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The effect of risk of mortality on the foraging behaviour of animals faced with time and digestive capacity constraints

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ABSTRACT

This article examines the effect of risk of mortality on the optimal diet of an animal foraging for two food types. The foods are characterized by different nutritional or energetic values per unit volume, and the forager has constraints on both the amount of time it has available for foraging and on the volume of food that can be processed per unit time. Such a situation characterizes the diet choice problem faced by many herbivores. The two food types may occur in the same habitat, or they may occur in different habitat patches; in the latter case, they cannot be encountered simultaneously. Unlike earlier analyses of these diet problems, here we consider the risk of mortality when foraging and allow risk to differ between habitats. Optimal time allocation strategies and the resultant functional responses are calculated for both one- and two-habitat situations. Mortality risk can substantially change the forager's time allocations and, consequently, its functional responses. Increasing mortality risk in both habitats proportionally can increase use of the habitat that has the greater risk. Time allocation often responds in a non-monotonic fashion to changes in the density of a particular food. As a result, functional responses may decrease with increasing food abundance over one or more ranges of abundance. Experimental findings on the response of grasshopper foraging to the risk of spider predation are compared with the theory. Finally, the possible indirect interactions between the food species in this simple food web are discussed.

Keywords: constrained diets, foraging behaviour, functional response, habitat selection, optimal diet, predation risk, time allocation.

INTRODUCTION

There is growing recognition in the ecological literature that consumer foraging behaviour must be studied if we are to understand consumer–resource interactions. Foraging behaviour influences the functional relationship between resource density (plus other variables) and the consumption rate of those resources – that is, the consumers' functional response (Holling, 1959). Most analyses of consumer functional responses have assumed that consumers either have no constraints on their foraging behaviour, or, if they have

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limited time for foraging, they always forage for the maximum amount of time available. However, most organisms are limited in their consumption behaviour by the capacity of their digestive systems, the amount of time available for foraging, or both. For instance, low food densities often lead to available time constraining intake. Low food quality, measured by energy or nutrients per volume, often means that the size and passage rate of the digestive system constrain food intake (Belovsky, 1986a,b). Herbivores have frequently been shown to be limited by both time and digestive constraints in their attempts to maximize their intake rate of energy or nutrients and hence maximize fitness (Belovsky, 1984, 1986a; Belovsky and Schmitz, 1991, 1994). One important consequence of these two constraints is that adaptive foraging produces a variety of functional response forms that do not occur in the absence of both constraints (Abrams, 1989, 1990a; Schmitz, 1995).

In a community context, foragers are not only confronted by choices among foods, but must also consider the risk of being captured by predators, and must balance this risk against the goal of maximizing energy or nutrient intake. The importance of mortality risk for foraging is widely accepted (Lima and Dill, 1990), but, until recently, the impact of risk on diet choice in herbivores had not received much attention. It has been shown that mortality risk from predators can alter herbivore foraging behaviour (Rothley *et al.*, 1997) and thus change the impact of herbivores on plant communities (Schmitz *et al.*, 1997).

In this article, we examine the effect of mortality risk (due to predators or other factors) on both the optimal foraging behaviour and functional responses of foragers that are constrained by time, digestive capacity or both, while feeding on two resources. These constraints apply to a variety of herbivore species (Belovsky, 1984, 1986a,b; Belovsky and Schmitz, 1991, 1994; Yamauchi and Iwasa, 1995), but the models do not include assumptions that restrict the results to herbivores. The analysis predicts how diet selection should change as a function of resource abundances and of the mortality risks associated with feeding on each resource type. We also show how diet selection determines the forager's functional responses. Some predictions of the models are compared with experimental results previously obtained on a system with spider predators, grasshopper herbivores, and forbs and grasses representing low- and high-quality foods for the herbivores. We conclude by examining the range of predator-mediated indirect effects that may occur in ecological communities when the foragers satisfy the assumptions of our models.

MODELS

Simplifying assumptions

The models below make a number of simplifying assumptions. However, these assumptions have several other justifications in addition to their simplicity. Similar assumptions have been made in a number of previously published theoretical studies (e.g. Belovsky, 1978, 1984, 1986a,b, 1997; Abrams, 1990a,b; Belovsky and Schmitz, 1991, 1994; Schmitz, 1995) and maintaining these assumptions facilitates comparison with previous work. In addition, these simple models have been very successful in predicting the diet of many herbivore species (Belovsky, 1986a,b, 1997; Grantham *et al.*, 1995), suggesting that the simplifying assumptions may be reasonably accurate. Belovsky (1986a) found that the assumptions used here predicted 88% of the variance in the proportions of grasses and forbs in the diets of 27 species of mammals, birds and insects.

Food density of food type i is denoted R_i and an individual predator's intake rate per unit time while foraging for food type i is an increasing function of food density, $f_i(R_i)$. The proportion of available time that is spent foraging for resource i is denoted t_i, so the realized intake rate (i.e. the functional response to food i) is $t_i f_i(R_i)$. The parameter A_i denotes the nutritional (or energetic) content per unit volume of food i. The maximum food intake rate set by limitations on the digestive system occurs when $\Sigma_i\, t_i f_i(R_i) = D$, where D is gut capacity. The instantaneous risk of mortality due to foraging for food type i is m_i, and the expected probability of survival to reproduction of an individual that forages relative to survival of a non-foraging individual is $\exp[-\Sigma_i\, m_i t_i]$. This formulation assumes that the risk of starvation is negligible. Reproduction can be expressed as an increasing function, b, of nutrient intake rate, $\Sigma_i\, t_i A_i f_i(R_i)$. In previous work and in the following analysis, b is assumed to be linear. In this case, we can assume that A_i is measured in units of net reproduction per unit food intake. The resulting fitness expression is:

$$W = (\Sigma_i\, t_i A_i f_i(R_i)) \exp[-\Sigma_i\, m_i t_i] \tag{1}$$

There are two sets of constraints on foraging. First, because t_i is expressed as a fraction of total time available for foraging, $0 \le \Sigma_i\, t_i \le 1$. Secondly, because the capacity of the digestive system is limited, $\Sigma_i\, t_i f_i(R_i) \le D$. The possible optimal times must either: (1) satisfy $\mathrm{d}W/\mathrm{d}t = 0$ and $\mathrm{d}^2 W/\mathrm{d}t^2 < 0$ as well as all constraints; or (2) be a value of t where a constraint is satisfied as an equality (i.e. is binding) and where W decreases as t_i moves away from the constrained value in any permissible direction.

The effect of mortality risk when there is one food type

Because it has not been studied before, we begin our analysis by considering the simplest situation that has risk of mortality while foraging and both time and processing constraints on food intake. Such an analysis could apply to a system with a single, specialist herbivore, or to a generalist herbivore in an environment with a single food type. This leads to the following three possible expressions for optimal foraging time, depending on m and R:

$$\begin{array}{ll} t = 1/m & \text{if } m \ge \max[1, f(R)/D] \\ t = 1 & \text{if } m \le 1 \text{ and } f(R) \le D \\ t = D/f(R) & \text{if } f(R) \ge \max[D, Dm] \end{array}$$

These alternatives imply that there are two possible relationships between food density and realized food intake: (1) when mortality risk is low, intake goes up as $f(R)$ until this function reaches D; intake is constant at D for higher values of R; or (2) when mortality risk is high (condition (1) is satisfied), intake goes up as $f(R)/m$ until this quantity reaches D, after which intake is again constant. If mortality risk is proportional to predator population density, this implies that foraging is independent of predator abundance, P, unless P is above a threshold, in which case foraging time varies inversely with P.

Mortality risk with two food types in separate habitats

Separate habitats means that a consumer is restricted to feeding on one food type at a time; this can be true of an apparently homogeneous habitat in which the foragers are small in size relative to the food items (as with many insect herbivores consuming plants). When there are two food types, equation (1) becomes $W = (t_1A_1f_1(R_1) + t_2A_2f_2(R_2))\ \exp[-m_1t_1 - m_2t_2]$. This is subject to the following constraints:

$$0 \le t_1 \le 1;\ 0 \le t_2 \le 1;\ 0 \le t_1 + t_2 \le 1 \text{ (time constraints)}$$

$$t_1f_1(R_1) + t_2C_2f_2(R_2) \le D \text{ (digestive capacity constraint)}$$

In the following analysis, we assume (without loss of generality) that resource 2 is the more nutritious per unit volume (i.e. $A_2 > A_1$). The linear form of the instantaneous risk and reproductive rate components of the fitness function imply that, in general, there do not exist intermediate, unconstrained values of both variables t_1 and t_2 that maximize fitness (i.e. the set of two equations, $\mathrm{d}W/\mathrm{d}t_1 = 0$ and $\mathrm{d}W/\mathrm{d}t_2 = 0$, do not have a unique solution). The only exception is when $A_1f_1(R_1)/m_1 = A_2f_2(R_2)/m_2$, in which case, any values of the two time allocations give equal fitness when the digestive capacity is not limiting. If no constraints interfere, it is optimal to spend time only in the habitat that provides the greater ratio of rewards to risks per unit time (i.e. $Af(R)/m$). However, this simple rule is no longer true when the solution is constrained.

The optimal foraging strategy

For a pair of time allocations to represent a fitness maximum, it is necessary that all *feasible* changes in t_1 and t_2 reduce fitness. This can occur when either: (1) $\mathrm{d}W/\mathrm{d}t_i = 0$ for one of the t_i, and one constraint is binding; or (2) two constraints are binding. There are nine time allocation rules, each of which is optimal over certain ranges of resource densities and mortality risks. Of these nine, six are specialist solutions, and three involve consumption of both food types. For each solution, certain inequalities must be satisfied to ensure that fitness decreases as one or both t_i move away from the solution in a

Table 1. Time allocation rules for the two-resource model

(1) $t_1 = 1$; $t_2 = 0$ if $m_1 \le \min[1, m_2 + 1 - A_2f_2(R_2)/(A_1f_1(R_1))]$; and $f_1(R_1) \le D$
(2) $t_2 = 1$; $t_1 = 0$ if $m_2 \le \min[1, m_1 + 1 - A_1f_1(R_1)/(A_2f_2(R_2))]$; and $f_2(R_2) \le D$
(3) $t_1 = D/f_1(R_1)$; $t_2 = 0$ if $f_1(R_1) \ge \max[D, m_1D]$; and $(A_2 - A_1)/(A_1D) \le (m_2f_1(R_1) - m_1f_2(R_2))/(f_1(R_1)f_2(R_2))$
(4) $t_1 = 0$; $t_2 = D/f_2(R_2)$ if $f_2(R_2) \ge \max[D, m_2D]$; and $(A_2 - A_1)/(A_2D) \ge (m_2f_1(R_1) - m_1f_2(R_2))/(f_1(R_1)f_2(R_2))$
(5) $t_1 = 1/m_1$; $t_2 = 0$ if $m_1 \ge \max[1, f_1(R_1)/D]$; and $A_1f_1(R_1)/m_1 > A_2f_2(R_2)/m_2$
(6) $t_2 = 1/m_2$; $t_1 = 0$ if $m_2 \ge \max[1,\ C_2R_2/D]$; and $A_1C_1R_1/m_1 < A_2C_2R_2/m_2$
(7) $t_1 = A_2D/(f_1(R_1)(A_2 - A_1)) - f_2(R_2)/(m_2f_2(R_1) - m_1f_2(R_2))$; $t_2 = f_1(R_1)/(m_2f_1(R_1) - m_1f_2(R_2)) - DA_1/(f_2(R_2)(A_2 - A_1))$ if $A_1f_1(R_1)/m_1 > A_2f_2(R_2)/m_2$; and $(m_2f_1(R_1) - m_1f_2(R_2))\{f_1(R_1)f_2(R_2)(A_2 - A_1) - D(A_2f_2(R_2) - A_1f_1(R_1))\} \ge f_1(R_1)f_2(R_2)(A_2 - A_1)(f_1(R_1) - f_2(R_2))$, and $f_1(R_1)f_2(R_2)(A_2 - A_1)/(A_2D) \le m_2f_1(R_1) - m_1f_2(R_2) \le f_1(R_1)f_2(R_2)(A_2 - A_1)/(A_1D)$
(8) $t_1 = \{A_1f_1(R_1) - A_2f_2(R_2) - (m_1 - m_2)A_2f_2(R_2)\}/\{(m_1 - m_2)(A_1f_1(R_1) - A_2f_2(R_2))\}$; $t_2 = \{(m_1 - m_2)A_1f_1(R_1) - (A_1f_1(R_1) - A_2f_2(R_2))\}/\{(m_1 - m_2)(A_1f_1(R_1) - A_2f_2(R_2))\}$ if $(m_1 - m_2)(A_1f_1(R_1) - A_2f_2(R_2)) > 0$; and $(A_1f_1(R_1) - A_2f_2(R_2))/(A_2f_2(R_2)) \ge m_1 - m_2 \ge (A_1f_1(R_1) - A_2f_2(R_2))/(A_1f_1(R_1)$, and $(m_1 - m_2)\{D(A_1f_1(R_1) - A_2f_2(R_2)) + (A_2 - A_1)f_1(R_1)f_2(R_2)\} \ge (A_1f_1(R_1) - A_2f_2(R_2))(f_1(R_1) - f_2(R_2))$
(9) $t_1 = (D - f_2(R_2))/(f_1(R_1) - f_2(R_2))$; $t_2 = (f_1(R_1) - D)/(f_1(R_1) - f_2(R_2))$ if either $f_1(R_1) > D > f_2(R_2)$ or $f_1(R_1) < D < f_2(R_2)$; and $\{f_1(R_1)f_2(R_2)(A_2 - A_1)(f_1(R_1) - f_2(R_2))\} \ge \{f_1(R_1)f_2(R_2)(A_2 - A_1) - D(A_2f_2(R_2) - A_1f_1(R_1))\}(m_2f_1(R_1) - m_1f_2(R_2))$, and $(m_1 - m_2)\{f_1(R_1)f_2(R_2)(A_2 - A_1) - D(A_2f_2(R_2) - A_1f_1(R_1))\} \le (A_1f_1(R_1) - A_2f_2(R_2))(f_1(R_1) - f_2(R_2))$

permissible direction, and to ensure that the solution itself does not violate a constraint. The possible time-allocation rules and the conditions under which they apply are given in Table 1.

Cases 1–6 in Table 1 are all specialist solutions in which only a single food is consumed. In these cases, the nutrient intake rate in one habitat is significantly better than in the other, and/or risk is significantly lower. Cases 1 and 2 represent situations in which mortality risks are not very high and the resource densities are sufficiently low relative to digestive capacity that the gut is never filled. The third and fourth solutions arise when resource densities are high enough that the gut capacity becomes limiting, and risks of mortality are low enough that it is advantageous to forage as much as gut constraints allow. The fifth and sixth solutions reflect a sufficiently high mortality risk that foraging time is an optimal balance between intake and mortality risk, and digestive capacity is high enough that it does not constrain foraging. The optimal strategy under these cases is to forage for an intermediate amount of time in the habitat that provides the highest ratio of nutrient (or caloric) intake to mortality risk.

The remaining solutions (7–9) in Table 1 represent generalist foraging behaviours in which both resources are taken. Under solution 7, only the digestive capacity constraint is binding; clearly, this pertains to cases with abundant food. Under solution 8, only the maximum time constraint is binding; this is likely to occur when food is relatively rare. Under solution 9, both time and digestive capacity simultaneously constrain foraging; Belovsky (1986a) presented data suggesting that this is true for many generalist grassland herbivores.

For solution 7 to be optimal, it is necessary for the more nutritious resource (here resource 2) to be sufficiently rare or to be associated with a high enough risk that it has the smaller value of $A_i f_i(R_i)/m_i$ (i.e. the ratio of caloric or nutrient intake rate to mortality risk per unit time). It is also necessary that the more nutritious resource (resource 2) has a lower ratio of intake volume to mortality risk per unit time, $f_i(R_i)/m_i$. (If this is not the case, then the last set of inequalities for solution 7 in Table 1 can never be satisfied.) Time spent in habitat 2, t_2, decreases with increasing R_1 and increases with increasing R_2. Time spent in habitat 1, t_1, decreases with increasing R_2. However, the sign of $\partial t_1/\partial R_1$ is indeterminate, and unimodal change in t_1 with increasing R_1 is possible. Increases in mortality risk in habitat 2 or proportional increases in both mortality rates increase t_1 and decrease t_2.

Under solution 8, when time allocation between habitats is adjusted optimally, all available time is used for foraging, but the intake rate is still less than the gut capacity. This implies a relatively low food abundance. A necessary condition for this solution to be optimal is that the habitat with the greater mortality risk per unit time, m_i, also has the greater energy or nutrient gain rate per unit time, $A_i C_i R_i$. Under solution 8, the time allocated to foraging on resource 1 increases as the density of resource 1 increases and decreases as the density of resource 2 increases; time allocated to consuming resource 2 must change in the opposite manner. Proportional increases in mortality risk in both habitats or increases in risk in habitat 1 both result in lower consumption of resource 1 and greater consumption of resource 2.

Under solution 9, both time allocations are constrained simultaneously by total time available and by digestive capacity. Mortality risks affect whether this potential solution is a local fitness maximum, but risks do not affect the time allocations when this solution is optimal. This foraging behaviour has been discussed in the context of models with no mortality risk by Abrams (1990a) and Schmitz (1995). When there is risk, there are two sets of conditions under which the solution is optimal. The first is when the density of the less nutritious food is high and that of the more nutritious food is low, and mortality risk is relatively low in both habitats. The second is when the density of the less nutritious food is low and that of the more nutritious food is high, but mortality risk is much higher in the habitat with the more nutritious food. Under the first set of conditions, time allocated to habitat 1 (less nutritious food) decreases with an increase in either R_1 or R_2; t_2 increases with either R_1 or R_2. The opposite is true under the second set of conditions, with high mortality risk and high food abundance in habitat 2. Under this second set of conditions, the roles of the two resources are reversed; R_2 becomes less fitness-enhancing than R_1 because of its associated predation risk, but, because of its greater abundance, R_2 can be used to fill the digestive system.

Time allocations and functional responses under the optimal strategy

The foraging strategy specified by these nine solutions is quite complicated, and is a function of four variables: the two mortality risks and two food densities. The number of variables may be reduced to three if, for example, predation risk is the main mortality factor, if the same predator occurs in both habitats, and if the predator's foraging is not affected by prey densities. In this case, the m_i may be factored into a predator density (P) multiplied by a capture rate coefficient (M_i). When this is possible, the time allocations become functions of the two food densities and the predator density. When different predators (or other

Table 2. Functional responses of foragers under each of the nine possible time allocations for the model with two habitats and linear $f_i(R_i)$

Solution	Functional responses
1	$C_1R_1t_1 = C_1R_1$ $C_2R_2t_2 = 0$
2	$C_1R_1t_1 = 0$ $C_2R_2t_2 = C_2R_2$
3	$C_1R_1t_1 = D$ $C_2R_2t_2 = 0$
4	$C_1R_1t_1 = 0$ $C_2R_2t_2 = D$
5	$C_1R_1t_1 = C_1R_1/(m_1)$ $C_2R_2t_2 = 0$
6	$C_1R_1t_1 = 0$ $C_2R_2t_2 = C_2R_2/(m_2)$
7	$C_1R_1t_1 = A_2D/(A_2 - A_1) - (C_1C_2R_1R_2)/(m_2C_1R_1 - m_1C_2R_2)$ $C_2R_2t_2 = (C_1C_2R_1R_2)/(m_2C_1R_1 - m_1C_2R_2) - A_1D/(A_2 - A_1)$
8	$C_1R_1t_1 = C_1R_1(A_1C_1R_1 - A_2C_2R_2 - (m_1 - m_2)A_2C_2R_2)/((m_1 - m_2)(A_1C_1R_1 - A_2C_2R_2))$ $C_2R_2t_2 = C_2R_2((m_1 - m_2)A_1C_1R_1 - (A_1C_1R_1 - A_2C_2R_2))/((m_1 - m_2)(A_1C_1R_1 - A_2C_2R_2))$
9	$C_1R_1t_1 = C_1R_1(D - C_2R_2)/(C_1R_1 - C_2R_2)$ $C_2R_2t_2 = C_2R_2(C_1R_1 - D)/(C_1R_1 - C_2R_2)$

mortality risks) occur in the two habitats, no reduction in the number of independent variables is possible. The functional responses to the two resources are $f_1(R_1)t_1$ and $f_2(R_2)t_2$. For illustrative purposes, we will assume linear functions: $f_i(R_i) = C_iR_i$. Table 2 gives the functional responses to each food type for the nine possible time allocations in Table 1, assuming linear $f_i(R_i)$.

Because of the difficulty of visualization with more than two independent variables, we will illustrate the time allocations and functional responses as functions of one or two variables. The situations that are likely to be of interest to ecologists are the effects on intake rate of each food of changing the abundance of one of the foods or changing either the general risk or risk in a particular habitat. These situations will be considered below. We will focus on the case where solution 9 describes the optimal diet in the absence of predation, because Belovsky's (1986a,b, 1997) work suggests that this solution characterizes the diet of a wide variety of generalist herbivores.

The qualitative changes in time allocations with changes in the mortality risk in a single habitat are not surprising. The solutions in Table 1 show that increasing the risk in one habitat either reduces or does not affect the time allocated to that habitat. Increasing risk in the other habitat either increases or does not affect the use of the focal habitat. However, increasing risk in both habitats simultaneously can result in interesting and non-obvious changes in the time allocations. Mortality will increase in both habitats if, for example, it is caused by a predator that occurs in both habitats and risks are proportional to predator density, $m_i = M_iP$. Under solution 7, the use of habitat 1 increases with proportional increases in both risks (e.g. an increase in P), even if there is a greater risk per unit time in habitat 1 than in habitat 2. Under these conditions, use of habitat 1, with its greater energy gain rate per unit time, enables total foraging time (and thus total exposure to extra mortality) to be reduced. Figure 1 shows a common shape for the overall response of each t_i to increasing risk. This figure also describes the consumption rates of each resource, since these rates are directly proportional to time allocations. The two curves in Fig. 1 describe situations in which mortality is equal in the two habitats (dashed line) or twice as great in

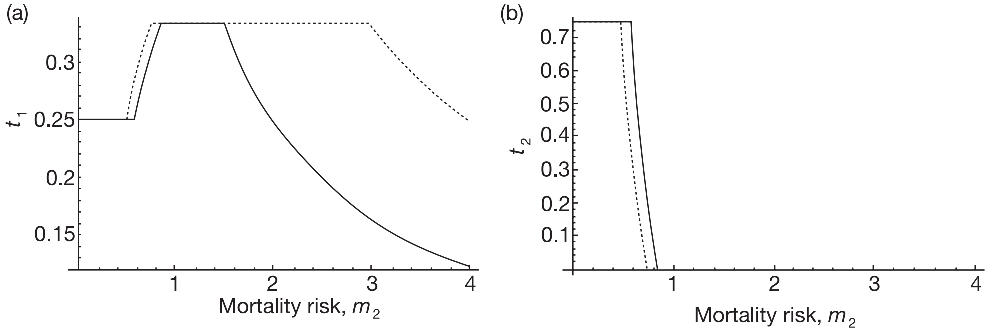

Fig. 1. Time spent in habitat 1 (a) and habitat 2 (b) as a function of mortality risk, which is assumed to be proportional to predator density in both habitats; the x-axis gives mortality risk in habitat 2. The parameter values are: $C_1 = C_2 = 1$; $A_1 = 0.5$; $A_2 = 1.5$; $D = 1$. The resource densities are $R_1 = 3$ and $R_2 = 0.33$. In each part of the figure, the solid line represents a system where the mortality risk in habitat 1 is twice that in habitat 2, while the dashed line assumes equal risk in the two habitats. As the instantaneous mortality associated with foraging in either habitat increases from zero, the optimal time allocations are given by solutions 9, 7, 5 and 3 as R_2 increases.

habitat 1 as in habitat 2 (solid line). As the instantaneous mortality associated with foraging in either habitat increases from zero, the optimal time allocations are given by solutions 9, 7, 5 and 3 in succession. The four segments of the curves in Fig. 1a correspond to these four solutions. In both situations illustrated in Fig. 1, there exists a wide range of mortality rates for which use of habitat 1, with the lower quality resource, is greater in the presence of mortality risk than in its absence. Even when mortality risk is twice as large in habitat 1 as in habitat 2, use of habitat 1 is at least as great as it would be with zero risk, provided that risk per unit time spent in habitat 2 is less than approximately 1.99 in this example. In both of these situations, use of habitat 2 remains constant at $t_2 = 0.75$ when mortalities are low (and solution 9 applies), and then rapidly declines to zero where solution 7 applies, as shown in Fig. 1b. It is only when mortality is more than approximately 3.03 times as great in habitat 1 as in habitat 2 that increasing mortality proportionately in both habitats fails to increase use of habitat 1 over some range of mortalities.

Figure 2 examines the response of time allocations to mortality when the ratio of m_1 to m_2 is greater than 3.03; in Fig. 2, the ratio is 5. Here, the increase in both mortalities shifts the solutions from solution 9 to 8 to 2 to 6. Use of habitat 2 increases with mortality when solution 8 is optimal, is constant at solution 2, and decreases for solution 6. Use of habitat 1 declines to zero when solution 8 is optimal (and is zero for solutions 2 and 6). Increasing the mortality risk in both habitats can only increase the amount of time spent in habitat 2 when mortality in habitat 1 is sufficiently greater than that in habitat 2.

There are a number of interesting features of the dependence of the time allocations and functional responses on food densities. As noted by Abrams (1990a), even when there is no mortality risk, the functional response to the lower quality food may decrease as the density of that food increases; this is true of solution 9 in the model with mortality. Here we illustrate time allocations and functional responses for a situation with greater risk associated with the habitat containing the higher quality food, and with a linear $f(R)$.

Figures 3 and 4 represent time allocations and functional responses (the latter assuming linear $f_i(R_i)$) as a function of R_1 and R_2 for foods 1 and 2 respectively (for a representative set of parameters). It is clear that both quantities can have rather intricate dependencies on resource densities when the more nutritious resource is characterized by a greater mortality risk. Figure 5 shows two cross-sections from Figs 3 and 4, illustrating more clearly how the time allocations to each habitat and food consumption rates change with the density of

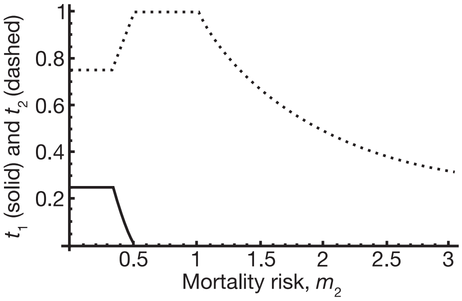

Fig. 2. The time spent in habitats 1 and 2 as a function of mortality risk. The assumptions, parameters and food densities are the same as in Fig. 1, except mortality is five times higher in habitat 1 than in habitat 2.

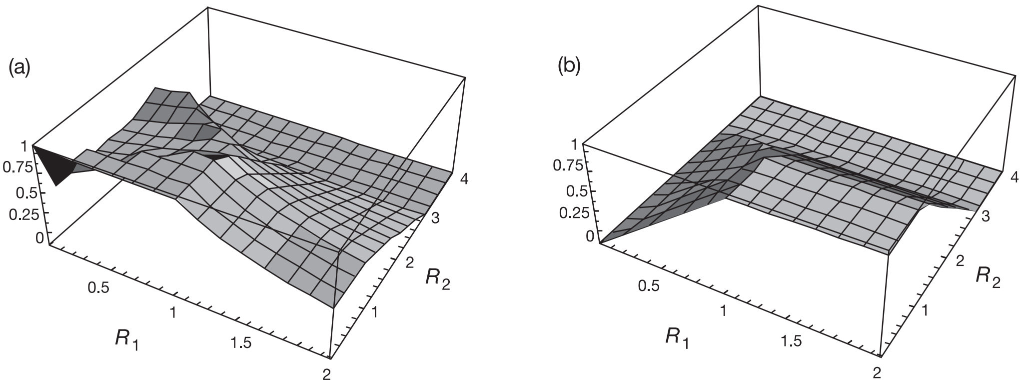

Fig. 3. The time spent in habitat 1 (a) and the functional response to the resource therein (b) for a range of food densities for the case of significant mortality only in the habitat containing the high-quality food ($m_1 = 0.001$, $m_2 = 2$). Parameter values are the same as in Fig. 1.

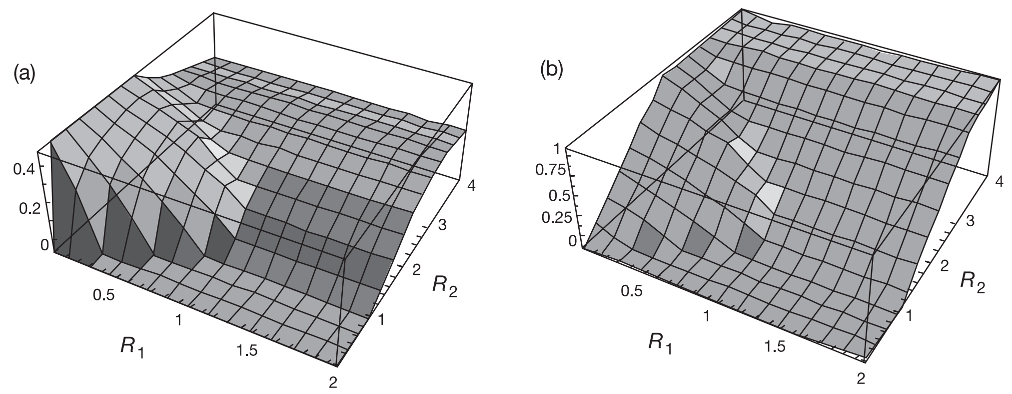

Fig. 4. The time spent in habitat 2 (a) and the functional response to the resource therein (b) for the situation illustrated in Fig. 3.

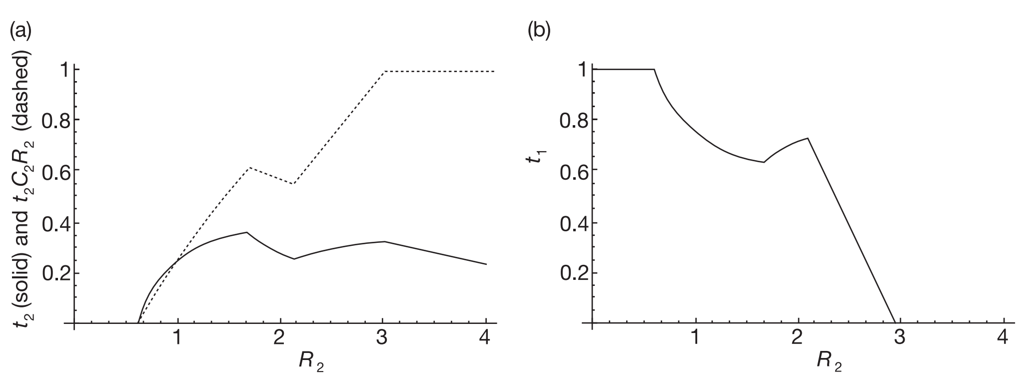

Fig. 5. Two cross-sections through the time allocations shown in Figs 3 and 4 for a fixed density of the less nutritious resource, $R_1 = 0.6$. Each 'corner' in the curve represents a transition between strategies. As R_2 increases, the sequence of optimal solutions goes from solution 1 to 8 to 9 to 7 to 4.

food 2 for a particular value of R_1. The shifts between strategies are evident as non-differentiable ‘corners’ in the curves. As R_2 is increased from a density of 0 to 4 in Fig. 5, the sequence of optimal solutions goes from solution 1 to solution 8 to solution 9 to solution 7 to solution 4. The signs of the derivatives of t_1 and of t_2 with respect to R_2 change with each transition between the three generalist solutions: 8, 9 and 7. It is clear from Fig. 5 that the functional response to food 2 decreases with increasing R_2 over a range of densities when R_1 is less than 1 (these occur when solution 9 describes the optimal time allocations). The ingestion rate of food 1 is unaffected by R_2 when R_2 is low (solution 1), decreases with R_2 when R_2 is slightly larger (solution 2), increases with R_2 for still larger densities (solution 9), and finally declines to zero (solution 7).

In models without constraints, a two-habitat choice problem is characterized by monotonic responses of time allocations to resource densities (Abrams, 1987). However, non-monotonic responses of time allocations to resource densities occur for a wide range of parameters in this model. Concepts of satiation and switching have dominated discussions of foraging on two or more foods; these clearly do not provide an adequate basis for understanding the responses of models with both digestive constraints and mortality risk.

The representations of functional responses assume that intake per unit time within a habitat increases linearly with food density. Non-linearity in the f_i does change the details of the functional response diagrams. However, because the f_i are assumed to be increasing functions, the order of the transitions between different solutions for the optimal t_i as an R_i is increased is not altered by the non-linearity.

Mortality risk with two food types in the same habitat

If the two food types occur in the same habitat, it is not necessary to give up access to one food to forage on the other. This case requires more consideration of the form of the intake function, f, because handling one food item often precludes capture and/or ingestion of another. However, here we will assume that the intake rate functions are linear: $f_i(R_i) = C_iR_i$. This assumption reveals the effects of digestive limitation and risk without the complications of food items being dropped from the diet because of effects of handling on encounter, which are well-known from optimal foraging theory (Stephens and Krebs, 1986). Given this assumption that the encounter rate of one food while foraging is unaffected by the presence of the other food, the two adaptive variables are t, the total time spent foraging, and q, the proportion of encounters with the low-quality item that result in consumption. (It is never advantageous to ignore an encountered, high-quality food item.) The expression for forager fitness is:

$$(A_1C_1R_1q + A_2C_2R_2)t \exp[-mt]$$

where C_1 and C_2 are the encounter rates per unit resource density with each resource. The constraints on the variables are: $0 \leq q \leq 1$, $0 \leq t \leq 1$, $(C_1R_1q + C_2R_2)t < D$. We again assume that resource 1 is the lower quality resource in terms of energy or nutrient gain per unit volume consumed ($A_1 < A_2$). The possible optimal strategies are determined as before:

(1) $q = 1$; $t = 1$; when $C_1R_1 + C_2R_2 \leq D$; and $m < 1$. Here maximizing both foraging time and acceptance of the lower quality food still does not violate the gut capacity constraint, and the mortality rate is low enough that it is optimal to forage for all available time.

(2) $q = (D - C_2R_2)/(C_1R_1)$; $t = 1$; if $C_1R_1 + C_2R_2 \geq D$; $D > C_2R_2$; and $m < 1$. The mortality rate is still low enough that $t = 1$ is optimal, but acceptance of the lower quality food is <100% because it is abundant, and accepting all encountered items would violate the gut capacity constraint.

(3) $q = 1$; $t = 1/m$; if $m \geq \max[1, (C_1R_1 + C_2R_2)/D]$. With this solution, the mortality rate is high enough that an intermediate foraging time is optimal, and resource densities are low enough that all encountered items may be accepted without violating the gut capacity constraint.

(4) $q = 0$; $t = D/C_2R_2$; if $C_2R_2 \geq \max[D, mD]$. This is the solution when the more nutritious resource type is abundant enough and mortality rate is low enough that the gut can be filled with the more nutritious food in less than the total available time without foraging intake being outweighed by mortality risk.

(5) $q = (mD - C_2R_2)/(C_1R_1)$; $t = 1/m$; if $mD \geq C_2R_2$; and $C_1R_1 + C_2R_2 \geq Dm$; and $m \geq 1$. This is a situation where the risk per unit time is relatively high and total food density is high. Foraging time is an optimal balance between risks and rewards, while the proportion of low-quality food items taken is set by the gut capacity constraint. The proportion of low-quality items encountered that are consumed decreases as the abundance of either food increases. The total amount of low-quality food consumed is independent of its density.

Note that in all potential solutions except for case (4), the time spent foraging is independent of the abundances of both resources, and is only affected by the mortality risk. Case (4) represents the comparatively unlikely situation in which the more nutritious resource is so abundant that gut capacity based on consumption of this resource alone determines foraging time. In this single-habitat model, the only disadvantage of accepting the lower quality food is the possibility that doing so fills the digestive system, thus requiring a reduction in intake of the better food. In general, the optimal strategy can be described as follows: accept the lower quality food to the maximum extent that does not reduce consumption of the higher quality food, and optimize foraging time based on the amount of risk.

Functional responses under the simultaneous encounter scenario are given by tqC_1R_1 for the lower quality resource and tC_2R_2 for the higher quality resource. Table 3 lists the responses after substituting the formulas for t and q given above. The overall functional response again consists of several qualitatively different segments. The non-zero segments of the functional response to the less nutritious resource 1 either (1) increase linearly with R_1 and are independent of R_2, or (2) decrease linearly with R_2 and are independent of R_1. Decreasing segments of the functional response do not occur in this case. However, consumption of resource 1 may increase (solution 5), decrease (solution 3) or be unaffected (solutions 1, 2, 4) by mortality risk, m. The various segments of the functional response to resource 2 are either constant or increase linearly with R_2. The functional response to resource 2 is always independent of R_1; it may be independent of (solutions 1, 2, 4), or decrease with (solutions 3, 5), mortality risk. The functional response to the low-quality resource may increase with increased risk of mortality. When the total resource abundance is more than enough to fill the digestive system, increasing mortality either shifts the solution from 2 to 5 (when R_2 alone cannot saturate digestive capacity) or from 4 to 5 (when R_2 alone does not saturate capacity). In either case, once instantaneous mortality risk m exceeds 1, solution 5 obtains, and the consumption rate of the less nutritious resource increases, while that of the more nutritious resource decreases.

Table 3. Functional responses of foragers under each of the five possible time allocations for the model with simultaneous foraging for both foods (descriptions of each numbered strategy are given in the text)

Solution	Functional responses
1	$qtC_1R_1 = C_1R_1$ $tC_2R_2 = C_2R_2$
2	$qtC_1R_1 = D - C_2R_2$ $tC_2R_2 = C_2R_2$
3	$qtC_1R_1 = C_1R_1/m$ $tC_2R_2 = C_2R_2/m$
4	$qtC_1R_1 = 0$ $tC_2R_2 = D$
5	$qtC_1R_1 = (Dm - C_2R_2)/m$ $tC_2R_2 = C_2R_2/m$

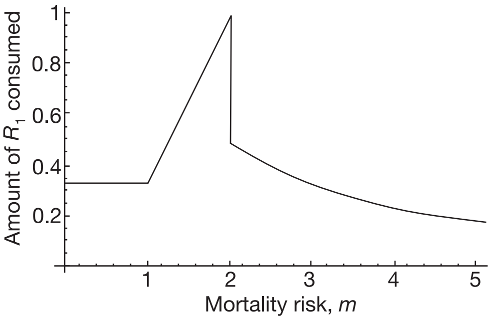

Fig. 6. The functional response of the consumer to the lower quality resource as a function of mortality risk when both foods occur in the same habitat. The graph is scaled so that 1 is the maximum possible consumption rate, given resource densities. Parameter values and resource densities are: $C_1 = C_2 = 1$; $A_1 = 1$; $A_2 = 2$; $D = 1$; $R_1 = 1.5$; $R_2 = 0.5$.

However, greater increases in mortality risk eventually result in solution 3, at which both consumption rates decrease with increasing mortality risk. Figure 6 illustrates the functional response on the lower quality food as a function of mortality for a case with high total food abundance.

DISCUSSION

The importance of the digestive capacity constraint in determining functional response shape

There has been comparatively little consideration of functional responses when a forager has two or more available foods (see review in Abrams, 1987). Within the small body of theory that is available for multiple foods, there has been even less consideration of constraints, or of the interaction of those constraints with mortality risk. The digestive capacity constraint is the main factor responsible for producing the complexity of the functional responses revealed here and in similar models without mortality risk (Abrams, 1990a; Schmitz, 1995). This can be shown by a comparison with the functional responses predicted by the two-habitat foraging problem without this constraint. Without the digestive capacity constraint, the optimal policy in this situation becomes: Forage exclusively on the food with the higher values of $f_i(R_i)/m_i$, except when two conditions are met: $(m_1 - m_2)(A_1f_1(R_1) - A_2f_2(R_2)) > 0$ and $(A_1f_1(R_1) - A_2f_2(R_2))/(A_2f_2(R_2)) \geq m_1 - m_2 \geq (A_1f_1(R_1) - A_2f_2(R_2))/(A_1f_1(R_1))$. Under these conditions, both foods should be taken with time allocations given by solution 8 in the two-habitat model:

$$t_1 = [A_1f_1(R_1) - A_2f_2(R_2) - (m_1 - m_2)A_2f_2(R_2)]/[(m_1 - m_2)(A_1f_1(R_1) - A_2f_2(R_2))]$$

$$t_2 = [(m_1 - m_2)A_1f_1(R_1) - (A_1f_1(R_1) - A_2f_2(R_2))]/[(m_1 - m_2)(A_1f_1(R_1) - A_2f_2(R_2))]$$

Although these formulas are somewhat lengthy, the forms of these time allocations when plotted against food densities are relatively simple. Each t_i increases as a function of the density of the food in its habitat and decreases with the density of the food in the other habitat. A food (and its habitat) should always be ignored when the food is sufficiently rare relative to the other food, and always taken exclusively when it is sufficiently common relative to the other food. Thus, although time constraints alone have some effect on diet choice, they do not lead to the large range of complex responses shown when digestive capacity is constrained.

Time minimizers and energy maximizers

In a seminal paper on foraging theory, Schoener (1971) distinguished animals that maximized energy intake from those that minimized the amount of time spent to achieve a given ration. The importance of this distinction has been questioned (e.g. Stephens and Krebs, 1986) because, when there are no constraints – or only time constraints – both goals are achieved by the same choice of diet (i.e. that which maximizes energy gain per unit time). However, the distinction does have implications for diet choice when there are digestive capacity constraints. Increasing mortality risk increases the fitness pay-off achieved by reducing foraging time. As a consequence, risks frequently favour a diet shift to higher use of low-quality (but abundant) food items (Rothley *et al.*, 1997; Schmitz *et al.*, 1998; see the following section). This is what is predicted under a time-minimizing strategy.

Comparison with experimental work

The work reported here was motivated by the recent findings of Schmitz *et al.* (1997, 1998) and Rothley *et al.* (1997), who explored the foraging behaviour of grasshoppers faced with risk of predation from spiders. The grasshoppers appear to be constrained by digestive capacity in the absence of spiders, and their two major food types, grasses and forbs, have a clumped distribution, suggesting that a two-habitat model may be appropriate. In the presence of a single spider per enclosure, grasshoppers shifted their foraging from feeding primarily on an apparently high-quality food (grasses, corresponding to resource 2 in our models) to an apparently low-quality food (forbs, corresponding to resource 1) (Schmitz *et al.*, 1997). This shift is consistent with solutions 7 or 9 in the two-habitat model. However, we do not yet know whether the necessary conditions for either of these solutions are met, because not all of the parameters of the model can be estimated from available data. Because quantitative observations of spider locations were not made, it is also not possible to provide precise values for the relative risks of mortality (m_i) for grasshoppers on the two vegetation types. However, additional support for the model presented here is provided by Rothley and co-workers' (1997) experiments involving three different spider densities. Although consumption of forbs increased in treatments with a single spider, it decreased in treatments with two spiders. Grass consumption decreased monotonically with spider density. Both of these trends are predicted by the two-habitat model.

Although different species of plants occur within centimetres of each other, a grasshopper perched on one plant is constrained to eating that type until it moves to another plant individual. This makes the situation closer to the two-habitat model than the one-habitat model. However, the qualitative nature of the predicted diet shift in response to greater predation is similar in both one- and two-habitat models. Rothley and co-workers' (1997) results cannot be used to distinguish between these alternative models. The shape of the grasshopper's intake rate versus food density while foraging in a patch has not been quantified, but Belovsky (1986a) suggested that they spend a significant time searching for high-quality food items.

The experiments by Schmitz (1994) and by Schmitz *et al.* (1997, 1998) were not designed to examine the dependency of grasshopper functional responses on all variables that were explored here. It would be of interest to determine how time allocations to the two food types responded to changes in their relative and absolute densities. If the theory presented here is applicable, it should be possible to observe decreases in forb consumption with increased forb densities over at least some sets of grass and forb densities. By manipulating the densities of predators and of both plant types, it may be possible to produce the full range of responses reviewed here.

There are some additional observations that are relevant to the theory developed here. Belovsky (1986a,b) successfully predicted the proportions of forbs and grasses in the diets of a large number of species of generalist herbivores, based on a model that ignored foraging-associated risk of mortality. Although risk can greatly modify the optimal food choice in these situations, the models considered here also predict that relatively low risk of mortality does not change the optimal diet. Thus, Belovsky's results are not inconsistent with the theory derived here. Because many of the species studied by Belovsky were large mammals living in predator-depleted environments, a low risk of foraging-related mortality is plausible.

Possible extensions of the foraging models

The models considered here are among the simplest possible models of foraging for two foods with both mortality risk from foraging and constraints on time and digestive capacity. Two important types of modification of these models are: (1) non-linear functional components and (2) facultative anti-predator behaviour. In general, risk is likely to increase faster than linearly with the proportion of time spent foraging, and reproduction is frequently a non-linear function of foraging intake (Abrams, 1992). It is not known how much such non-linearities will alter the qualitative features of the solutions given here. Most organisms are capable of adjusting the amount of risk that they experience by vigilance behaviour or other types of anti-predator behaviour within a habitat (Lima and Dill, 1990; Lima, 1998). Most of this behaviour also has the effect of reducing foraging intake (Lima and Dill, 1990; Lima, 1998; Schmitz *et al.*, 1998). It is likely that the foraging–predation trade-off is at least somewhat different in different habitats. Adding these features to the models considered here is likely to result in a number of new phenomena. However, it is unlikely to change the general message that constraints on time and food intake rates change foraging strategies in important ways.

A variety of other modifications of this basic model would be informative. Neither available time nor digestive capacity is likely to operate as the totally inflexible constraint we have assumed here. Instead, the costs due to other foregone activities are likely to be low until total foraging time approaches a large fraction of available time, after which costs increase rapidly in an accelerating manner. Similarly, the digestion-related costs of food intake are likely to be low until they approach a certain (large) value, and then increase at a rapid and accelerating rate. A partial analysis of these modifications for two-food models (Abrams, 1989) gives some basis for believing that these modifications might not greatly change the qualitative features of the present analysis. Finally, animals may have some control of their gut passage rate, with slower rates resulting in greater nutrient extraction. In this case, the parameter D is subject to some degree of adaptive modification; Yamauchi and Iwasa (1995) have explored the relationship between passage rate and diet choice in a model without any effect of foraging decisions on mortality risk.

Indirect effects caused by optimal foraging

Our results have important implications for the indirect interaction between prey via their shared predator. The best-known of these indirect effects is mutually detrimental, and is generally termed 'apparent competition' (Holt, 1977). However, there are many circumstances when the indirect effect can actually be mutualistic (Abrams and Matsuda, 1996; Abrams *et al.*, 1998). In particular, if predator density is constrained by some factor other than its diet, the interactions between prey are generated by the effect of each prey species on the predator's functional response to the other prey. The two models considered here (foods in the same or different habitats) produce a range of indirect interactions between prey (foods). As discussed previously (Abrams, 1990a,b, 1996), solution 9 of the two-habitat model results in a (+, −) interaction between the two foods via their consumer's functional response; increases in the low-quality food increase predation on the high-quality food, whereas increases in the high-quality food decrease predation on the better food. However, both of the other generalist solutions (7 and 8) are characterized by mutually positive indirect effects; increases in the food in the other habitat decrease time spent in the focal habitat. Changes in the density of one or both foods may switch the optimal solution from (9) to (7) or (8) (or vice versa), changing the nature of the indirect effect when the forager population is regulated by some factor other than food supply. This means that the qualitative nature of the indirect effect generated by the functional response may depend on the magnitude of the change in food density.

When both foods occur in the same habitat, the less nutritious food does not affect consumption of the more nutritious food, while increases in the more nutritious food reduce (or do not change) consumption of the less nutritious food. Thus, the interaction mediated by the predator's functional response is a commensalism (+, 0).

When predator per capita population growth rate is solely a function of food supply, changes in the forager population produce a (–, –) interaction between food species whenever there is a stable equilibrium density (Holt, 1977). However, this is often not the case when the equilibrium is unstable (Abrams *et al.*, 1998). Although unstable systems have not been investigated here, the non-linearity of the functional responses guarantees that interactions in unstable systems will at least differ quantitatively from those discussed in the previous two paragraphs, which were based on a fixed predator population (Abrams *et al.*, 1998). In a more general model, the forager population will have some direct effects (usually negative) on its own per capita growth rate, but its population size will be affected by food consumption (Abrams and Matsuda, 1996). In this more general case, effects mediated by functional and numerical responses often have different signs, and a detailed model is required to determine the sign of the indirect effect of one food species on the other's density.

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