a lower perceived risk of predation. At a Mojave Desert site (Bouskila 1995) and at a Sonoran Desert site during the summer (Brown 1989), kangaroo rats (*Dipodomys* sp.) had lower GUDs in the open than bush microhabitat. Rattlesnakes (*Crotalus cerastes*), lying in ambush under shrubs, account for this pattern. Crested larks (*Galerida cristata*) on sand dune habitats in the Negev, also exhibited lower GUDs in the open than bush microhabitat – gerbils in this same system show the opposite pattern (Brown *et al.* 1997). Larks escape by either running along the ground or jumping up into the air and taking flight. Site lines and lack of escape obstructions may explain the larks' preference for the open (see Lima 1998 for a general discussion of risk responses in birds).

Predation risk may vary across landscapes, and titrations of food and safety can reveal both within and between habitat heterogeneities in risk. In general, animals in higher risk habitats should show even sharper responses to microhabitat or temporal variation in risk (Lima & Bednekoff 1999; Brown 2000). Korb & Linsenmair (2002) measured GUDs of fungus-rearing termites in a savanna and forest habitat of Ivory Coast. Higher GUDs in the gallery forest suggest that it is the high-food, high-risk habitat. When the researchers simulated predation events near food patches, GUDs increased in the savanna habitat while, as an extreme response, foraging ceased in the forest.

Grand & Dill (1997, 1999) used IFD theory with unequal competitors to evaluate habitat-specific differences in the cost of predation. They created two habitats, one safe and one risky. They used distributions of fish (juvenile coho salmon, *Oncorhynchus kisutch*) to estimate the amount of food reward that would be required to equalize the fish's habitat-specific activity patterns. Having estimated the cost of predation, they then added the required amount of food to the risky habitat and obtained the predicted shift in fish activity. Relative to a safe patch, either fewer fish used the risky patch or more food must be provided from the risky patch to attract the same level of feeding activity (Holbrook & Schmitt 1988; Gotceitas 1990; Utne *et al.* 1993)

Temporal variation in perceived predation risk

The earth spins on its tilted axis and revolves around the sun. This assures daily (day–night), seasonal, and other regular and irregular temporal patterns of climate that may be associated with differences in the types and abundances of resources and predators. Diurnal and nocturnal rodents facing diurnal hawks and nocturnal owls attest to the power of the day–night cycle to direct adaptations and niche coevolution (Kronfeld-Schor *et al.* 2001). In rodents, what we might call the 'squirrel' plan emphasizes colour vision and predator detection at a distance. The 'mouse' plan emphasizes detection at shorter range with enhanced night vision and auditory acuity. Soaring hawks (*Buteo* sp.) and owls show the predators' responses to day–night contingencies and to the strategies of the rodents. Hawks are lithe flying machines with acute vision for detecting prey and striking at a distance for which sound plays a lesser role. In contrast, the 'owl' plan suggests a stealthy yet somewhat unwieldy flying boxcar, that bristles with visual and auditory specializations effective for detecting prey at night. This and other temporal cycles guarantee rich variation in the quality and quantity of predation risk that reverberates through the behaviours and niche characteristics of most taxa.

Despite the importance of day–night variation, there are few titrations of this variation. Some animals simply do not exhibit foraging both day and night, and for those that do, little data has been collected. Two rodent studies illustrate the variety of ways animals may approach diurnal variation in predation risk. Rodents of the genus *Microtus* can be active both night and day. *Microtus arvalis* in hayfields in Germany showed a strong habitat by time interaction in perceived predation risk. Daytime GUDs were lower in mowed than unmowed pasture (perhaps as a consequence of weasel predation); night-time GUDs were higher in mowed than unmowed pasture (perhaps driven by owl predation). Based on GUDs, the unmowed habitat during the night was perceived as the safest while the mowed habitat at night was viewed as the riskiest circumstance (Jacob & Brown 2000).

Two spiny mice, *A. russatus* and *A. caharinus*, coexist in rocky desert habitats of Israel and partition time, with the former species active during the day and the latter at night (Jones *et al.* 2001). *Acomys russatus* exhibits sharply higher perceived predation risk (higher GUDs) in the open than in microhabitats under and around boulders. Furthermore, *A. russatus* will forager during the night as well, with a shift towards night-time foraging with the removal of *A. caharinus*. However, *A. russatus*, even in the absence of its competitor, reveals in its patch use behaviour greater fear of night than day.

Small mammal biologists know that moonlight can adversely affect trapping success of rodents. Illumination makes owls more lethal predators (Kotler *et al.* 1988; Longland & Price 1991), and many nocturnal rodents use illumination as an indirect cue of increased predation risk (Brown *et al.* 1988; Kotler *et al.* 1991; Vasquez 1994). Patch

use titrations of free-living rodents have found that GUDs increased with moonlight in the Indian crested porcupine (Brown & Alkon 1990) and Namib desert gerbil (*Gerbillurus tytonis*, Hughes *et al*. 1995). Other studies have found very small (South American desert rodents, Yunger *et al*. 2002) or more complex relationships between patch use and moonlight. At a Mojave desert site dominated by sidewinder rattlesnakes, GUDs of kangaroo rats only increased with moonlight during cold seasons when snakes were inactive (Bouskila 1995). For the desert pocket mouse, *Chaetodipus penicillatus*, Meyer & Valone (1999) also found seasonal variation in whether there was or was not a positive relationship between GUDs and moonlight. The common spiny mouse, in response to moonlight, reduced the number of food patches visited rather than altering GUDs within visited food patches Mandelik *et al*. (2003).

The above studies illustrate the context dependencies of moonlight effects. But, the conversion of GUDs into quitting harvest rates reveals just how costly moonlight can be for kangaroo rats at a Sonoran Desert site (Brown 1989). Using data from this study, we construct Fig. 4 to show the decline of foraging costs ($J min^{-1}$) over 8 days of waning moon. With each daily reduction in moon phase, the foraging cost of predation declines *c*. 30 and 20 $J min^{-1}$ in the open and bush microhabitat respectively. The strong moonphase by microhabitat interaction reveals that nearer to full moon, the open microhabitat is riskier than the bush by *c*. 180 $J min^{-1}$, but by the end of the 8 days, the risk premium for the open microhabitat is down to *c*. 100 $J min^{-1}$.
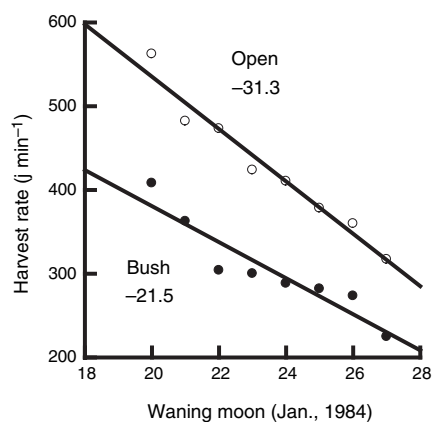
Figure 4 The effect of a waning moon on the foraging cost of predation for Merriam's kangaroo rat at a Sonoran desert site (see Brown 1989). The cost of predation declined both in the bush (solid circles) and the open (open circles) microhabitat from 20 to 27 January 1984. With each day of a waning moon, the cost of foraging in the bush and open microhabitat declines 21.5 $J m^{-1}$ and 31.3 $J m^{-1}$ respectively. 18 January was a full moon and 25 January was the last quarter moon.

Predator scents provide a temporal or spatial cue of predation risk that is not directly tied to solar or lunar rhythms. GUDs and patch use can be used to titrate for the presence or magnitude of the effects of predator odours on the foraging cost of predation. At least for small mammals, results suggest that predator scents, in general, contribute much less to the cost of predation than microhabitats, actual presence of predators, or moonlight. While factors such as cover had strong impacts on perceived predatory risk, the presence of predator scents did not influence GUDs of the common vole (Pusenius & Ostfeld 2002), fox squirrel (Thorson *et al*. 1998) or two species of spiny mouse (Jones & Dayan 2000). Predator odour did raise the GUDs of Merriam's kangaroo rat, but only in the bush microhabitat and only in the winter (Herman & Valone 2000).

BROADER CONTEXTS OF FEAR

In vertebrates, fear may be an emotional state that calibrates the costs and benefits of engaging in risky activities. If we define fear more expansively as the assessment of and response to the foraging cost of predation, then there are a number of broader contexts within which it may be possible to titrate for predation risk and its consequences. These include ontogenetic niche shifts and the timing of developmental events, fear in plants and fear in big fierce predators. While we only discuss each of these briefly, each represents a promising area for advances in theory and empiricism.

A frog in Central America lays its eggs in branches above water. The eggs later hatch, and the tadpoles fall into the water for the next stage of their ontogenetic journey. Presumably, the act of laying eggs arboreally affords protection and/or better oxygenation. But regardless, there is a tree snake that preys on the unprotected egg masses. Upon sensing the snake's vibrations in the branches, distinct from wind or rain vibrations, the eggs may hatch prematurely – as an adaptation. Such flexibility in the timing of hatching represents a tradeoff between development and safety (Warkentin 1995). The tadpoles presumably balance a perception of risk of predation with lost opportunities associated with early metamorphosis.

The metamorphosis of tadpoles into adult toads and frogs has been studied more extensively in the context of environmental cues of habitat quality. The predator-sensitive life-history stage can vary its morphology or tactics for metamorphosis (Skelly & Werner 1990; Relyea & Werner 2000; Altwegg 2002). Tadpoles may accelerate (or delay) their development and the date at metamorphosis in response to risk. Presumably, they balance present dangers with future life-history consequences (Relyea 2001). In one species of mosquito, the adult females seek

out ponds free from the predators of their larvae (Stav *et al.* 1999; Kiflawi *et al.* 2003; Blaustein *et al.* 2004). The larvae of this species forage boldly and in a manner unresponsive to predation risk. The opposite happens for another mosquito species. The mothers pay no attention to the predator characteristics of their oviposition sites whereas the larvae modify their behaviour according to local contingencies of predation risk (L. Blaustein, personal communication).

Plants respond directly to herbivory by producing more defensive chemicals or structures such as spines. Recent findings reveal how plants assess the risk of herbivory via distress chemicals or incidental chemical releases from neighbouring plants experiencing herbivory. The production of and response to such chemicals may provide a means for titrating a plant's perception of risks from herbivores. For example, a species of bean plant (Guerrieri *et al.* 1999) when attacked by aphids secretes pheromones that alert parasitoid wasps to the availability of aphids. As a consequence, the aphids' patch quality declines both through their herbivory and through increased risk of parasitism.

A final aspect of titrating food and safety concerns fear of hunting in the predators themselves. Does a big fierce carnivore such as a mountain lion hunting mule deer experience fear of its prey? It should. Behaviourally responsive prey have the potential to harm their predators. While struggling with the prey, a predator might be injured or in rare instances killed. A mountain lion can lose an eye or break a bone from struggling with a kicking mule deer. Some types of prey are more dangerous than others, and diet selection by a predator should be responsive to this. Even a minor injury can be life threatening to a predator that relies on peak performance to capture prey. A fearless mountain lion can easily kill a porcupine (*Erithizon dorsatum*), but a single quill causing a swollen paw may doom the handicapped mountain lion to starvation. The different tactics that a predator chooses to attack a particular prey individual may trade off the predator's risk of injury and its probability of successfully capturing the prey.

Predators that risk injury while hunting and capturing their prey have at least two ways of balancing food and safety. First, they may rank prey according to scales of ease of capture vs. difficulty of capture (scaled for prey profitability once captured); and according to risk of injury. Obviously, prey that pose little threat and that are easy to subdue should be ranked highest, while those that are dangerous and hard to subdue should be lowest. A predator may reveal interesting aspects of its state and prospects in its ranking of risky, but easy to catch prey with safe, but hard to catch prey. For example, porcupine may be relatively risky but easy prey for a mountain lion. Mule deer may be safer, yet more evasive prey. A mountain lion in a productive environment, in a good state, and with good food prospects

may want to avoid porcupines and stick to hunting mule deer. However, a hungry, desperate mountain lion may include porcupines in its diet (John Lanudre, unpublished data).

Predators may be able to vary their hunting tactics along a continuum from timid to bold. A red-tail hawk may jettison a fox squirrel in its talon if the grip provides an opportunity for the squirrel to bite (Temple 1987). A hungrier or more desperate hawk may elect to trade off safety (life-threatening bite to its leg) for food (successful capture of the squirrel) by continuing the struggle and tightening its grip. Owls that choose to attack at greater speeds may have a higher probability of prey capture and a higher probability of injury. Predators with prey that can cause injury possess boldness as a behavioural strategy. By adjusting the level of boldness (willingness to risk injury) the predator can strike the optimal balance between the likelihoods of successful prey capture and injury to itself. Modelling and identifying these boldness tactics and using them as indicators of how fierce predators titrate food and safety pose future research opportunities and challenges.

CONCLUSIONS AND PROSPECTUS

Predation is a foraging cost, and it can be measured quantitatively or qualitatively. Foraging theory, particularly the theories of optimal patch use and density-dependent habitat selection, provide the conceptual tools. Measurements of quitting harvest rates, GUD, activity levels in time and space, and habitat distributions can all provide empirical data for measuring the foraging costs of predation and its consequences.

There is much scope for expanding the conceptual tools. Various forms of interference competition and any risk of catastrophic loss should impose a foraging cost that is analogous to the foraging cost of predation. Furthermore, foragers can weather the risk of predation by preserving survivorship and forgoing opportunities to harvest food and produce offspring. Alternatively, a forager may respond through increased fecundity as it compensates for predation risk by demanding a higher feeding rate from risky situations. How do these two approaches to managing predation risk manifest in the cost of predation, and how can they be differentiated experimentally? The conceptual tools should be expanded and tailored to deal with plants – how is the cost of predation the same or different for plants? Predator–prey foraging games between animals, in which both prey and predator are clever and behaviourally responsive, alter foraging costs in ways not yet fully understood or modelled. Can such games provide behavioural titrations of prey and/or predators that reveal interesting aspects of the game and the predator–prey interaction?

Empirical tools should also be expanded and improved. Remote sensing, camera traps, PIT (passive integrated transponder) tags and readers all provide promising tools for improving current methodologies for measuring GUDs or habitat distributions. Video camera or signal detection systems will be able to ascribe decisions directly to individuals based on gender, age and condition. Such remote sensing will provide the actual temporal sequence of actions leading to a particular GUD or habitat distribution. Physiological measures of stress, such as hormones and corticosterones, may provide valuable tools for titrating stresses such as predation risk and risk of injury (Wingfield *et al.* 1998; Cockrem & Silverin 2002). Such physiological measures of risk may complement other measures such as GUDs and habitat use. As such, several probes of the cost of predation may yield a more accurate and multi-faceted picture of the risks and opportunities faced by a foraging animal (Eilam *et al.* 1999).

As Laundre *et al.* (2001) notes, animals live in a landscape of fear. This landscape is in addition to landscapes of productivity, soil and physical features, vegetation structure, food availability and climate. All of these interact to influence ecosystems. Many of these landscapes can be measured directly, sometimes with the use of satellite imaging and other remote sensing techniques. However, often the most important landscape to an animal is its landscape of fear. This landscape can best be assessed through behavioural titrations that allow animals to reveal their foraging cost of predation.

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